

## Predicted changes in vegetation structure affect the susceptibility to invasion of bryophyte-dominated subarctic heath

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- **Background and Aims** A meta-analysis of global change experiments in arctic tundra sites suggests that plant productivity and the cover of shrubs, grasses and dead plant material (i.e. litter) will increase and the cover of bryophytes will decrease in response to higher air temperatures. However, little is known about which effects these changes in vegetation structure will have on seedling recruitment of species and invasibility of arctic ecosystems.
- **Methods** A field experiment was done in a bryophyte-dominated, species-rich subarctic heath by manipulating the cover of bryophytes and litter in a factorial design. Three phases of seedling recruitment (seedling emergence, summer seedling survival, first-year recruitment) of the grass *Anthoxanthum alpinum* and the shrub *Betula nana* were analysed after they were sown into the experimental plots.
- **Key Results** Bryophyte and litter removal significantly increased seedling emergence of both species but the effects of manipulations of vegetation structure varied strongly for the later phases of recruitment. Summer survival and first-year recruitment were significantly higher in *Anthoxanthum*. Although bryophyte removal generally increased summer survival and recruitment, seedlings of *Betula* showed high mortality in early August on plots where bryophytes had been removed.
- **Conclusions** Large species-specific variation and significant effects of experimental manipulations on seedling recruitment suggest that changes in vegetation structure as a consequence of global warming will affect the abundance of grasses and shrubs, the species composition and the susceptibility to invasion of subarctic heath vegetation.

**Key words:** *Anthoxanthum alpinum*, *Betula nana*, bryophytes, deciduous shrubs, global warming, graminoids, invasibility, litter, recruitment, seedling emergence.

### INTRODUCTION

Recent climate change leaves its mark on numerous natural processes (Walther *et al.*, 2002; Walker *et al.*, 2006). Increasing temperatures change the phenological development of species with important implications for complex direct and indirect interactions, and there is evidence of dynamic changes in the ranges of plants as a response to warming (Walther *et al.*, 2002, 2005).

For arctic regions, results of open-top chamber experiments within the International Tundra Experiment (ITEX) examining the effects of temperature increase on community structure show that (a) plant productivity will increase, (b) the cover of shrubs, grasses and dead plant material (i.e. litter) will increase, whereas (c) the cover of bryophytes will decrease (Walker *et al.*, 2006). Large-scale field surveys using aerial photography show that there is an ongoing range expansion and colonization of new areas by deciduous shrubs such as *Betula nana* and *Salix* spp. in arctic areas over the past 50 years (Tape *et al.*, 2006). Also long-term (25 years) satellite observation data show increasing plant productivity in the low arctic, where dwarf shrubs and graminoids dominate (Jia *et al.*, 2009).

The magnitude and speed of shifts in the range of species depend on specific traits of the colonizing species such as fecundity and production of viable diaspores ('diaspore pressure'), dispersal ability (seed morphology, vectors, dispersal distances) and germination behaviour of species (Graae *et al.*, 2009; Milbau *et al.*, 2009; Shevtsova *et al.*, 2009) but also on the susceptibility to invasion (generally termed 'invasibility' – which will be used for brevity) of the recipient community (Davis *et al.*, 2005). Invasibility is determined by resource availability, disturbance and suitability of the physical environment (abiotic factors), resource uptake by residents and negative and positive interactions between residents and invaders (cf. Davis *et al.*, 2005). Thus, the establishment of a new species in a community can be envisioned as a series of filters selecting, from a global species pool, those species that (a) reach a site, (b) possess the physiological constitution to cope with the abiotic environmental conditions and (c) establish successful interactions with organisms at the same or higher trophic levels (Lortie *et al.*, 2004). Interactions may be positive or negative (e.g. Brooker *et al.*, 2008), direct through competition or facilitation between living plants (plant–plant–interactions) or indirect (Ladd and Facelli,

2008) through various (mechanical, microclimatic and chemical) effects of dead plant material ('after-death interactions' *sensu* Facelli and Pickett, 1991). Results of a meta-analysis suggested that the effects of litter on seed germination and seedling emergence are mostly negative (Xiong and Nilsson, 1999). However, the sign of these after-death interactions, through litter as well as bryophyte–vascular plant interactions, on seedling emergence strongly depends on environmental conditions and varies among species (e.g. Mallik *et al.*, 1988; Eckstein and Donath, 2005; Serpe *et al.*, 2006; Donath and Eckstein, 2008, 2010). There is experimental evidence that a cover of bryophytes and litter acts partly through similar mechanisms (cf. Donath and Eckstein, 2010): (a) an increasing amount of bryophytes or litter on top of seedlings reduces the fluctuations in temperature (Eckstein and Donath, 2005; Gornall *et al.*, 2007, 2009; Soudzilovskaia *et al.*, 2011) owing to insulation effects; (b) light quantity and quality beneath a bryophyte or litter cover are significantly reduced (Keizer *et al.*, 1985; Fahnestock *et al.*, 2000; Jensen and Gutekunst, 2003; Eckstein and Donath, 2005); (c) bryophytes and litter may release allelopathic substances interfering with seed germination (e.g. Ruprecht *et al.*, 2008, 2010; Soudzilovskaia *et al.*, 2011); and (d) bryophytes and litter present a physical barrier for seedlings (Jensen and Gutekunst, 2003; Eckstein and Donath, 2005; Jeschke and Kiehl, 2008; Donath and Eckstein, 2010; Graae *et al.*, 2011; Soudzilovskaia *et al.*, 2011). Additionally, (e) soil moisture is usually increased beneath a litter cover, whereas a bryophyte cover may lead to increased (Mallik *et al.*, 1988; Donath and Eckstein, 2010) or decreased soil moisture levels compared with control without cover (Serpe *et al.*, 2006; Gornall *et al.*, 2007; Soudzilovskaia *et al.*, 2011). Finally, (f) seeds entrapped within a bryophyte or litter layer cannot establish soil contact for germination or, if germinating within the cover layer, run a high mortality risk through desiccation.

Higher temperatures may lead to earlier germination of subarctic species (Milbau *et al.*, 2009), which may improve seedling recruitment due to a prolongation of the growing season. The fact that net effects of warming are highly specific to species and depend on the phase of recruitment considered (e.g. seed germination, seedling establishment) (Graae *et al.*, 2009; Shevtsova *et al.*, 2009) indicates that increased temperatures have the potential to directly alter community composition.

Additionally, global warming may also exert effects on recruitment via changes in vegetation structure which affect the invasibility. However, the importance of different components of vegetation structure (moss and litter cover) and their interactions for processes of seedling recruitment in arctic regions is largely unknown (Soudzilovskaia *et al.*, 2011). In light of climate-induced changes of these components, studies addressing their impact on community invasibility become particularly important for understanding future species distributions.

In the present paper, the cover of bryophytes and litter was experimentally manipulated to identify the effects of expected changes in vegetation structure on different aspects of seedling recruitment of two common and widespread species of subarctic vegetation. Seedlings were measured during the whole first growing season to differentiate between seedling emergence,

seedling survival during summer and first-year recruitment. The following questions were addressed. (a) How does manipulation of bryophyte and litter cover influence seedling recruitment? (b) Do the two vascular plant species investigated respond differently to the manipulations of vegetation structure, i.e. are there significant vegetation structure manipulation  $\times$  species interactions? (c) Do the changes in vegetation structure exert different effects on the phases of recruitment, i.e. seedling emergence, summer seedling survival and first-year recruitment?

## MATERIALS AND METHODS

### Study site

The study was carried out in subarctic tundra, approx. 4 km south of the Abisko Scientific Research Station, northern Sweden (68°19'N, 18°51'E, 520 m a.s.l.). The study site was situated on a gently sloping, northerly inclined heath just above the subalpine mountain-birch forest within the low-alpine zone. The vegetation was species-rich (24 species m<sup>-2</sup>) and dominated by bryophytes, specifically *Homalothecium nitens* and *Hylocomium splendens*. It belongs to the *Cassiope tetragona* vegetation type (Påhlsson, 1998), which is characterized by only moderate snow cover during winter, early snow-melt and a calcareous or base-rich substrate with high pH (6.7 at the study site, own measurements). The most abundant and frequent plant species are listed in the Appendix.

### Study species

Since we were interested in the response of common and widely distributed species of life-forms that are predicted to benefit from climate warming, *Anthoxanthum alpinum* (graminoid) and *Betula nana* (deciduous shrub) (Nilsson, 1987), which are henceforth referred to by their generic names, were selected. Both species tolerate a wide range of environmental conditions and thus occur in various heath types on acidic and calcareous substrate (Andersson *et al.*, 1985; Nilsson, 1987). Adult *Betula* shrubs occurred frequently at the study site, whereas tillers of *Anthoxanthum* grew within some 100 m of the study site.

Seeds of the study species were collected a few days before sowing in natural populations in the Abisko region and were brought to the laboratory where 30 seed batches consisting of 100 seeds each were counted and stored in Eppendorf caps. A viability test with a 1% tetrazolium-chloride solution (Bennett and Loomis, 1949) on three additional seed batches per species showed that the viability of the seeds used in the experiments was 64.4%  $\pm$  7.8 and 81.1%  $\pm$  2.9 (mean  $\pm$  s.e.) for *Betula* and *Anthoxanthum*, respectively.

### Experimental design

In September 2008, 90 experimental plots (19  $\times$  19 cm), widely distributed across the heath slope, were established and marked. These were used (a) for sowing the study species (30 plots each = 60 plots) or (b) as 'no-seeding controls' to correct for seedlings of the study species appearing naturally (30 plots). To limit environmental heterogeneity

with respect to soil water conditions, plots were restricted to micro-sites on level ground or in shallow depressions. A completely randomized design where each plot was randomly assigned to one of the treatment combinations was used.

Manipulation of the vegetation structure (factors: bryophyte manipulation and litter manipulation) consisted of the six combinations of the factors 'bryophytes removed' (45 plots, B<sub>-</sub>) or 'bryophytes intact' (45 plots, B<sub>nat</sub>) with the factor 'litter removed' (30 plots, L<sub>-</sub>), 'litter intact' (30 plots, L<sub>nat</sub>) or 'litter added' (30 plots, L<sub>+</sub>), i.e. B<sub>-</sub>/L<sub>-</sub>; B<sub>-</sub>/L<sub>nat</sub>; B<sub>-</sub>/L<sub>+</sub>; B<sub>nat</sub>/L<sub>-</sub>; B<sub>nat</sub>/L<sub>nat</sub> (control); B<sub>nat</sub>/L<sub>+</sub>. To improve the estimate of the amounts of bryophytes and litter per plot, bryophytes and litter were collected on another 30 and 20 plots, respectively, which were not included in the experiment.

In the bryophyte removal plots, the living (green) parts of all bryophytes (plus all lichens) were carefully picked by hand to a depth of approx. 2 cm, below which only dead (partly decomposed) bryophyte tissues were present. Removed material was collected for each plot, dried at 60 °C to constant mass and weighed. In litter-removal plots, all dead plant parts (predominantly senesced leaves of *Vaccinium uliginosum*, *Salix reticulata* and *Betula nana*, cf. the Appendix) were removed. Back in the laboratory, the bench dry weight of litter of each plot was determined to estimate the average amount of litter per plot. Thereafter the collected material was pooled, thoroughly mixed, and equal weight batches corresponding to the average litter mass per plot were prepared. These were brought back to the field and evenly dispersed on each of the litter-addition plots. Consequently, the litter amount in these plots was, on average, twice the natural amount.

After manipulation of vegetation structure, 2 times 30 plots (6 treatments × 5 replicates) were sown with seeds of each of the two species and 30 plots received no seeds (to account for naturally occurring seedlings of *Betula nana*). A seed batch (100 seeds) of one of the study species was carefully sown into the central 10 × 10 cm of each plot on 17 September 2008. Plots were covered with gauze cloth fixed to the ground to avoid the redistribution of seeds and litter. It was removed in early spring after snowmelt. Seedlings of the study species were counted four times during the vegetation period, i.e. in late May, early July, early August and late August. At each date, seedlings of the new cohort were recorded and marked, and dead seedlings of each cohort counted. Using these data the following were calculated: (a) cumulative seedling emergence – the cumulative number of seedlings that emerged over the vegetation period (expressed as percentage of sown seeds); (b) seedling survival – the number of seedlings that survived in each plot at the end of the vegetation period (expressed as percentage of seedling emergence); and (c) first-year recruitment – the number of seedlings that survived until the end of the vegetation period (expressed as a percentage of sown seeds). First-year recruitment is a composite measure, representing the product of seedling emergence and seedling survival. For *Betula*, data were corrected for seedlings germinating naturally on the study site by subtracting the average number of *Betula* seedlings from control plots of the corresponding treatment ( $n = 5$ ).

### Statistical analysis

A full-factorial GLM three-way analysis of variance was calculated testing for the effects of species (*Betula*, *Anthoxanthum*), litter (L<sub>-</sub>, L<sub>nat</sub>, L<sub>+</sub>) and bryophytes (B<sub>-</sub>, B<sub>nat</sub>) on seedling emergence, seedling survival and first-year recruitment. Data were Box–Cox transformed before analysis. As a measure for the relative contribution of each factor and the interactions to the total variability, the ratio of the sum of squares of the factor or interaction of interest to the total sum of squares (i.e. for all factors, their interactions and the error) was used. Additionally, using the data of three counting occasions (4 July, 1 August and 28 August) a four-way repeated measures ANOVA was calculated (with time as a within-subject factor) on the percentage of new and dead seedlings. All statistical analyses were done using Statistica 9.0 (Statsoft, 2010).

## RESULTS

The study site was dominated by bryophytes (Fig. 1), both with respect to biomass ( $753 \text{ g m}^{-2} \pm 180$ , mean  $\pm$  s.d.,  $n = 75$ ) and cover ( $93.5 \% \pm 7.8$ ,  $n = 10$ ). On average,  $1 \text{ m}^2$  contained  $75.6 \text{ g m}^{-2}$  of litter (s.d. = 19.6,  $n = 50$ ). Cover of shrubs and herbs were 21.5 % and 6.2 %, and their average heights 16 cm and 8 cm, respectively (Fig. 1).

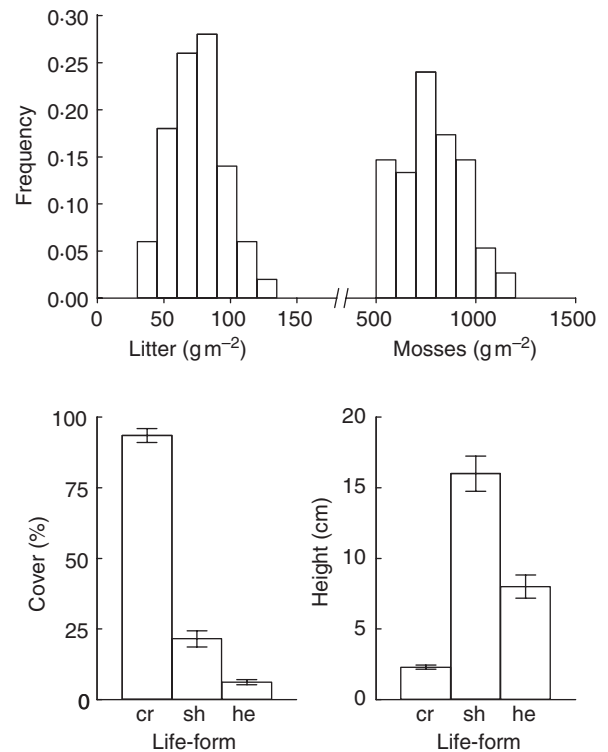


FIG. 1. Frequency distribution of litter ( $75.6 \text{ g m}^{-2} \pm 19.6$ , mean  $\pm$  s.d.,  $n = 50$ ) and bryophyte mass ( $753 \text{ g m}^{-2} \pm 180$ ,  $n = 75$ ), and cover (%) and height (cm) of cryptogams (cr), shrubs (sh) and herbs (he) (in the lower panels data are means  $\pm$  s.e.,  $n = 10$ ). For upper panel, note the break in the x-axis. Frequency distributions for litter and bryophytes are based on ten classes (litter: min = 0 g, max = 150 g, class width = 15 g; bryophytes: min = 500 g, max = 1500 g, class width = 100 g).

For cumulative seedling emergence only the main effects of litter and bryophytes were significant, explaining 12.4 % and 13.7 % of the total variation, respectively (Fig. 2 and Table 1). There were no significant differences between species. Across species and bryophyte treatments, cumulative seedling emergence was significantly lower in the litter addition treatment ( $L+ : 3.29 \pm 1.01$ , mean  $\pm$  s.e.,  $n = 20$ ) than in the litter-removal plots ( $L- : 7.46 \pm 1.38$ , Tukey test,  $P < 0.05$ ); emergence under natural litter amounts ( $L_{nat} : 6.05 \pm 1.21$ ) was intermediate. Across all other factors, cumulative seedling emergence differed significantly between bryophyte treatments; it was 2.3 times higher after removal of bryophytes than in plots, where bryophyte cover had not been manipulated ( $7.8 \% \pm 1.16$  vs.  $3.4 \% \pm 0.68$ , mean  $\pm$  s.e.,  $n = 30$ ).

In general, differences between cumulative seedling emergence and first-year seedling recruitment were much lower in *Anthoxanthum* than in *Betula* (Fig. 2) which suggests that mortality during the growing season was much higher in the latter (Figs 2 and 3). In fact, seedling survival differed significantly between species, which explained more than 70 % of the total variation (Table 1).

As a consequence, first year seedling recruitment was significantly higher in *Anthoxanthum* ( $4.8 \% \pm 0.77$ ) than in *Betula* ( $0.6 \% \pm 0.4$ ). Differences between the species

explained more than half of the total variation in first year seedling recruitment (Table 1). Additionally, there was a significant effect of the bryophyte treatment on recruitment (bryophytes removed,  $4.17 \% \pm 0.90$ ; bryophytes intact,  $1.27 \% \pm 0.31$ ) and the response to manipulation of the bryophyte layer varied significantly between species ( $S \times B$  interaction): recruitment of *Betula* did not vary between bryophyte treatments while the percentage recruitment in *Anthoxanthum* was significantly greater in plots where bryophytes were removed ( $7.4 \% \pm 1.12$ ) than in plots with intact bryophyte layer ( $2.3 \% \pm 0.48$ ).

Across treatments, there were 7.5 times more seedlings of *Betula* than of *Anthoxanthum* on 30 May (Fig. 3, columns), showing the earlier germination of *Betula*. However, there was a net decline in seedling numbers in *Betula* during summer, i.e. when mortality was significantly higher than establishment of new seedlings in early July and early August. In contrast, *Anthoxanthum* had a peak of new seedlings between late May and early July and summer seedling mortality was very small in this species (Fig. 3, symbols). In the statistical analysis this was reflected by highly significant species  $\times$  time interactions (repeated measures ANOVA, data not shown; seedling establishment:  $F_{2,96} = 10.2$ ,  $P < 0.0001$ ; seedling mortality:  $F_{2,96} = 8.3$ ,  $P < 0.0001$ ). Additionally, there was a significant bryophytes  $\times$  species  $\times$  time interaction (repeated measures ANOVA, data not shown;  $F_{2,96} = 4.19$ ,  $P = 0.018$ ) which was mainly caused by high seedling mortality of *Betula* in early August on plots where bryophytes had been removed.

## DISCUSSION

The results of the present field experiment suggest that beyond a facilitation of adult vascular plant growth and reproduction (Gornall *et al.*, 2009), a reduction in bryophyte cover may also improve the chances for successful recruitment of graminoids and shrubs in bryophyte-dominated subarctic heath systems. Bryophyte removal had a consistent positive effect on seedling emergence and also on first-year recruitment (Table 1 and Fig. 2). We presume that a bryophyte layer exerts negative effects on germination and establishment of vascular plants by acting as mechanical barrier and/or through microclimatic and chemical effects (e.g. Keizer *et al.*, 1985; Mallik *et al.*, 1988; Serpe *et al.*, 2006; Jeschke and Kiehl, 2008; Graae *et al.*, 2011; Soudzilovskaia *et al.*, 2011). It has been shown that removal or reduction of the bryophyte layer decreases average temperatures and temperature amplitudes in arctic and subarctic areas (Gornall *et al.*, 2007; Soudzilovskaia *et al.*, 2011). These, together with possible bryophyte effects on soil moisture, may lead to lower microbial biomass, nutrient concentrations and decomposition rates under deep than under shallow bryophyte layers (Gornall *et al.*, 2007, 2009). Changes in vegetation structure may thus have strong implications for ecosystems processes (Wookey *et al.*, 2009), which, in this study, were consistent among study species with regard to seedling emergence.

However, evidence was also found for strong species-specific responses to variation in bryophyte and litter cover with respect to other phases of recruitment. For instance, species identity accounted for  $>70\%$  of the variation in

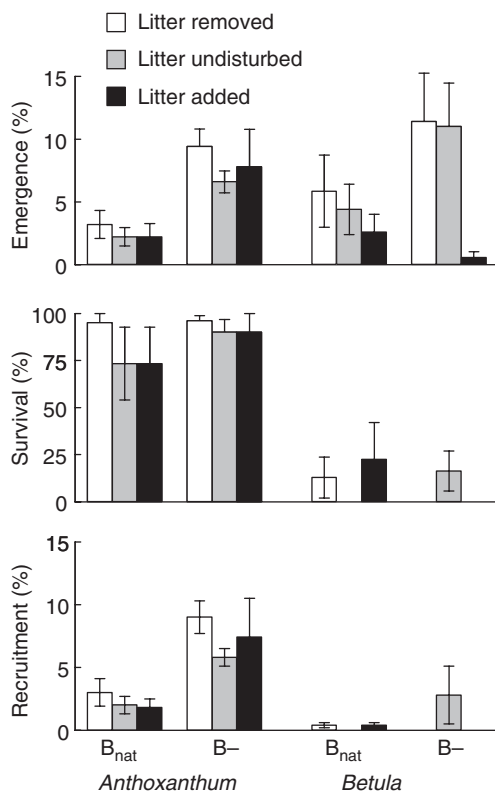


FIG. 2. Percentage of cumulative seedling emergence (upper panel), seedling survival (middle panel), and first-year recruitment (lower panel) of *Anthoxanthum alpinum* and *Betula nana* under different treatment combinations manipulating vegetation structure (bryophyte and litter cover). Treatments:  $B_{nat}$ , natural bryophyte cover;  $B-$ , bryophytes removed. Litter removed, undisturbed or added as indicated. Data are means  $\pm$  s.e. ( $n = 5$ ).

TABLE 1. Results of a three-way GLM testing for the effects of species (S), litter (L) and bryophytes (B) on cumulative seedling emergence, seedling survival and first-year recruitment of *Anthoxanthum alpinum* and *Betula nana*

	d.f.	Emergence			Survival			Recruitment		
		MS	P	ev(%)	MS	P	ev(%)	MS	P	ev(%)
Intercept	1	<b>165.99</b>	<b>&lt;0.0001</b>		<b>6.54</b>	<b>&lt;0.0001</b>		<b>20.58</b>	<b>&lt;0.0001</b>	
Species (S)	1	0.359	0.5115	0.5	<b>4.19</b>	<b>&lt;0.0001</b>	<b>71.5</b>	<b>10.54</b>	<b>&lt;0.0001</b>	<b>56.9</b>
Litter (L)	2	<b>4.29</b>	<b>0.0088</b>	<b>12.4</b>	0.008	0.7665	0.3	0.0825	0.4418	0.9
Bryophytes (B)	1	<b>9.45</b>	<b>0.0014</b>	<b>13.7</b>	0.005	0.6769	0.1	<b>0.9873</b>	<b>0.0028</b>	<b>5.3</b>
S × L	2	1.960	0.1026	5.7	0.021	0.4983	0.7	0.1273	0.2868	1.4
S × B	1	1.944	0.1305	2.8	0.056	0.1716	1.0	<b>0.8448</b>	<b>0.0054</b>	<b>4.6</b>
L × B	2	1.400	0.1926	4.0	0.044	0.2321	1.5	0.2716	0.0751	2.9
S × L × B	2	1.346	0.2049	3.9	0.026	0.4170	0.9	0.2164	0.1242	2.3
Residual	48	0.821		57.0	0.029		24.1	0.0993		25.7

Data were Box–Cox transformed before analysis.

Abbreviations: d.f., degrees of freedom; MS, mean square; P, error probability; ev(%), explained variance.

Significant effects are indicated in bold.

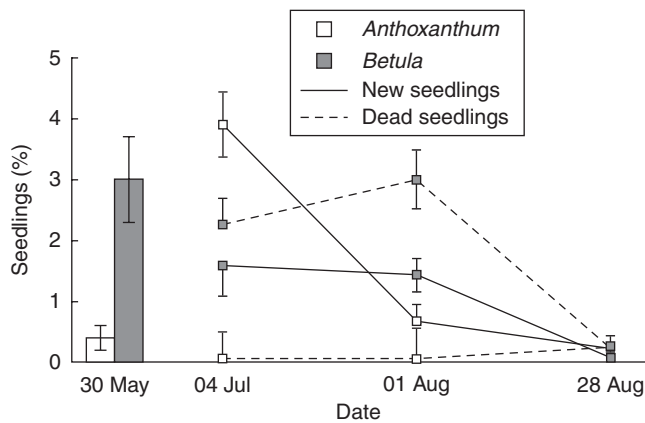


FIG. 3. Percentage of seedlings of *Anthoxanthum alpinum* (open column) and *Betula nana* (shaded column) present on 30 May, and new (continuous line) and dead seedlings (dashed line) counted on 4 July, 1 August and 28 August across treatments (*Anthoxanthum*: open squares, *Betula*: shaded squares). Data are means  $\pm$  s.e.,  $n = 30$ . There were highly significant species  $\times$  time interactions on seedling establishment (repeated measures ANOVA, data not shown,  $F_{2,96} = 10.2$ ,  $P < 0.0001$ ) and seedling mortality ( $F_{2,96} = 8.3$ ,  $P < 0.0001$ ).

survival (Table 1) and  $>50\%$  of the variation in first-year recruitment. High summer mortality of *Betula* (Fig. 3), especially in plots where bryophytes had been removed (significant species  $\times$  bryophyte interaction on first-year recruitment; cf. Table 1) resulted in much lower first-year recruitment of that species in comparison with *Anthoxanthum*. This may indicate that seedlings of *Betula* are more sensitive to summer drought. Grasses of habitats with intermediate to low fertility, such as *Festuca rubra* and *Anthoxanthum odoratum* (closely related to *Anthoxanthum alpinum*) are characterized by high morphological and physiological plasticity (Fransen *et al.*, 2001) which entail high competitive ability in heterogeneous environments. High nutrient turnover and biomass production of grasses (Vázquez de Aldana and Berendse, 1997) suggest that *Anthoxanthum alpinum* or other grass species may benefit from nutrient mineralization as a consequence of bryophyte removal (Gornall

*et al.*, 2007, 2009) and/or climate warming (cf. Parsons *et al.*, 1995; Wookey *et al.*, 2009).

Finding differences between two species as in the present study might appear rather trivial. However, we would hold that these differences were large and concerned significant aspects of species performance. Our findings are in line with other papers that emphasized large species-specific variation concerning seed germination and seedling recruitment in subarctic species (Milbau *et al.*, 2009; Shevtsova *et al.*, 2009; Graae *et al.*, 2011) and differential responses to litter effects (Myser, 1994; Quedsted and Eriksson, 2006; Hovstad and Ohlson, 2009; Donath and Eckstein, 2010). Most importantly, variation in species-specific responses is a prerequisite for vegetation changes. Consequently, in concert with the results of other studies, the present results suggest that global warming will significantly affect species composition of subarctic heath systems, given that seeds of species currently not present in these communities will reach the sites. Additionally, there are likely to be effects on species abundance and/or dominance that may have cascading consequences for ecosystem properties and processes such as nutrient cycles, carbon balance, energy budget and hydrology (Wookey *et al.*, 2009).

Although manipulation of the litter layer involved comparatively lower absolute masses (Fig. 1), a doubling of litter amounts had significant negative effects on seedling emergence. This may be because the added litter that was hetero-specific to the study species may have exerted negative physical and/or chemical effects (Xiong and Nilsson, 1999; Eckstein and Donath, 2005; Hovstad and Ohlson, 2009). In line with recent studies that showed species-, litter type- and litter species-specific effects on seedling emergence and recruitment (Myser, 1994; Quedsted and Eriksson, 2006; Donath and Eckstein, 2008, 2010; Hovstad and Ohlson, 2009) the present study suggests that changes in litter cover also have the potential to alter species composition of subarctic communities.

In essence, changes in vegetation structure, i.e. cover of bryophytes and litter, may affect temperature, light, soil moisture and the chemical environment of seeds and seedlings, and bryophytes and litter may present a physical barrier for

seedling growth or act as a seed trap (Facelli and Pickett, 1991; Donath and Eckstein, 2010, and references therein). Thus, predicted changes in vegetation structure as an indirect consequence of global warming may influence a plethora of mechanisms, each of which may have consequences for successful species recruitment and thus invasibility. The decline of bryophytes and lichens will be a consequence of increased water stress due to higher temperatures (Potter *et al.*, 1995). Additionally, increased mineralization of nutrients owing to higher temperatures will be beneficial for biomass production of life-forms with high nutrient productivity (Eckstein and Karlsson, 1997) such as graminoids, herbs and deciduous shrubs (Walker *et al.*, 2006). Increased biomass production and cover of vascular plant life-forms will reduce light penetration to the ground so that light-demanding cryptogams will be outcompeted (e.g. Parsons *et al.*, 1994, 1995; Wookey *et al.*, 2009). This may, in turn, create safe sites for seed germination.

However, idiosyncratic species-specific responses make it difficult to predict the effects of changes in community composition and diversity on ecosystem properties and processes. In this context, comparative ecological studies with many species are urgently needed to clarify which species traits, life-forms or functional types are consistently related to successful recruitment in response to climate-induced changes in vegetation structure.

In conclusion, significant effects of experimental manipulations on seedling recruitment and differential response of species to these manipulations suggest that changes in vegetation structure as a consequence of global warming will affect the abundance of grasses and shrubs, the species composition and the susceptibility to invasion of subarctic heath vegetation.

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## APPENDIX

Characteristic plant species (B, bryophyte; L, lichen) of the study site based on ten vegetation relevés 1 m<sup>2</sup> in size. Species cover was estimated using a nine-level ordinal scale (cf. van der Maarel, 1979). Only species with frequency  $\geq 60\%$  are given. Calc. denotes the species demands with respect to calcareous or base-rich substrate according to Nilsson (1987) for vascular plants and Mårtensson (1955, 1956) for bryophytes (I, indifferent to calcareous/base-rich substrate; C, preferentially on calcareous/base-rich substrate; C, needs calcareous/base-rich substrate).

Species	Frequency (%)	Median cover	Calc.
<i>Homalothecium nitens</i> (B)	100	7.0	C
<i>Hylocomium splendens</i> (B)	100	6.5	I
<i>Vaccinium uliginosum</i>	100	4.5	I
<i>Empetrum hermaphroditum</i>	100	4.5	I
<i>Carex parallela</i>	100	3.0	C
<i>Andromeda polifolia</i>	100	3.0	I
<i>Salix reticulata</i>	100	3.0	C
<i>Carex vaginata</i>	100	3.0	I
<i>Betula nana</i>	100	3.0	I
<i>Equisetum arvense</i> ssp. <i>boreale</i>	100	3.0	I
<i>Ptilidium ciliare</i> (B)	90	6.0	I
<i>Arctostaphylos alpina</i>	90	3.0	I
<i>Equisetum scirpoides</i>	80	2.0	C
<i>Dicranum scoparium</i> (B)	70	4.0	I
<i>Barbilophozia floerkei</i> (B)	70	3.0	I
<i>Dryas octopetala</i>	70	3.0	C
<i>Polygonum viviparum</i>	70	2.0	I
<i>Peltigera aptosa</i> (L)	70	1.0	–
<i>Aulacomnium turgidum</i> (B)	60	4.0	C
<i>Cetraria cucullata</i> (L)	60	3.0	–
<i>Rhododendron lapponicum</i>	60	2.5	C
<i>Pyrola norvegica</i>	60	2.5	C
<i>Bartsia alpina</i>	60	1.5	C