How do bryophytes govern generative recruitment of vascular plants?

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Summary

• Interactions between vascular plants and bryophytes determine plant community composition in many ecosystems. Yet, little is known about the importance of interspecific differences between bryophytes with respect to their effects on vascular plants. We compared the extent to which species-specific bryophyte effects on vascular plant generative recruitment depend on the following underlying mechanisms: allelopathy, mechanical obstruction, soil moisture and temperature control.

• We sowed 10 vascular plant species into monospecific mats of six chemically and structurally diverse bryophytes, and examined 1-yr seedling recruitment. Allelopathic effects were also assessed in a laboratory phyto-assay.

• Although all bryophytes suppressed vascular plant regeneration, there were significant differences between the bryophyte species. The lack of interactions indicated the absence of species-specific adaptations of vascular plants for recruitment in bryophyte mats. Differences between bryophyte species were best explained by alterations in temperature regime under bryophyte mats, mostly by reduced temperature amplitudes during germination. The temperature regime under bryophyte mats was well predicted by species-specific bryophyte cushion thickness. The fitness of established seedlings was not affected by the presence of bryophytes.

• Our results suggest that climatically or anthropogenically driven changes in the species' composition of bryophyte communities have knock-on effects on vascular plant populations via generative reproduction.

Introduction

Bryophytes play important roles in many ecosystems, especially in rain forests and cold biomes (Longton, 1997; Tan & Pocs, 2000), where they are abundant and in close contact with vascular plants. Interactions between bryophytes and vascular plants comprise a large spectrum of relations, including resource competition (Chapin *et al.*, 1987), as well as suppression and facilitation, mostly attributed to the altered microclimatic conditions for vascular plants within bryophyte patches (van Tooren & During, 1990; J. L. Gornall *et al.* unpublished data). Although these interactions have been shown to be species specific for vascular plants (Sohlberg & Bliss, 1984; van Tooren & During, 1990), virtually nothing is known about the importance of interspecific differences between bryophytes with respect to their effects on vascular plants (but see Ohlson & Zackrisson, 1992), or about the functional traits of bryophyte species that are responsible for such effects (Cornelissen *et al.*, 2007).

Bryophyte mats have been shown to greatly affect vascular plant seedling emergence (Sthilaire & Leopold, 1995; Sedia & Ehrenfeld, 2003; Dostal, 2007) and survival (Zamfir *et al.*, 1999; Sedia & Ehrenfeld, 2003; Otsus & Zobel, 2004; Spackova & Leps, 2004; Morgan, 2006; Dostal, 2007; Donath & Eckstein, 2010). Usually the effect is negative, as a result of allelopathic effects on germination

(Steijlen *et al.*, 1995; Zamfir, 2000), reduced moisture availability (Equihua & Usher, 1993) or the creation of a physical barrier that prevents seeds from reaching the soil (McIlvanie, 1942; Morgan, 2006), thereby increasing the likelihood of desiccation, predation, a chemically unfavourable environment or destruction by fire. Furthermore, bryophyte mats reduce light intensity and the red : far red ratio below the cushions, which may suppress germination (Haeussler & Tappeiner, 1993). Among these effects, allelopathy seems to be the most controversial. Steijlen *et al.* (1995) suggested that it only affects germination, but not subsequent seedling survival, whereas Equihua & Usher (1993) found no allelopathic effects of bryophytes at all. Positive effects of bryophytes on seedling emergence and survival (Bell & Bliss, 1980; Sohlberg & Bliss, 1984) have been reported mostly from harsh environments, where facilitation prevails over competition (Bertness & Callaway, 1994; Callaway & Walker, 1997). Facilitation has been attributed to improved moisture conditions, higher soil temperature, reduced wind speed and a seed trap effect (Bell & Bliss, 1980; Sohlberg & Bliss, 1984; van Tooren & During, 1990; Groeneveld *et al.*, 2007; Jeschke & Kiehl, 2008).

Experimental manipulations, climatic gradient studies and microfossil analyses suggest that climate change will strongly affect the abundance and species' composition of bryophytes in many plant communities (Potter *et al.*, 1995; Molau & Alatalo, 1998; Weltzin *et al.*, 2000, 2001; Dorrepaal *et al.*, 2004; Bauer *et al.*, 2009; Lang *et al.*, 2009). Changes in bryophyte community composition will, in turn, affect species-specific interactions between vascular plants and bryophytes, including reproduction, the most crucial aspect of community composition. Vascular plant seedlings are more sensitive to bryophyte influence, positive as well as negative, than the established vascular vegetation (Spackova *et al.*, 1998), because of their great dependence on microsite conditions (Eriksson & Ehrlen, 1992; Steijlen *et al.*, 1995).

Sparse data suggest that distinct bryophyte species may have distinct effects on seedling germination and survival (Cross, 1981; Zamfir, 2000; Serpe *et al.*, 2006), attributed to differences in mat thickness (Zamfir, 2000). However, as yet, little is known about the generality of interspecific differences between bryophytes in this respect, or about the mechanisms underpinning these differences.

The aims of this study were to assess the differences between bryophyte species with regard to their effects on vascular plant generative recruitment, including germination and first-year seedling establishment, and to unveil the mechanisms underlying these effects. We tested the following suppositions:

- Bryophyte effects on the recruitment of vascular plants are species specific for bryophytes (i.e. there is a significant difference between bryophytes) as well as for vascular plants (i.e. there is an interaction effect between vascular plants and bryophyte species, indicating that the effects of bryophytes differ according to the vascular plant species).
- The mechanisms underpinning the effects of bryophytes on vascular plant recruitment include phenolic leakages that inhibit germination, mechanical obstruction that prevents seeds from reaching the soil and alters the light regime, alteration of the soil microclimate (moisture and temperature regimes) and retarded seedling growth in thicker and denser cushions with reduced light availability. With respect to this research question, we aimed to find easy-to-measure bryophyte traits (Cornelissen *et al.*, 2007) that could be used as proxies for these factors.

Previous studies on the effects of bryophyte mats on vascular plant recruitment have featured experimental removal of the bryophyte mat (but seeZamfir, 2000) or the sowing of seeds in bryophyte mats at their natural habitats (Ohlson & Zackrisson, 1992; Hanssen, 2002). However, neither of these methods targets the effects of bryophytes *per se*, because the former method causes considerable soil disturbance, affecting germination by itself via an enhanced mineralization rate, and the latter does not allow the separation of the effects of bryophytes from the effects of microhabitat. By contrast, our experimental bryophyte cushion transplantations ensured identical soils in different control and bryophyte treatments, allowing the explicit examination of bryophyte (species') effects.

We ran this study in a subarctic forest where bryophytes co-dominate the understory vegetation and therefore greatly determine the abiotic and biotic conditions for co-occurring species (Longton, 1988; Grime, 1998). Although many vascular plant species in polar regions possess vegetative reproduction, reproduction by seeds here is an extremely important process enabling longer term genetic flexibility of plant populations and long-distance dispersal (Welling & Laine, 2002; Alsos *et al.*, 2007). The climate is harsh here and seedling recruitment success is mediated by soil temperature (Milbau *et al.*, 2009; Shevtsova *et al.*, 2009) and moisture regimes (Bell & Bliss, 1980; Sohlberg & Bliss, 1984), allowing us to properly test for the importance of bryophyte-driven modifications of soil microclimate vs effects of mechanical obstruction and allelopathic suppression, the latter being unraveled through a complementary controlled laboratory experiment.

Materials and Methods

Study site and plants used in the experiments

The field experiment was carried out in Abisko (north Sweden, 68°21′N, 18°49′E, *c.* 200 km north of the Arctic Circle and *c.* 385 m above sea level). A complementary laboratory experiment was conducted in the laboratory of VU University Amsterdam. Table 1 shows the list of bryophyte

and vascular plant species used in the study and their origin. All vascular plant species used in the experiments are very common in the subarctic and the bryophytes are subdominant in the forest understory. A few vascular plants used in the field experiment were not used in the laboratory experiment owing to their expected long germination time.

Field experiment

The experiment was conducted during October 2007–September 2008 close to the Abisko Scientific Research Station, in a homogeneous area, free of trees and large shrubs, in the mountain birch (*Betula pubescens*) heath-woodland. We removed all ground vegetation including large roots down to 10-cm depth. We covered the soil with a layer of 2.5-cm-thick mineral wool in order to secure good moisture-holding capacity and isolation from the ground, possibly containing viable roots, seeds and traces of *Empetrum nigrum* ssp. *hermaphroditum*, the latter known to inhibit the germination of vascular plants through allelopathic secondary compounds (Nilsson *et al.*, 2000). On top of the mineral wool we placed plastic trays ($50 \times 30 \times 8$ cm^3) with the bottoms cut out and filled these with commercial garden soil (Änglamark, Sweden). Extra soil was added around the plots to level the surface.

The experiment followed a fully factorial three-factor design (Fig. 1), featuring the following treatments. (1) The presence vs absence of active charcoal additions in the soil. This treatment aimed to immobilize mobile (allelopathic) phenolic compounds and thereby enabled the separation of the chemical and physical effects of bryophytes. Each bryophyte treatment had four charcoal-treated and four control replicates. (2) Bryophyte treatment with seven levels: six bryophyte species and bare soil without bryophytes, hereafter referred to as 'control', each replicated eight times. (3) Vascular plant treatment with 10 levels, that is species (see Table 1). All 10 levels were applied to each bryophyte treatment replicate.

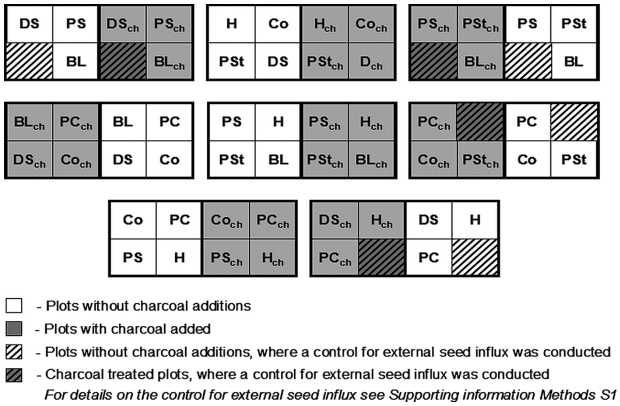

Fig. 1 Schematic drawing of experimental plots. Bryophyte treatment coding: Co, Control; BL, *Barbilophozia lycopodioides*; DS, *Dicranum scoparium*; HS, *Hylocomium splendens*; PC, *Ptilidium ciliare*; PS, *Pleurozium schreberi*; PSt, *Polytrichum strictum.* Charcoal addition treatment coding: subscript 'ch' indicates charcoal added.

Table 1 Plant species used in the study and their origins

Species	Growth form	Origin	Use in laboratory experiment	Use in field experiment
Bryophytes				
Hylocomium splendens (Hedw.) B.S.G.	Pleurocarpous moss; loose turfs	Abisko area	Yes	Yes
Pleurozium schreberi (Brid.) Mitt.	Acrocarpous moss; loose turfs	Abisko area	Yes	Yes
Dicranum scoparium Hedw.	Acrocarpous moss; dense turfs	Abisko area	Yes	Yes
Polytrichum strictum (Brid.)	Acrocarpous moss; dense turfs	Abisko area	Yes	Yes
Barbilophozia lycopodioides (Wallr.) Cogn.	Cushion-forming liverwort	Abisko area	Yes	Yes
Ptilidium ciliare (L.) Hampe.	Cushion-forming liverwort	Abisko area	Yes	Yes
Vascular plants				
Dryas octopetala L.	Dwarf shrub	Abisko area	No	Yes
Empetrum nigrum L. (ssp. *hermaphroditum*)	Dwarf shrub	Abisko area	Yes	Yes
Vaccinium myrtillus L.	Dwarf shrub	Abisko area	No	Yes
Betula pubescens ssp. *Czerepanovii* (Orlova) Hämet-Ahti	Tree	Abisko area	Yes	Yes
Pinus sylvestris L.	Tree	Karesuando, Sweden	Yes	Yes
Epilobium angustifolium L.	Forb	Abisko area	Yes	Yes
Silene dioica (L.) Clairv.	Forb	Abisko area	Yes	Yes
Solidago virgaurea Praecox.	Forb	Abisko area	Yes	Yes
Carex rostrata Stokes	Graminoid	Abisko area	No	Yes
Deschampsia flexuosa L.	Graminoid	Abisko area	No	Yes
Festuca ovina L.	Graminoid	Sheffield, UK	Yes	No

Table 2 Statistical tests applied in the study: hypotheses, analysis methods, statistical results (*F* values for ANOVAs and simple regressions, *t*-values for mixed-model regressions, degrees of freedom (df) and *P* values) and implications for subsequently conducted analyses

Number	Hypothesis	Method	*F* or *t* (in case of mixed-model regressions) and df	*P*	Implications for subsequent analyses
Field experiment					
F1	Amounts of soil phenolics are affected by charcoal additions, bryophyte species and their interaction	Two-way ANOVA	Charcoal: $3.17_{1,41}$ Bryophyte: $3.43_{6,41}$ Interaction: $0.43_{6,41}$	0.082 0.008 0.852	
F2	Number of seedlings is affected by bryophyte treatment, vascular plant species' identity, charcoal additions and interactions between them	Three-way ANOVA	Bryophyte: $88.2_{6,420}$ Vasc. plant: $17.6_{9,420}$ Charcoal: $0.01_{1,420}$ Bryo × Vasc: $6.34_{4,420}$ Bryo × Char: $0.98_{6,420}$ Vasc × Char: $0.73_{9,420}$ Bryo × Vasc × Char: $0.94_{54,\ 420}$	< 0.001 < 0.001 0.921 < 0.001 0.436 0.677 0.608	In further analyses, we do not have to distinguish between charcoal-treated and -untreated plots
F3	Number of established seedlings is affected by vascular species' identity and bryophyte treatment (including control) as well as by their interaction	Two-way ANOVA	Bryophyte: $89.5_{6,490}$ Vasc. plant: $17.9_{9,490}$ Interaction:$6.43_{54,480}$	< 0.001 < 0.001 < 0.001	
F4	Seedling fitness, expressed as average mass of an individual seedling, is affected by vascular species' identity and bryophyte treatment (including control) as well as by their interaction	Two-way ANOVA	Bryophyte: $1.47_{6,103}$ Vasc. plant: $9.98_{9,103}$ Interaction: $1.24_{35,103}$	0.207 < 0.001 0.199	
F5	Number of established seedlings is affected by vascular species' identity and bryophyte species (control treatment excluded) as well as by their interaction	Two-way ANOVA	Bryophyte: $3.92_{5,420}$ Vasc. plant: $9.02_{9,420}$ Interaction: $1.91_{\ 45,420}$	0.002 < 0.001 0.194	Insignificance of interactions (also registered in the analysis F6) suggests that the numbers of vascular plant seedlings can be pooled together per plot for further analyses
F6	Seedling fitness, expressed as average mass of an individual seedling, is affected by vascular species' identity and bryophyte treatment (including control) as well as by their interaction	Two-way ANOVA	Bryophyte: $1.44_{5,98}$ Vasc. plant: $5.51_{8,98}$ Interaction: $0.69_{27,98}$	0.211 < 0.001 0.845	
F7	The total number of established seedlings of all vascular plants pooled together per plot is affected by bryophyte identity (control excluded)	One-way ANOVA	Bryophyte: $3.661_{5,41}$	0.008	
F8	Number of seedlings established in bryophyte cushions is linearly affected by species' identity, soil temperature regime, soil moisture regime, phenolic leachates and level of mechanical obstruction	Mixed-model regression with bryophyte identity as random factor	Detailed results are reported in Table 3		

Table 2 Continued

Number	Hypothesis	Method	*F* or *t* (in case of mixed-model regression) and df	*P*	Implications for subsequent analyses
F9	This test was conducted for each of the following individual temperature proxies: *May temperature amplitude* *June temperature amplitude* *July temperature amplitude* *August temperature amplitude* *Vegetation season temperature amplitude* *Year temperature amplitude* *Sum positive temperatures May* *Sum positive temperatures September* *Sum positive temperatures vegetation season* *Mean temperature May* *Mean temperature September* *Mean temperature October* Hypothesis: (The) temperature proxy can fully explain variation in seedling number in bryophyte cushions so that there is no significant variation associated with the bryophyte species' identity that is not explained by the temperature proxy	Single-factor, mixed-model regressions with bryophyte identity as random factor	For May temperature Amplitude: Intercept: -1.02_{26} Regression: 2.94_{26} For results for other proxies, see Supporting Information Table S1	 0.316 0.007	
F10	This test was conducted for each of the individual temperature proxies listed for the test F9 Hypothesis: Bryophyte cushion density and thickness both significantly affect (the) temperature proxy, and can fully explain variation in the proxy, so that there is no significant variation associated with the bryophyte species' identity that is not explained by thickness and density	Single-factor, mixed-model regressions with bryophyte identity as random factor	For May temperature amplitude: Density: -2.08_{5} Thickness: -6.33_{5} For results for other proxies, see Supporting information Table S1	 0.129 0.008	
Laboratory experiment					
L1	The amount of phenolic leachates differs between bryophytes in the laboratory conditions	One-way ANOVA	Bryophyte: $51.28_{5,24}$	< 0.001	
L2	Phenolic leachates measured in the soil under bryophytes and phenolic leachates from the distinct bryophyte species registered in the laboratory are linearly related	Regression on per-species mean values	Regression: $0.14_{1,5}$	0.701	
L3	The number of viable seedlings is affected by bryophyte species' identity, vascular plant species' identity and interaction between them	Two-way ANOVA	Bryophytes: $9.83_{6,140}$ Vasc. plants: $26.4_{4,140}$ Interaction: $1.3_{24,140}$	< 0.001 < 0.001 0.174	It is possible to pool all the vascular plants together and conduct the analysis for the total number of viable seedlings
L4	The number of viable seedlings pooled across all vascular plants depends on the amount of phenolic leachates	Mixed-model linear regression	Regression: -5.09_{23}	< 0.001	

We arranged the trays in pairs and divided each tray into four plots with plastic barriers. We randomly assigned each pair of trays to four bryophyte treatments out of seven, so that both trays in each pair had the same combination of treatments. In each pair, we treated the soil in one tray with charcoal, whereas soil in the other tray was kept intact. We sowed a mix of vascular plant seeds (50 seeds per species, but 10 seeds for *Pinus* because of their expected high germination ratio) into the central part of all plots.

We collected monospecific (visually > 95% of the same species) cushions of bryophytes in the forest within a 3-km radius around the experimental site and transplanted them to the trays, one species per plot (one-quarter of a tray), so that the plots were completely covered. The cushions were collected at random, but we avoided atypical habitats and damaged or atypically thin, thick, loose or dense cushions, using as a reference for typical cushion thickness and density the data reported in Elumeeva *et al.* (2011).

Following Steijlen *et al.* (1995), we injected active charcoal in multiple spots into the soil in the charcoal-treated plots using a syringe. We sowed a mix of vascular plant seeds (50 seeds per species, but 10 seeds for *Pinus* because of their expected high germination rate) into the central part of each plot. During the experiment we also conducted a control for the external seed influx (for details, see Supporting information Methods S1).

In September 2008, seedlings were harvested, identified, counted, oven dried (70°C) and weighed per species.

The transplanted bryophyte cushions were regularly visually inspected for vitality. During the whole experimental period 2007–2008, no harmful effects of transplantation or charcoal additions were observed on the bryophyte cushions, which seemed to have established perfectly in the new location.

We measured the soil moisture content of every plot hourly between 20 May 2008 and 10 September 2008 with ECH_2O EC-5 sensors (Decagon, Hopkins, MN, USA). We assessed the amount of phenolic leakage in the soil by collection in resin capsules (Unibest, Walla Walla, WA, USA), which were installed in May 2008 into the soil on each plot, at 1-cm depth, and collected in September 2008, simultaneous with the seedling harvest. We analysed the capsules for phenolic compounds using the Folin–Ciocalteau method.

For each species, we measured in eight replicates the cushion thickness and density (mass to volume ratio) and the level of mechanical obstruction experienced by seeds and seedlings caused by the presence of bryophytes (for details, see Methods S3; for data, see Table S2). We tested the cushion thickness and density as potential easily measurable proxies for the mechanical obstruction level and for the differential effects on soil moisture and temperature regimes. The data on the average cushion densities were also used as reference data for natural cushion density in the laboratory and obstruction experiments.

Statistical analysis of the field experiment

Table 2 gives an overview of the statistical analyses used in this study. All tests applied to the number of seedlings registered per plot were also applied to the total mass of seedlings measured per vascular plant species per plot. As these two groups of analyses revealed generally similar results, we describe and report only the analyses referring to the number of seedlings as the response variable.

We tested the effects of charcoal additions and bryophyte species on soil phenolics with two-way ANOVA (Table 2, analysis F1). We used three-way ANOVA to examine the effects of bryophyte treatment, vascular plant species, charcoal additions and their interactions on the number of seedlings (Table 2, analysis F2). As this analysis revealed that charcoal treatment did not affect the seedling number or interact with bryophyte species or vascular species, in further analyses we pooled charcoal-treated and -untreated plots.

We tested the effects of bryophyte treatment on field seedling establishment and fitness by two two-way ANOVAs using bryophyte and vascular species as independent factors and (1) number of seedlings and (2) average mass of an individual seedling, calculated per plot per species, as dependent factors. These tests were conducted in two steps: first, taking the control into account, mainly aiming at the detection of differences between control and bryophyte treatments (Table 2, analyses F3 and F4, respectively); and, second, without control, aiming at the detection of differences between bryophytes *per se* (Table 2, analyses F5 and F6, respectively). As, at the second step, none of the ANOVAs detected an interaction between the vascular plant and bryophyte species, we ran one-way ANOVAs on the total seedling number of all vascular plants pooled per plot as independent factor and bryophyte treatment (excluding the control) as dependent factor, followed by a Tukey *post hoc* test (Table 2, analysis F7).

As proxies for the soil temperature regime, we considered per-plot averages of temperature per month, whole summer and whole year, amplitudes of daily fluctuations and the sums of positive day averages per month. As proxies for soil moisture regime, we considered per-plot monthly averages, whole summer averages and amplitudes of daily fluctuations. From these proxies, we selected those that showed significant differences between bryophyte species, as detected by ANOVAs in the case of temperature and Kruskal–Wallis test in the case of moisture, the latter as a result of the non-equality of error variances. The proxies selected in this way expressed different aspects of alternation of temperature and moisture regimes provided by bryophytes. However, the moisture proxies were autocorrelated, as were those of temperature. Therefore, they could not be used individually in a multiple regression analysis to test their relationships to seedling emergence. In order to obtain one summary proxy for

soil temperature and one for soil moisture, we ran a principal component analysis (PCA) individually on the sets of temperature and moisture proxies, and used the principal component obtained from each analysis as a combined proxy for temperature and moisture regimes in further analysis.

We assessed the combined effects of soil temperature and moisture regimes, phenolic leachates and level of mechanical obstruction on the number of seedlings in different bryophyte cushions by a mixed multiple regression model with a random intercept (Zuur *et al.*, 2009), with bryophyte species as a random factor, seedling number per plot as dependent variable, and per-plot temperature and moisture proxies, obtained by PCA, per-plot values of phenolic leachates and the per-species mean value for obstruction as explanatory variables (Table 2, analysis F8). Mixed-model analysis was chosen to account for the fact that observations within a species are unlikely to be independent. Variation between observations that was not explained by the set of explanatory variables and was associated with species' identity was accounted for by a random intercept (see Methods S2 for full details on the method and references therein for further reading).

Only the temperature regime was a significant predictor of seedling number/mass (see the Results section for details). Having ascertained this, we tested each of the individual temperature proxies as explanatory variables for seedling number and mass in a series of single-factor, mixed-model regressions (Table 2, analysis F9). In order to determine which bryophyte traits could be used as easy-to-measure proxies for changes in temperature regime under distinct species, we tested the relation of cushion density and thickness to each of the temperature proxies individually with mixed-model multiple regression analysis, considering per-plot temperature proxy as dependent variable, bryophyte thickness and density as explanatory variables and bryophyte species as a random factor (Table 2, analysis F10).

Laboratory experiment

This experiment aimed to assess the effects of bryophyte phenolic leachates alone on germination and the early survival of vascular plants. We collected intact bryophyte cushions in October 2007 in the Abisko area and air dried them to preserve their structure. Before the start of the experiment, we cleaned the cushions of soil, roots, vascular plant litter and lower senescing and dead parts. We rehydrated the bryophytes with specially prepared water, resembling the chemical composition of Abisko rainwater (Malmer & Nilgård, 1980), hereafter called 'Abisko rainwater'.

We placed each bryophyte cushion on two sheets of glass fiber filter paper (Whatman®, Schleicher & Schuell, s-Hertogenbosch, Netherlands, GF/A, 90 mm in diameter) arranged on top of each other in a Petri dish. We used five replicates for each bryophyte species and a control consisting of filter paper in a Petri dish without bryophyte. The amount of bryophyte material per Petri dish represented the natural cushion structure of each species. The Petri dishes were placed in a glasshouse and kept moist with Abisko rainwater. After 5 d, we removed the bryophytes from the filters, oven dried and weighed them. From each Petri dish, we oven dried one-quarter segment of one randomly selected filter and analyzed it for phenolic content with the Folin–Ciocalteau method (Waterman & Mole, 1994). We expressed the phenolic content of the filters on an area basis, which is a realistic way of comparing bryophytes differing in thickness and density. However, within the same species, we corrected the data for differences between weights of bryophyte cushions used for filter saturation, which never exceeded 10%.

After the bryophytes had been removed, filter pairs were separated and each filter was placed in a new sterile Petri dish. On each pair of filters, seven segments were defined, four in a complete filter and three in the filter cut for phenolic analysis. On each segment, we placed 20 seeds of a randomly assigned species, so that each ex-pair of filters contained all seven vascular plant species involved in the experiment. All seeds had been stratified at 4°C for 3 months before the experiment in order to break dormancy. The Petri dishes with seeds and filters were placed in a glasshouse (temperature, 15°C; moisture, 60%) with natural daylight and supplemented artificial daylight during the night hours in order to mimic the subarctic summer.

The experiment lasted for 1 month, during which we kept the seeds and seedlings moist with demineralized water and counted the germinated seeds every 3 d. After 2 wk, we randomized the position of Petri dishes in order to avoid location artifacts. At the end of the experiment we counted the total number of viable seedlings per species per replicate dish. We opted to analyze the number of viable seedlings instead of the number of germinated seedlings because many seedlings rotted soon after germination. *Silene dioica* and *Empetrum nigrum* did not germinate at all in any treatment and were omitted from further analysis.

Statistical analysis of the laboratory experiment

We compared the amounts of phenolics in the filters with one-way ANOVA using bryophyte treatment level as independent factor (Table 2, analysis L1). We compared per-bryophyte species' mean values of phenolics in the filters with those measured in the field using linear regression (Table 2, analysis L2). We compared the numbers of viable seedlings using two-way ANOVAs with bryophyte treatment and vascular plants as independent factors (Table 2, analysis L3). The lack of significant interaction effects between vascular plant species and bryophyte species (see the Results section) allowed us to pool the vascular plant seedlings for further analysis. We tested the effect of (log-transformed) phenolic leachates on the total number

of viable seedlings by mixed-model linear regression with bryophyte species as random factor (Table 2, analysis L4). As the phenolic amounts registered in the control were negligible, we excluded the control data from analyses L1, L2 and L4 (Table 2).

Methodological note on statistics

For all analyses, we tested the assumptions of normality (with the Kolmogorov–Smirnov test), homogeneity of variances (graphically and with Levene's test) and multi collinearity (only for regressions) and, where necessary, applied natural logarithm or rank transformations (needed only for ANOVAs). In order to check for any location artifact, we ran all the above-mentioned ANOVAs with the filter pairs and tray pairs in the laboratory and field experiments, respectively, as an additional factor, which was found to be nonsignificant in all cases. Analyses were conducted with SPSS v.15, Chicago, IL, USA and R2.11, R Foundation for Statistical Computing, Vienna, Austria.

Results

Field experiment: seedling recruitment

Soil phenolic content was marginally lower in charcoal-treated plots ($P = 0.082$) and differed between bryophyte treatments ($P = 0.008$) (Table 2, analysis F1; Fig. S1), but there was no significant interaction between the two treatments ($P = 0.85$). Charcoal additions did not affect seedling number or interact with other bryophyte or vascular plant treatments (Table 2, analysis F2).

Although seedling number was affected by vascular plant treatment (see Fig. S2 for details) and its interaction with bryophyte treatment ($P < 0.001$ in all cases, see Table 2, analysis F3), analysis conducted without control (Table 2, analysis F5) revealed significant vascular plant and bryophyte treatment effects ($P < 0.001$, in both cases), but no significant interaction effect ($P = 0.2$). This suggests that the significant interaction in the former analysis was exclusively a result of the distinct responses of the vascular plants to control vs bryophyte treatments and not to the different responses of distinct vascular plants to distinct bryophytes. The subsequent ANOVAs on seedling number of all vascular plants pooled together (Table 2, analysis F7) indicated a significant effect of distinct bryophyte species ($P = 0.008$, Fig. 2).

Per-species average seedling mass (analyses F4 and F6 in Table 2) did not differ between bryophyte species' treatments (whether or not including control plots), and there was no interaction with vascular plant species. Logically, there were significant differences between vascular plant species ($P < 0.001$, in both cases). Therefore, we concluded that the fitness of established seedlings was not affected by bryophyte treatment.

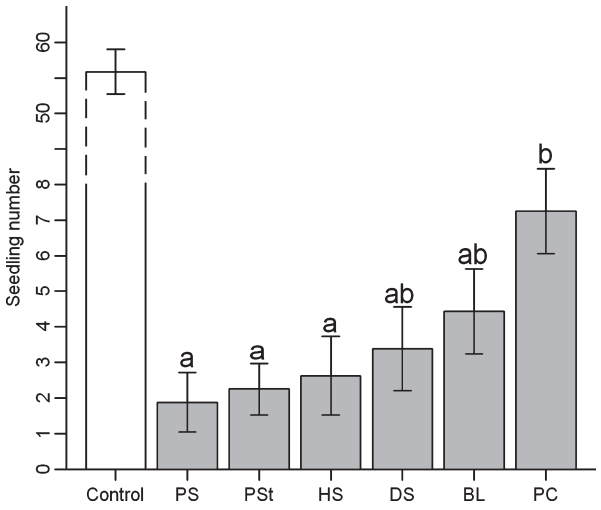

Fig. 2 Number of seedlings (all vascular plants pooled together) germinated in the field experiment as affected by different bryophyte treatments. Mean values and standard errors ($n = 8$) are shown. Different letters indicate differences detected by Tukey *post hoc* test. Note that the values for controls are shown exclusively for comparison. They were not included in the analysis. Also, control values are shown in a distinct range. Bryophyte species' codes: BL, *Barbilophozia lycopodioides*; DS, *Dicranum scoparium*; HS, *Hylocomium splendens*; PC, *Ptilidium ciliare*; PS, *Pleurozium schreberi*; PSt, *Polytrichum strictum*.

Field experiment: mechanisms underpinning seedling recruitment

Mixed-model multiple regression analysis (Table 2, analysis F8) revealed that only the temperature regime was a significant predictor of field seedling establishment in different bryophyte cushions ($P = 0.009$ and $P = 0.07$ for the first and second PCA axes), but moisture regime, mechanical obstruction and phenolic leachates were not noteworthy (Table 3). Species' identity (i.e. intercept), expressing the factors not included in the modeled explanatory variables, did not play a significant role in explaining the variation in seedling number (coefficient of variation (CV) of the intercept, 0.00002).

Among the individual temperature proxies (Table 2, analysis F9), diurnal temperature amplitude in May best predicted seedling establishment ($P = 0.007$, Fig. 3; see also Tables 4 and S1 for further details). In none of the analyses based on the individual temperature proxies (Table 2, analysis F9) did we detect a noteworthy variation of the intercept. For May temperature amplitudes, the variation was the smallest (CV = 0.00003); for the other proxies, CVs are not shown. This indicates that all the variation in seedling number as affected by bryophyte species (Table 2, analysis F7) was a result of the species-specific temperature regimes, mostly May temperature amplitudes, and there were no other unknown factor(s) associated with the bryophyte species' identity that influenced seedling establishment. (For

Table 3 Results of the mixed-model multiple regression analysis of the total number of seedlings found after 1 yr in bryophyte mats vs factors potentially triggering the germination and early seedling survival (temperature and moisture regimes, mechanical obstruction and phenolic leachates)

				Pearson correlation coefficient			
	P value	*T* value	df	1st PCA axis temp. regime	2nd PCA axis temp. regime	1st PCA axis moist. regime	Obstruction
1st PCA axis temperature regime	0.01	−2.65	26				
2nd PCA axis temperature regime	0.09	−1.76	26	−0.11			
1st PCA axis moisture regime	0.61	−0.51	26	0.01	−0.05		
Obstruction	0.28	−1.25	4	0.25	−0.25	0.05	
Phenolics	0.11	−1.92	26	−0.29	0.32	0.07	−0.5

Temperature and moisture regimes are expressed as projections of multiple respective proxies on the first and second axes of principal component analyses (PCAs) conducted individually on sets of temperature and moisture proxies. For the regression analysis, PCA axes for temperature and moisture regimes, and phenolic leachates, were nested within bryophyte species, and the mean value for obstruction was considered as a species-specific trait. We show Pearson coefficients of intercorrelation between the predictors, and the significance of each predictor for seedling establishment in bryophyte mats.

Table 4 Absolute values and standard errors of individual proxies of soil temperature regime under bryophyte cushions

Bryophyte species	A May**	A June*	A July^{+}	A Veg*	A Year^{+}	S May^{+}	S Sep^{+}	M Sep^{+}	M Oct*
Pleurozium schreberi	4.0 ± 0.2	6.8 ± 0.3	6.7 ± 0.4	5.7 ± 0.3	2.6 ± 0.1	363 ± 19	204 ± 3	5.2 ± 0.1	−0.3 ± 0.1
Hylocomium splendens	4.3 ± 0.3	7.4 ± 0.6	7.5 ± 0.5	6.3 ± 0.4	2.8 ± 0.2	395 ± 24	207 ± 7	5.3 ± 0.2	−0.1 ± 0.2
Polytrichum strictum	4.7 ± 0.2	7.8 ± 0.3	8.1 ± 0.4	6.7 ± 0.3	3.0 ± 0.1	445 ± 22	213 ± 5	5.5 ± 0.1	−0.2 ± 0.1
Dicranum scoparium	5.1 ± 0.2	7.7 ± 0.3	7.2 ± 0.4	6.4 ± 0.3	2.9 ± 0.1	446 ± 11	196 ± 4	5.0 ± 0.1	−0.4 ± 0.1
Ptilidium ciliare	6.2 ± 0.3	9.3 ± 0.4	9.5 ± 0.5	8.0 ± 0.4	3.5 ± 0.2	504 ± 32	196 ± 5	5.0 ± 0.1	−0.7 ± 0.1
Barbilophozia lycopodioides	6.3 ± 0.5	9.1 ± 0.3	8.5 ± 0.2	7.6 ± 0.2	3.4 ± 0.1	503 ± 31	187 ± 6	4.8 ± 0.2	−0.7 ± 0.1

Only proxies that showed a significant relation ($P < 0.05$) or at least a tendency ($0.05 < P < 0.15$) in a regression analysis are shown.
**, $P < 0.01$; *, $0.01 < P < 0.05$; $^{+}$, $0.05 < P < 0.15$.
A May, A June, A July, A Veg, A Year, temperature amplitudes of May, June, July, vegetation season and whole year, respectively; S May and S Sep, sums of positive temperatures in May and September; M Sep and M Oct, mean temperatures in September and October.

the per-species absolute values of May amplitude temperature, as well as other temperature proxies, see Table 4.)

Cushion thickness was a significant predictor for all temperature proxies that were related to seedling establishment (Table 2, analysis F10; for result details, see Table S2). Cushion density was not a significant predictor for any of the temperature proxies.

Laboratory experiment

The amount of phenolic leachate and the number of viable seedlings were strongly affected by bryophyte treatment (Table 2, analysis L1, $P < 0.001$); the two liverworts, *Barbilophozia* and *Ptilidium*, leached the most phenolics (mean ± SE of 0.52 ± 0.12 and 0.17 ± 0.04 mg m^{-2}, respectively, which are 10-fold higher than other species, $P < 0.001$, Tukey test) and had the fewest viable seedlings (70% and 40% lower than the control, respectively). However, per-species' levels of phenolic leachates were not related to those registered in the field (Table 2, analysis L2).

The number of viable seedlings was significantly affected by both vascular species' identity and bryophyte species' identity ($P < 0.001$ in both cases), but there was no interaction between vascular plant species and bryophytes (Table 2, analysis L3). The total number of well-developed seedlings pooled across all vascular plant species was negatively related to the amount of bryophyte phenolic leachates (Table 2, analysis L4; Fig. 4).

Discussion

This study is the first assessment of interaction mechanisms between vascular plant seedlings and bryophyte species. All bryophytes in our study strongly suppressed the regeneration of vascular plants. This may be explained by the enormous proportion of seeds intercepted by bryophyte cushions (see Methods S3 for details). However, between bryophyte species, the difference in the number of established seedlings could not be attributed to mechanical obstruction, but rather to altered soil temperature regime. Clear differences between bryophyte species in terms of suppressive effects on seedlings strongly imply that the climatically and anthropogenically driven transformations in the structure and composition of bryophyte communities

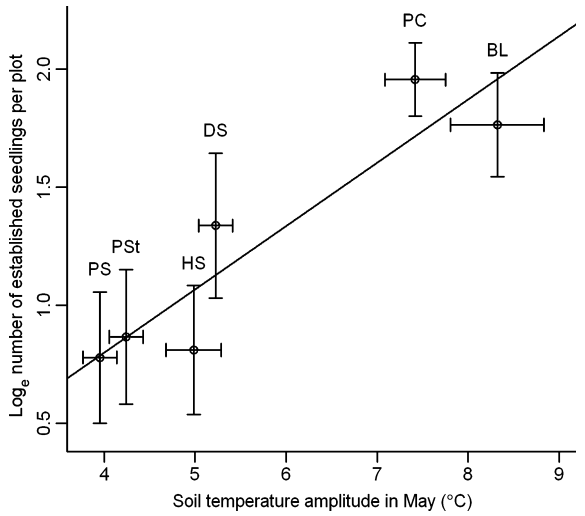

Fig. 3 Per-plot number of established vascular plant seedlings as a function of the May temperature fluctuations. Bryophyte species' codes: BL, *Barbilophozia lycopodioides*; DS, *Dicranum scoparium*; HS, *Hylocomium splendens*; PC, *Ptilidium ciliare*; PS, *Pleurozium schreberi*; PSt, *Polytrichum strictum*.

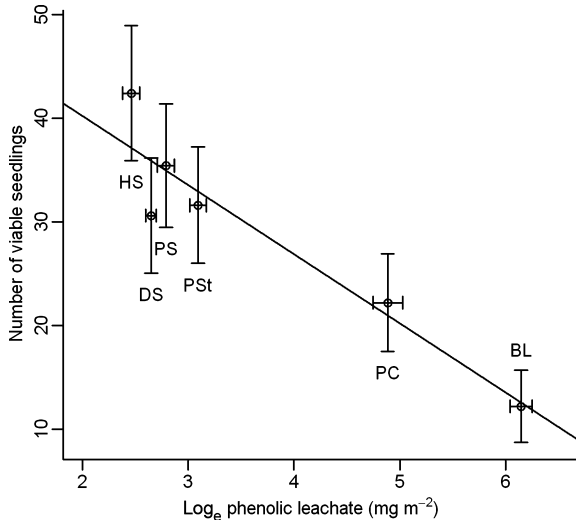

Fig. 4 Phenolic leachate (mg m^{-2}) measured in the laboratory vs number of viable seedlings. Bryophyte species' codes: BL, *Barbilophozia lycopodioides*; DS, *Dicranum scoparium*; HS, *Hylocomium splendens*; PC, *Ptilidium ciliare*; PS, *Pleurozium schreberi*; PSt, *Polytrichum strictum*.

(Molau & Alatalo, 1998; Nygaard & Odegaard, 1999; Makipaa & Heikkinen, 2003; Lang *et al.*, 2009) will affect the generative reproduction of vascular plants.

Interestingly, the suppressive effect of a bryophyte species on seedling performance coincided with its association with the forest understory, as reported in several subarctic vegetation surveys (Schoweld, 1992; Frego, 1996; Makipaa & Heikkinen, 2003; Locky *et al.*, 2005). The most widespread bryophytes of boreal and subartic forests, *Hylocomium splendens* and *Pleurozium schreberi*, were among the strongest suppressors of vascular plant seedlings. *Dicranum scoparium* had an intermediate position and liverworts, rather scarce in subarctic forests, formed the best sites for vascular plant regeneration in the field. This suggests that effective suppression of vascular plant seedlings is an important mechanism to maintain dominance in the forest understory, although *Polytrichum strictum*, which is less widespread than *Hylocomium* and *Pleurozium*, had a similar suppressive effect on vascular plant seedlings in our study. However, in contrast with other bryophytes investigated in this study, *Polytrichum* is a typical early successional species in subarctic forest (Benscoter, 2006; Benscoter & Vitt, 2008) and this might explain its lower abundance in the established forest.

To our surprise, we did not find interaction effects between bryophyte species and vascular plant species, suggesting that vascular plants do not possess species-specific adaptation mechanisms for recruitment in bryophyte cushions. This partly contradicts the results of Ohlson & Zackrisson (1992), who detected species-specific preferences of coniferous trees for habitats dominated by *Sphagna* vs *Pleurozium*. However, in that study, seeds were sown into existing bryophyte mats, and therefore it was not possible to distinguish between the effects of bryophytes *per se* and the effects of habitat, such as macro-light conditions, soil quality and moisture availability.

Allelopathy

We found a striking contrast between the results of laboratory and field experiments with respect to allelopathic effects of bryophytes. In the laboratory experiment, bryophyte phenolics negatively affected germination and, even more strongly, the early development of seedlings, as in some previous laboratory studies (Tsubota *et al.*, 2006; Kato-Noguchi *et al.*, 2010). By contrast, the field experiment revealed no difference in the amount of phenolics between bryophytes. In addition, seedling performance was not related to phenolics measured in the field. Consistently smaller amounts of phenolics in charcoal-treated soils indicated, however, that there was no error in the experimental treatments or measurements. Phenolic degradation and the composition of the microorganism community responsible for this process are strongly affected by plant inputs (Brant *et al.*, 2006). We speculate that, in our case, because of the difference in phenolic compound composition and the possible presence of other bryophyte leachates, the bryophyte-derived phenolics underwent distinct degradation, resulting in similar soil phenolic concentrations associated with different bryophytes. The striking difference between the results of the laboratory and field experiments highlights the danger of drawing conclusions about complex ecological processes based on laboratory experiments only, without field verification (Mokany & Ash, 2008; Soudzilovskaia *et al.*, 2010).

Moisture regime

Contrary to our expectations, bryophyte species did not vary greatly in their effect on soil moisture or associated effects on seedling establishment success. Moreover, the soil under some bryophytes was drier than the bare soil on control plots. This is probably a result of the generally low (300 mm yr^{-1}) level of precipitation in the Abisko area (Malmer & Nilgård, 1980), which often falls as drizzle and may be absorbed by bryophytes without reaching the soil. The absence of bryophyte-mediated moisture effects on vascular plant seedlings could be attributed to the lower sensitivity of seedlings to differences in moisture than to differences in temperature (Burton & Bazzaz, 1991), in combination with the relatively small differences in moisture found.

Temperature

Our data suggest that competition between bryophytes and vascular plant seedlings is mediated by the soil temperature regime under bryophyte mats. Our experimental set-up did not allow the unambiguous disentanglement of the importance of individual aspects of temperature regime. However, we detected a strong negative correlation between diurnal temperature fluctuations during the time of germination and the number of established seedlings. Similarly, Sthilaire & Leopold (1995) found better germination in mats of *Hypnum imponens* than in *Hylocomium splendens* and *Sphagnum girgensohnii* in the field, but not in the glasshouse at constant temperature. As Thompson *et al.* (1977) demonstrated the crucial importance of temperature fluctuations for breaking seed dormancy, we suggest that this mechanism is key to the suppression of vascular plant establishment in bryophyte mats in the subarctic, where understory vegetation is dominated by various bryophytes with distinct heat conductance. Thompson *et al.* (1977) reported that fluctuation ranges of 1–8°C were needed to break dormancy in light and 4–12°C in dark conditions. Our results are consistent with this temperature range.

Gornall *et al.* (2007, 2009) and Van der Wal & Brooker (2004) reported a reduction in soil temperature associated with bryophyte mat presence and thickness in high-arctic tundra (Van der Wal & Brooker, 2004). We also expected bryophytes to decrease the temperature during the growing season and thereby suppress the germination and seedling establishment of vascular plants. However, although soil temperature was lower under bryophytes at the beginning of the growing season, at the end it was higher, and the average soil temperature over the whole growing season did not differ between mats of different bryophyte species or from the control. As we harvested the experiment in September, our experimental set-up did not allow appropriate testing for the effects of the temperature regime at the end of the growing season on 1-yr-old seedlings. Jeschke & Kiehl (2008) reported that, in grasslands of Bavaria (Germany), removal of the moss layer improved the germination of vascular plants, but ultimate seedling survival was higher in moss mats, because the seedlings were better protected against frost. However, we do not expect this effect to be strong with respect to seedling survival in different bryophyte mats, because, in our as well as other experiments (Gornall *et al.*, 2007), the strongest difference between bryophytes with distinct canopy height was in the amplitude of temperature and not absolute temperature, and there is evidence (Prock & Körner, 1996) that the early season is the most critical period for the development of cold climate plants; late-season growth is generally much less important because, by that time, sufficient biomass has been produced to ensure successful winter survival.

We did not detect a correlation between the effects of moisture and temperature regimes on seedling establishment. Similarly, Van der Wal & Brooker (2004) reported, for high-arctic tundra, that the 'moss layer acts as an insulating blanket irrespective of soil moisture', after detecting a marginally significant impact of moisture on soil temperature, with only a < 1°C drop in temperature over the range of soil moisture contents from 10% to 60%. Considering that, in our study, the moisture range was much smaller (Fig. S3), the absence of correlation with temperature is not surprising. It is important to realize, however, that our study does not necessarily represent all relevant aspects of subarctic soil moisture and temperature regimes, but only those showing a clear relation to seedling establishment.

The absence of a bryophyte effect on the mass of individual vascular plant seedlings suggests that bryophytes exclusively affect germination and very early seedling establishment, but do not influence the fitness of established seedlings. This is supported by the responses to changes in temperature regime under bryophyte cushions: the strongest differences between bryophyte treatments were related to spring temperature fluctuations, which are known to affect germination, whereas differences related to the length of vegetation season were not significant. However, it is necessary to keep in mind that the commercial potting soil underneath the bryophytes probably created a favorable nutrient supply to the seedlings. Thus, the fitness of seedlings in control plots and bryophyte cushions in the species' natural habitats may vary more strongly owing to larger differences in soil nutrition regime.

Conclusions

Our study has clearly demonstrated the importance of bryophyte species for vascular plant generative reproduction, and thereby community composition. However, we did not find evidence of vascular plant species-specific adaptations for recruitment in bryophyte cushions. In the subarctic, bryophytes affect mostly germination and very early seed-

ling survival, but not the fitness of established seedlings. The difference between bryophyte species with respect to vascular plant seedling establishment success in bryophyte mats is best explained by the altered soil temperature regime, specifically by the reduction in temperature fluctuations during germination time.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Soil phenolic content under mats of distinct subarctic bryophyte species.

Fig. S2 Performance of individual vascular plant species in subarctic bryophyte mats.

Fig. S3 Volumetric soil moisture content measured over the summer months under subarctic bryophyte cushions.

Table S1 Results of the regression analyses of the dependences between individual proxies for soil temperature regime under bryophytes, vascular plant seedling establishment and bryophyte cushion thickness

Table S2 Mean values and errors for bryophyte cushion thickness, density and mechanical obstruction

Methods S1 Control for the external seed influx.

Methods S2 The use of the mixed-model regression technique.

Methods S3 Measurement of mechanical obstruction created by bryophyte cushions.

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