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Mosses modify effects of warmer and wetter conditions on tree seedlings at the alpine treeline

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Abstract

Climate warming enables tree seedling establishment beyond the current alpine treeline, but to achieve this, seedlings have to establish within existing tundra vegetation. In tundra, mosses are a prominent feature, known to regulate soil temperature and moisture through their physical structure and associated water retention capacity. Moss presence and species identity might therefore modify the impact of increases in temperature and precipitation on tree seedling establishment at the arctic-alpine treeline. We followed *Betula pubescens* and *Pinus sylvestris* seedling survival and growth during three growing seasons in the field. Tree seedlings were transplanted along a natural precipitation gradient at the subarctic-alpine treeline in northern Sweden, into plots dominated by each of three common moss species and exposed to combinations of moss removal and experimental warming by open-top chambers (OTCs). Independent of climate, the presence of feather moss, but not *Sphagnum*, strongly supressed survival of both tree species. Positive effects of warming and precipitation on survival and growth of *B. pubescens* seedlings occurred in the absence of mosses and as expected, this was partly dependent on moss species. *P. sylvestris* survival was greatest at high precipitation, and this effect was more pronounced in *Sphagnum* than in feather moss plots irrespective of whether the mosses had been removed or not. Moss presence did not reduce the effects of OTCs on soil temperature. Mosses therefore modified seedling response to climate through other mechanisms, such as altered competition or nutrient availability. We conclude that both moss presence and species identity pose a strong control on seedling establishment at the alpine treeline, and that in some cases mosses weaken climate-change effects on seedling establishment. Changes in moss abundance and species composition therefore have the potential to hamper treeline expansion induced by climate warming.

KEYWORDS
Arctic, *Betula pubescens*, bryophytes, climate change, *Pinus sylvestris*, plant interactions, precipitation, treeline expansion

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1 | INTRODUCTION

Shifts in the position of alpine and arctic treelines are among the most dramatic climate-driven plant migrations globally, and they may cause substantial climate feedbacks through altering soil carbon content and albedo (Chapin et al., 2005; Hartley et al., 2012; Mayor et al., 2017; Parker, Subke, & Wookey, 2015; Wilmking, Harden, & Tape, 2006). Treeline shifts are often considered to be driven by changes in temperature (notably through climate warming), given that worldwide their position is generally associated with a growing-season mean soil temperature of 6.7°C (Körner & Paulsen, 2004). However, across regions, treeline responses to climate warming are not consistent (Frost & Epstein, 2014) and in many cases treelines fail to advance upslope with increasing temperatures (Harsch, Hulme, McGlone, & Duncan, 2009). It has therefore been suggested that variation in other environmental factors may modify tree seedling responses to warming, including precipitation (Frost & Epstein, 2014; Hagedorn et al., 2014) and the composition of existing vegetation in which tree seedlings need to establish (Grau et al., 2012; Lett & Dorrepaal, 2018). The extend and mechanisms by which precipitation and resident plant community modify direct effects of warming on treeline advance has, however, seldom been explored experimentally (Hagedorn, Gavazov, & Alexander, 2019; Lett & Dorrepaal, 2018) and therefore remains poorly understood.

Treeline expansion beyond the vegetative spreading capacity of already present trees relies on successful seedling establishment above the current treeline. This partly depends on the abiotic conditions of the microhabitat such as temperature and soil moisture (Lett & Dorrepaal, 2018). Although warming can promote seedling establishment at treelines (Grau et al., 2012; Loranger, Zotz, & Bader, 2016; Okano & Bret-Harte, 2015), seedlings are sensitive to desiccation during the growing season, and this effect should be greater as temperatures increase. For this reason, increases in precipitation may promote seedling establishment more than warming or even stimulate warming responses (Kueppers et al., 2017; Lazarus, Castanha, Germino, Kueppers, & Moyes, 2018), but how temperature and precipitation interact is still unclear.

Beyond the current treeline, seedlings likely have to establish within the existing moss communities, which is frequently a dominant feature in tundra ecosystems (Beringer, Lynch, Chapin, Mack, & Bonan, 2001). Presence of moss has considerable impact on the immediate abiotic environment (Cornelissen, Lang, Soudzilovskaia, & During, 2007) because mosses buffer soil moisture and temperature fluctuations (Bueno, Williamson, Barrio, Helgadóttir, & Hik, 2016; Gornall, Jónsdóttir, Woodin, & van der Wal, 2007; Jackson, Martin, Nilsson, & Wardle, 2011; Soudzilovskaia, van Bodegom, & Cornelissen, 2013). Mosses can also affect soil nutrient availability (De Long et al., 2016) through their effects on soil temperature and their poor litter quality (Gornall et al., 2007; Lang et al., 2009). These effects of mosses on their environment can all greatly impact tree seedling establishment, both negatively and positively (Lett, Nilsson, Wardle, & Dorrepaal, 2017; Soudzilovskaia et al., 2011; Stuiver, Wardle, Gundale, & Nilsson, 2014; Wardle, Lagerström, & Nilsson, 2008; Wheeler, Hermanutz, & Marino, 2011). Furthermore, by reducing temperature (De Long et al., 2016) and soil moisture (Jackson et al., 2011) fluctuations, mosses could potentially mask both the separate and combined effect of warming and precipitation on tree seedlings. However, how and to which extent mosses may control seedling establishment under a future climate is not well understood.

Moss species show great variation in characteristics that may modify the microenvironment for coexisting vascular plants (During & van Tooren, 1990; Sohlberg & Bliss, 1987). For example, through variation in physical and chemical traits, such as mat thickness, moisture holding capacity and chemical composition, moss species vary in the extent to which they regulate the dynamics of soil temperature (Soudzilovskaia et al., 2013), soil moisture (Elumeeva, Soudzilovskaia, During, & Cornelissen, 2011) and soil nutrients (Lett et al., 2017). Moss species have been shown to differentially modify responses of establishing tree seedlings to warming or precipitation under controlled conditions where climate settings were kept constant (Lett et al., 2017; Stuiver et al., 2014). However, these effects on seedling establishment at natural settings for example, at or near the treeline have not been investigated. In addition, species identity may determine to which extent precipitation enhances positive warming responses, which also remains untested.

The aim of this study was to understand how the presence and species identity of mosses modify climate-warming effects on tree seedling establishment at the alpine treeline, in relation to the level of precipitation. We hypothesized that: (a) positive effects of warming on seedlings will be more pronounced with higher precipitation. (b) The positive effects of higher temperatures, precipitation and their interaction on seedlings will be greater when mosses are absent, because mosses will intercept moisture and buffer soil temperature changes. (c) How warming, precipitation and their interaction promote seedling survival and growth and how these effects are dampened by moss presence, will depend on moss species identity. As such, we expect that moss species that have the highest bulk density and moisture holding capacity will lead to the smallest effects of temperature and precipitation on seedlings, because they will have a greater buffering effect on soil temperature and soil moisture.

To test our hypotheses, we conducted a full-factorial experiment above the current subarctic–alpine treeline in northern Sweden, with four treatment factors as follows: natural precipitation (field sites with high and low natural precipitation), warming (presence vs. absence of open-top chambers (OTCs) to provide experimental warming), moss cover (presence vs. removal of mosses) and moss species identity (patches dominated by one of each of three moss species). The three moss species chosen at each site, (i.e. *Sphagnum* spp. (including *S. capillifolium* (Ehrh.) Hedw. and *S. fuscum* (Schimp.)) and the feather mosses *Hylocomium splendens* (Hedw.) Schimp. and *Pleurozium schreberi* (Brid.) Mitt.), are all common circumarctic species at the treeline ecotone. They differ in characteristics that are likely to be important for tree seedling establishment and for modifying climate-change impacts. In this experiment, we then monitored the survival and growth of planted tree seedlings of each of the two treeline forming species of the study region, that is, the deciduous broad-leaved *Betula pubescens* ssp. *tortuosa* (Ledeb.) Nyman and the evergreen conifer *Pinus sylvestris* L. We also measured various abiotic variables in the seedling microenvironment throughout the experiment in order to understand the mechanisms underpinning our results. Addressing these hypotheses in combination will allow us to understand how mosses may modify the effects of climate (and climate change) on tree seedling establishment and how this in turn may impact climate change-driven treeline expansion.

2 | MATERIALS AND METHODS

2.1 | Site description and experimental design

The experiment included eight field sites (between N68°18' to N68°31' and E18°12' to E18°54'), all situated at the current treeline (500–775 m a.s.l.) in Northern Sweden and encompassing a natural gradient in precipitation (Table 1). Four sites were situated on either side (north–south) of Lake Torneträsk and close to the Abisko National Park, which is a low precipitation area. These sites collectively served as the 'low precipitation' treatment (annual precipitation 571–755 mm/year, gridded data 4 × 4 pixels, Swedish Meteorological and Hydrological Institute [SMHI], 1961–1990; Table 1). The other four sites were situated further west towards the Swedish–Norwegian border, and this area is more oceanic and naturally receives higher annual precipitation. These sites collectively served as the 'high precipitation' treatment (annual precipitation 811–1155 mm/year, gridded data 4 × 4 pixels, SMHI, 1961–1990; Table 1). The four sites within each precipitation class were located at least 1 km apart and functioned as independent replicates for the experiment.

To verify the gridded data, we measured June–September rainfall in 2014 with one rain gauge (HOBO RG3-M) at each of the eight sites, and snow depth (as snow water equivalent, obtained by weighing the water in a core of snow taken through the entire snow pack) at plot level during maximum snow depth in March 2016. Rainfall tended to be higher at high precipitation sites ($p = .06$), whereas snow depth did not differ between sites during these periods (Figure S1). We have likely missed some of the precipitation that fell in the transitions between summer and winter due to inaccessibility of the sites. The precipitation estimated by gridded data was higher than measured at the closest meteorological stations (low precipitation sites: Abisko, 360 m a.s.l., mean annual temp. −0.8°C, precipitation 304 mm/year; high precipitation sites: Katterjåkk, 500 m a.s.l., mean annual temp. −1.7°C, precipitation 844 mm/year, SMHI, 1961–1990). This difference is likely caused by the higher elevation of the study sites than the meteorological stations. Precipitation level did not affect air temperature at the plot-level (see Section 2.3; Table S1).

Vegetation at the sites was typical treeless tundra-heath, with presence of dwarf shrubs and a high dominance of bryophytes. Within each site, there are numerous patches of up to 10 m across that are each dominated by one of three moss species, that is, *Sphagnum* spp. (including *S. capillifolium* and *S. fuscum* in pure colonies) and the feather mosses *H. splendens* and *P. schreberi*, hereafter referred to by their generic names. These species are all common above the treeline (Mårtensson, 1955, 1956) near Abisko, and in the boreal and arctic biomes in general (Longton, 1988).

At each of the eight sites, we established a full-factorial combination of the following treatments: 'moss species' (i.e. dominance by one of each of the three different species), 'moss removal' (presence vs. removal of the living moss cover) and experimental passive summer 'warming' (absence vs. presence of OTCs; Figure 1). Specifically, for each site we selected three pairs (one for

TABLE 1 Site characteristics of eight treeline sites situated along a precipitation gradient in the Abisko region in Northern Sweden

Site name	Precipitiation[a] (mm/year)	Precipitation category	Elevation (m a.s.l.)	Aspect	Vascular plant cover[c] (%)	Dominant bedrock[b]
Jieprenjåkk 1	755	Low	740	S	187	Metagreywacke, phyllite, limestone
Jieprenjåkk 2	571	Low	750	S	182	Metagreywacke, phyllite, limestone
Paddus 1	653	Low	775	N	176	Feldspathic metasandstone, meta-arkose
Paddus 2	653	Low	705	N	194	Feldspathic metasandstone, meta-arkose
Katterjåkk	1,155	High	550	NW	184	Granite
Vassijaure	1,155	High	570	N	171	Quartzite, metagreywacke
Pålnoviken 1	1,090	High	750	E	191	Metagreywacke, phyllite, limestone
Pålnoviken 2	811	High	660	S	171	Feldspathic metasandstone, meta-arkose

[a] Annual mean (1961–1991), gridded data Swedish Meteorological and Hydrological Institute 4 × 4 km pixels.

[b] Swedish Geological Survey.

[c] Point intercept measurement from July 2014 (see Table S2 for dominant species).

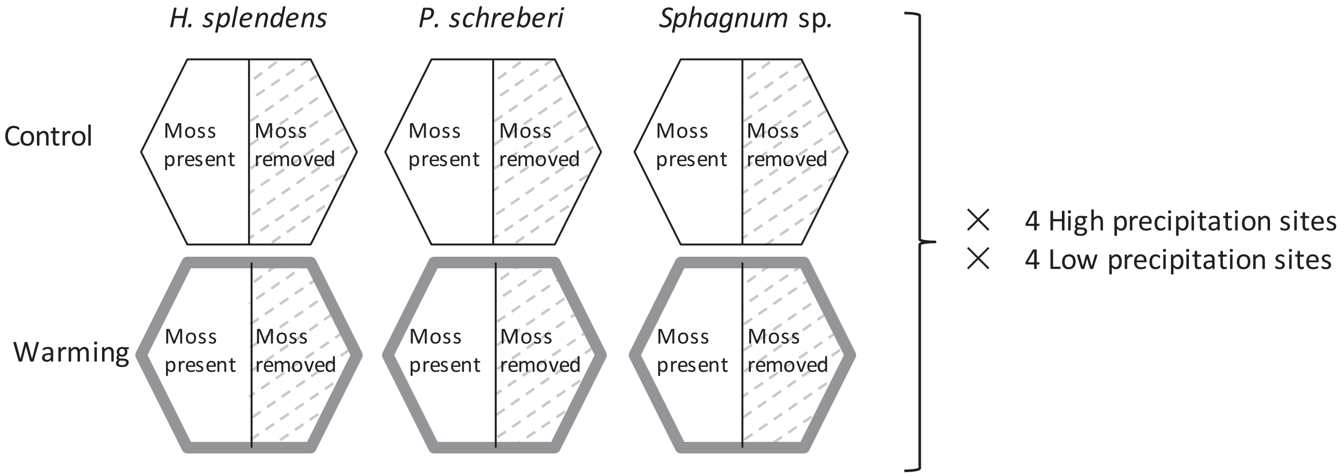


FIGURE 1 Experimental outline. Plots dominated by either one of *Hylocomium splendens*, *Pleurozium schreberi* and *Sphagnum* spp. were established in four low- and four high-precipitation sites. Plots were either left as control plots or subjected to warming with the use of open-top chambers. Mosses were removed in one half (randomly assigned, not visualized) of every plot

each moss species) of hexagonal plots (diameter 165 cm × 180 cm; 2.35 m^2 surface area per plot) in June 2011. The ground surface of each plot pair was fully covered by bryophytes and dominated (>90% cover) by one of the three moss species. For each pair of hexagonal plots, one randomly selected plot was passively warmed during the growing season with an OTC. Furthermore, we divided each hexagonal plot into two subplots along the north-south middle-line and removed all living moss material in one randomly selected subplot, while leaving the moss cover in the other subplot intact. This resulted in a total of 96 subplots that served as the experimental units, which collectively represented full-factorial combinations of the four treatments (precipitation, warming, moss species, moss removal).

Open-top chambers have been used widely throughout the arctic and subarctic region to assess climate-warming effects on plant and soil ecosystems at local spatial scales (Elmendorf et al., 2012). We placed OTCs on the plots each summer from 2011 to 2014 (inclusive) as soon as the sites were accessible after snow melt in mid-late June and left them in place until after birch leaf fall but before the first autumn storms in late September. We used transparent Perspex ITEX-type OTCs of the same size as the plots (diameter: 165 cm × 180 cm, height 47 cm; 0.95 m^2 exposed area in the centre; MacroLife; Arla Plast). To verify the warming effect of OTCs, air temperature was measured at 5 cm above the moss surface in the middle of the subplots with mosses present (see Section 2.3). OTCs increased average daily mean air temperature over the period from 29 June to 11 August 2012 by 0.8°C, relative to control plots ($p < .001$; Table S1).

As moss species are likely to differ in their environmental preferences, the moss removal treatment was included to separate effects of moss habitat from the effects of the living moss tissue itself. From the removal plots, we removed as much of the living moss biomass as possible by hand in spring 2011, while minimizing disturbance to vascular plants in the plots, as per De Long et al. (2016) and Wardle and Zackrisson (2005). Mosses were removed to the depth where their shoots begin to disintegrate, leaving a 100% organic soil behind with no moss parts left to start vegetative regeneration. The dry weight of removed moss per plot was 1,144 ± 227 g, 834 ± 247 g, 1,042 ± 147 g/m^2 (mean ± *SE*) for *Hylocomium*, *Pleurozium* and *Sphagnum*, respectively and did not differ between species or precipitation site. In both subplots, we left vascular plant vegetation intact (for dominating plant species and total vascular plant cover at the sites, see Table 1; Table S2). Regrowth of mosses was removed every subsequent spring. Removing of moss caused limited disturbance to vascular plants, as they have no roots. We observed no mortality or visual changes in the cover of the resident plants.

2.2 | Seedling transplantation and harvest

In Fennoscandia, both *B. pubescens* and *P. sylvestris* are treeline-forming species, although *B. pubescens* is the species that forms most treelines (Kullman, 2016). In the Abisko region, *B. pubescens* ssp. *tortuosa* forms the treeline, with presence of *P. sylvestris* below. For *B. pubescens* ssp. *tortuosa* (hereafter shortened to *B. pubescens*), we used seeds that we harvested from birch trees at the Abisko treeline the previous autumn. For *P. sylvestris* we used commercial seeds of a northern Swedish (68°00′) provenance (Svenska Skogsplantor AB).

We germinated and pregrew seedlings of *B. pubescens* and *P. sylvestris* in sand in plastic boxes in a greenhouse for 14 and 2 weeks prior to transplantation respectively. The evening before transplantation, we gently washed all seedlings free of sand and kept them between moist tissues at 5°C overnight. At the time of transplantation, *B. pubescens* had grown several leaves and a viable root system, whereas *P. sylvestris* seedlings had only developed their first cotyledons and a limited root system (tap root with beginning lateral roots). *B. pubescens* seedlings were grown to a larger size prior to transplantation because they are less robust than are *P. sylvestris* seedlings. To account for within-species variation in size at transplantation, we divided seedlings of *B. pubescens* into two size classes (visually) and distributed all seedlings within each size class randomly across subplots (large, 3–8 cm and 139–164 mg; small, 1–3 cm and 27–42 mg dry weight biomass). *P. sylvestris* seedlings varied very little in size (2–3 cm and 5–6 mg dry weight biomass) and were therefore not divided into size classes before random allocation to subplots. We transplanted five seedlings of *B. pubescens* and 24 seedlings of *P. sylvestris* into each subplot between 24 June and 10 July 2012, that is, 1 year after the treatments were implemented. Fewer *B. pubescens* seedlings were planted due to lower germination of seeds than intended. Seedlings were planted in groups of two or three for *B. pubescens* and 12 for *P. sylvestris* (Ø = 15 cm). No seedlings were planted within the 30 cm wide outer edge of each hexagonal plot or within 10 cm of the border between the two subplots. In subplots where mosses were present, we planted seedlings in the moss layer at a depth where seeds would likely have landed and germinated naturally, as in Lett et al. (2017).

We assessed seedling performance in each subplot by measuring seedling survival twice per growing season (early July and late August 2012, late June and mid-August 2013 and early July and early August 2014). As such, seedlings were considered alive if they had any green, non-wilted leaves. Missing seedlings were considered dead. Final survival, biomass and foliar N concentration were measured at the peak of the growing season in their third growing season (30 July–5 August 2014). To estimate survival, we counted the number of live seedlings present. For biomass and foliar N estimates, we harvested the above- and below-ground parts of the largest living seedling of each species in each subplot. Due to high mortality in some of the treatments, it was not possible to harvest seedlings for all 96 subplots. After returning to the laboratory, we rinsed seedlings in water, divided them into roots, stems and leaves (all green biomass, including green part of stem for *P. sylvestris*) and dried them at 70°C until constant weight to determine dry weight. Seedling growth was calculated on a whole-plant basis by subtracting the mean initial total seedling dry weight biomass for the same species and size group from the final total seedling biomass. We analysed ground leaves of the seedlings for N concentration using a EuroVector CN analyser coupled to an Isoprime Isotope Ratio Mass Spectrometer.

2.3 | Abiotic conditions

Soil and air temperature and soil moisture (volumetric water content) were measured and logged hourly throughout the period OTCs were in place in 2012, using 5TM soil moisture and temperature sensors and ECT air temperature sensors attached to EM50 data loggers (Decagon Devices Inc.), and TinyTag Talk2 dataloggers (Gemini Data Loggers Ltd.). Air temperature was measured at 5 cm above the moss surface in the middle of all moss-present subplots only. Soil temperature and moisture were measured in the seedling rooting zone, that is, at 5 cm below the moss or soil surface, in all subplots. For each plot, we calculated average daily minimum, mean and maximum soil temperature and average and daily means for air temperature and soil moisture data. These average values were calculated separately for each of the two subseasons of the OTC treatment period (early season: 29 June–11 August; late season: 12 August–24 September 2012), because the effects of OTCs on temperatures are higher in early summer when incoming solar radiation is higher (Bokhorst et al., 2013).

We measured NH_4^+ availability with nutrient resin capsules (PST1 capsule; Unibest), which we installed in early October 2013 at the approximate depth of the seedling roots (i.e. 5 cm below the moss or soil surface) in all subplots, as well as at 5 cm below the moss–soil interface in the moss-present subplots so that they were positioned in the same soil layer as those placed in the moss removal subplots. We installed two resin capsules at each depth in each plot. Nutrient resin capsules were harvested after 1 year, at the end of September 2014. This period was chosen due to the relatively low nutrient turnover and availability found in these ecosystems (Sundqvist et al., 2011). After collection, we extracted all capsules separately three times for 1 hr each time in 10 ml 1 M KCl (total of 30 ml; Gundale, From, Bach, & Nordin, 2014), and extracts were analysed for NH_4^+-N (FIAstar 5000 flow injection analyser, FOSS, Tecator; Höganäs).

2.4 | Data analysis

To analyse seedling survival over the course of the three growing seasons, we used mixed effects Cox proportional-hazards survival analysis, fitted with maximum likelihood, using the 'coxme' package in R (Therneau, 2018). A cox mixed-effects model evaluates the risk of mortality at a given time based on the survival at the same time. Time is thus implicit to the response variable and not included as a predictor in the analysis. Seedlings that had died since last counting event were considered to have died halfway between the two counting events. Survival of the two tree species was analysed separately, and the full models included 'warming', 'precipitation', 'moss removal' and 'moss species' as fixed effects and 'plot' nested in 'site' as random effect to take the nested design into account. For *B. pubescens*, where fewer seedlings were planted than for *P. sylvestris* and mortality was high, the model failed to converge when all interactions of the model were included and the four-way interaction (warming × precipitation × moss removal × moss species) was therefore excluded from the model.

To analyse seedling growth and leaf N concentration at harvest, we used linear mixed effects models (LMMs)—R package *nlme* (Pinheiro, Bates, DebRoy, Sarkar, & The R Development Core Team, 2018) with 'plot' nested within 'site' as random effect. Due to a high number of missing values in the feather moss-present subplots (i.e. no surviving seedlings available to determine growth or leaf N concentration), main effects and interactions for 'moss species', 'warming' and 'precipitation' could only be tested for the moss-removal subplots. Similarly, to test for the effect of 'moss removal' and its interaction with 'warming' and 'precipitation', we performed additional analyses for *Sphagnum* only, as this species, unlike the two feather mosses, had enough seedlings to be fully replicated for both the moss-present and moss-removal subplots. To analyse soil temperature and moisture, we used LMMs, with 'warming', 'precipitation', 'moss removal' and 'moss species' as fixed effects, and 'plot' nested in 'site' as random effect to take the nested design into account. We analysed air temperature with LMMs, with 'warming', 'precipitation' and 'moss species' as fixed effects, and 'site' as random effect. Resin-sorbed NH_4^+-N was analysed with LMMs with 'warming', 'precipitation', 'position in plot' and 'moss species' as fixed effects and 'plot' nested in 'site' as random effect. For all LMMs, we checked data for homoscedasticity and normality. To meet the assumptions for parametric testing, biomass data were square root transformed and early season soil moisture data were log transformed. We performed all data analyses and statistics in R version 3.6.3 (R Core Team, 2020).

3 | RESULTS

3.1 | Seedling survival

Higher precipitation increased *P. sylvestris* survival by almost 30% after three growing seasons in *Sphagnum* plots but not in either of the feather mosses (precipitation × moss species interaction, Table 2; Figure 2b; Figure S2). For *B. pubescens*, higher precipitation increased survival when mosses were removed and decreased survival when they were present (moss removal × precipitation interaction Table 2; Figure 2a), by 12% and 11% after three growing seasons respectively.

Warming did not affect survival of *P. sylvestris* in the presence or absence of mosses or any of the treatment combinations. For *B. pubescens*, the effect of warming depended on moss species and presence (warming × moss removal × moss species interaction; Table 2). As such, warming decreased survival of *B. pubescens* when *Hylocomium* was removed but this effect was reversed when *Hylocomium* was present (Figure 2a), by a decrease of 20% and an increase of 70% after three growing seasons respectively. Warming had no effect on *B. pubescens* survival in the presence of *Pleurozium* and *Sphagnum*, but where these mosses had been removed, warming increased survival in *Pleurozium* plots (Figure 2a), by 40% after three growing seasons.

Both *P. sylvestris* and *B. pubescens* survival was lower when mosses were present than when mosses had been removed and seedlings survived generally best in *Sphagnum* plots (moss removal and moss species main effects, Table 2). Furthermore, for both seedling species, removal of moss increased survival of seedlings growing in *Hylocomium* and *Pleurozium* by eightfold, whereas removal of *Sphagnum* had minor or no effects on survival (moss removal × moss species interaction; Table 2; Figure 2).

TABLE 2 Results from cox mixed effects models for *Pinus sylvestris* and *Betula pubescens* seedling survival for 2012–2014. The model for *B. pubescens* did not include the four-way interaction because too few seedlings survived in some treatment combinations

		B. pubescens		***P. sylvestris***	
Treatment	***df***	χ^2	***p***	χ^2	***p***
Warming (W)	1	0.0	.89	0.1	.71
Precipitation (P)	1	0.1	.73	0.1	.77
Moss removal (R)	1	67.7	**<.001**	667.9	**<.001**
Moss species (Moss)	2	96.8	**<.001**	16.5	**<.001**
W × P	1	0.3	.56	0.0	.98
W × R	1	0.1	.74	0.6	.44
W × Moss	2	1.2	.55	0.4	.83
P × R	1	5.9	**.015**	3.8	.051
P × Moss	2	1.5	.48	14.3	**<.001**
R × Moss	2	12.3	**.002**	35.4	**<.001**
W × P × R	1	0.1	.82	0.4	.54
W × P × Moss	2	0.7	.69	1.1	.59
W × R × Moss	2	10.9	**.004**	0.2	.93
P × R × Moss	2	4.6	.098	1.2	.56
W × P × R × Moss	2	—	—	1.5	.47

Note: Significant *p*-values ($p < .05$) in bold.

3.2 | Seedling growth and leaf nitrogen

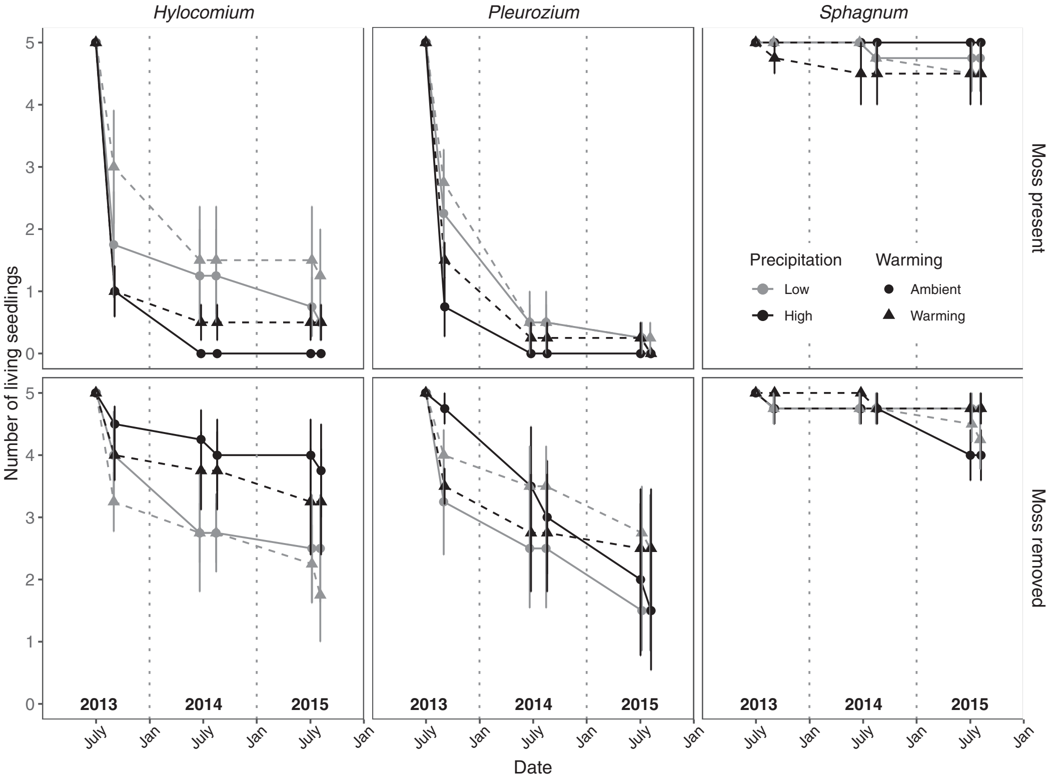
Warming and precipitation did not affect *P. sylvestris* growth in the *Sphagnum* plots, which were the plots that had sufficient seedling survival to allow analysis of how climate treatments were affected by moss presence (Table 3). Here removal of *Sphagnum* promoted the warming response of *B. pubescens* compared to such cases when mosses were present (moss removal × warming interaction; Table 3; Figure 3a). Apart from that, there were no statistically significant differences among treatments on *B. pubescens* seedling growth. Warming decreased leaf N in *P. sylvestris* seedlings, while none of the treatments affected *B. pubescens* leaf N (Figure 3c,d).

Moss removal subplots of the three species also had sufficient seedling survival to allow statistical comparisons (Figure 2; Figure S3; Table S3). Here the substrate of the three moss species and climate treatments had no effects on seedling biomass. *P. sylvestris* leaf N was increased in feather moss compared to *Sphagnum* plots, particularly in low precipitation sites (Figure S3; Table S3).

3.3 | Abiotic soil conditions

The warming treatment increased mean soil temperature (5 cm below the moss or soil surface) in the early season (29 June–11 August 2012) by 0.6°C (Table 4; Figure 4a). There was no effect of precipitation on soil temperature, and no statistically significant interactions ($p < .05$) among factors. Moss presence increased mean soil temperature by 0.9°C on average, and soil of *Sphagnum* plots

(a) *Betula pubescens*



(b) *Pinus sylvestris*

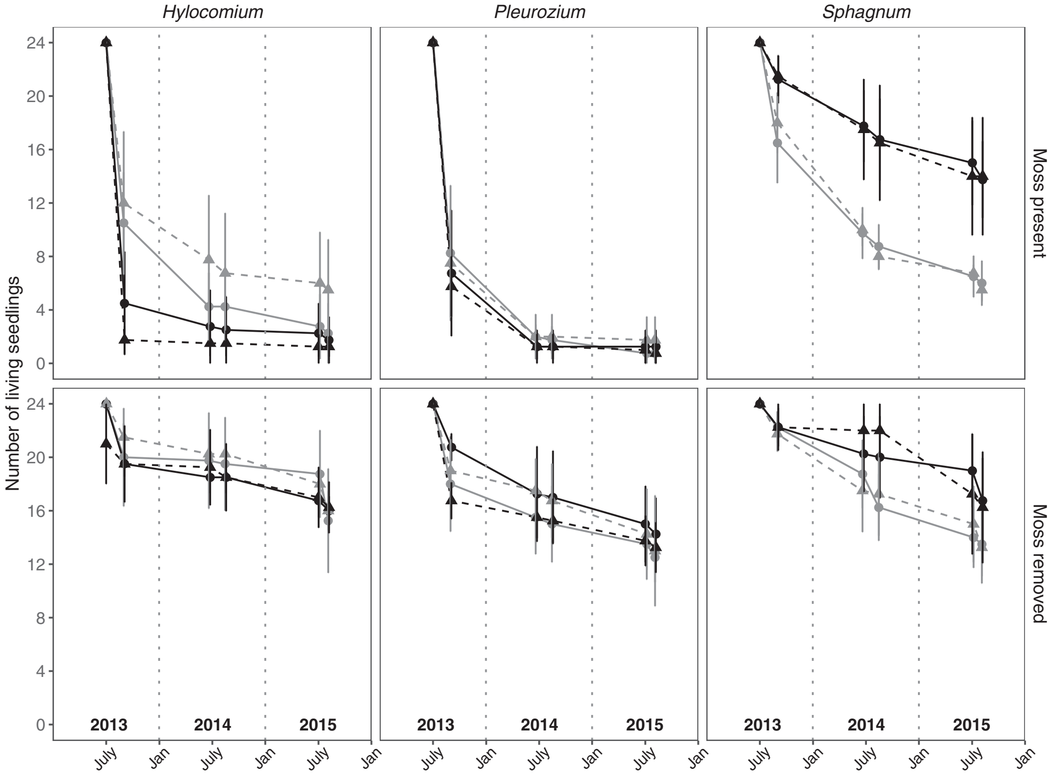


FIGURE 2 Mean survival (±*SE*, *n* = 4) from 2012 to 2014 of *Betula pubescens* (a, five planted seedlings) and *Pinus sylvestris* (b, 24 planted seedlings) at the subarctic alpine treeline in subplots with one of each of three moss species present or removed, subjected to summer warming (triangle, dashed line) or ambient conditions (circle, solid line) and at naturally high (black) or low (grey) precipitation sites. Survival was measured twice a year after planting in June 2013 (early July and late August 2013, late July and mid-August 2014, early July and early August 2015) and seedlings were harvested in the beginning of August 2015. See Table 2 for statistics

TABLE 3 Results from linear mixed effects models for seedling growth (biomass) and leaf N concentration of *Betula pubescens* and *Pinus sylvestris*. Analyses only includes *Sphagnum* plots, because too few seedlings survived in the *Hylocomium* and *Pleurozium* moss-present subplots to enable full model analyses

		B. pubescens				***P. sylvestris***			
		Biomass		**Leaf N**		**Biomass**		**Leaf N**	
Treatment	***df***	χ^2	*p*	χ^2	*p*	χ^2	*p*	χ^2	*p*
Warming (W)	1	2.7	.10	0.2	.66	0.5	.47	5.7	**.02**
Precipitation (P)	1	0.5	.46	1.5	.22	2.8	.09	0.3	.58
Sphagnum removal (R)	1	3.3	.07	0.3	.60	0.1	.73	0.4	.51
W × P	1	1.1	.29	1.0	.33	1.5	.21	0.1	.71
W × R	1	4.7	**.03**	0.1	.74	0.3	.59	0.2	.69
P × R	1	0	.89	2.3	.13	0.7	.42	3.2	.07
W × P × R	1	0.2	.63	0.5	.49	0.0	.96	1.1	.29

Note: Significant *p*-values ($p < .05$) in bold. Biomass data were square-root transformed.

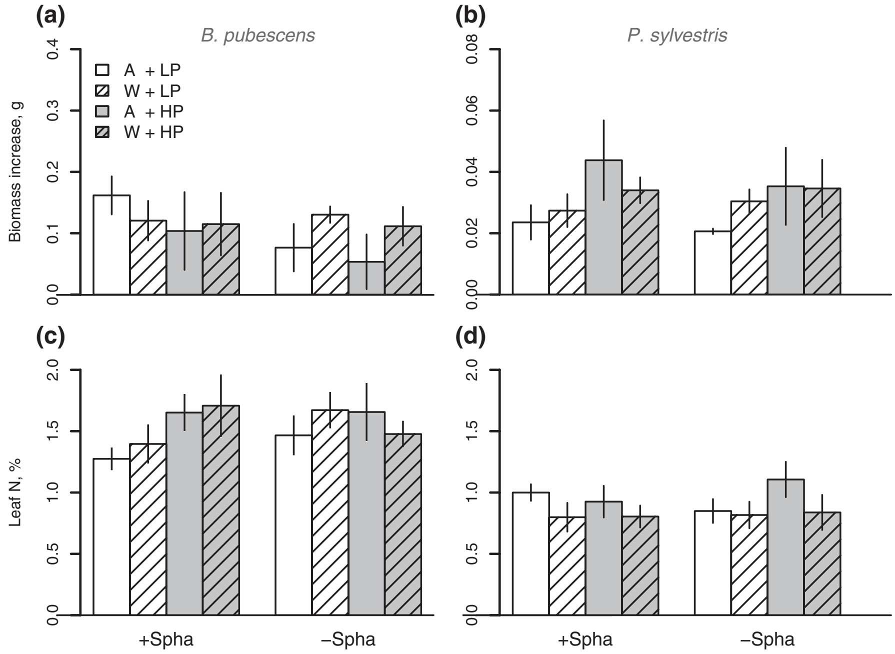


FIGURE 3 Growth (total biomass increase; a, b) and leaf nitrogen (N; c, d) concentration of *Betula pubescens* (a, c) and *Pinus sylvestris* (b, d) seedlings after three growing seasons at the subarctic alpine treeline in subplots with Spha, *Sphagnum* spp.) present (+) or removed (−), under experimentally warmed (W, hatched bars) or ambient (A, open bars) conditions, and at naturally low precipitation (LP, white bars) or high precipitation (HP, grey bars). Bars are means ± *SE* ($n = 4$). Data for *Hylocomium* and *Pleurozium* were not complete due to low seedling survival and therefore were not included in the analysis but found in Figure S3. Note differences in scale between tree species for biomass. See Table 3 for statistics

were 0.5°C warmer than that of the feather moss species (Table 4; Figure 4a). Warming increased average daily maximum temperature and this was most pronounced in moss present plots. Moss presence generally increased maximum temperature, and this was most pronounced at high precipitation sites (Figure S4). Average daily minimum temperature was lower in feather moss than *Sphagnum* plots, and minimum temperature was lower at high precipitation sites in *Hylocomium* plots (Figure S4).

Soil moisture at 5 cm below the moss or soil surface in the early season was generally lowest at the high precipitation sites and presence of moss increased this difference (precipitation × moss removal; Table 4; Figure 4b). Soil moisture was lower in moss than in soil where mosses had been removed. Furthermore, *Sphagnum* plots overall had higher soil moisture than did *Hylocomium* and *Pleurozium* plots (Table 4; Figure 4). For both soil temperature and moisture, the patterns in the second half of the warming period (12 August–24 September 2012) were similar to those for the early season (Table 4; Figures S4 and S5).

Resin-sorbed NH_4^+ was higher in *Hylocomium* and *Pleurozium* than *Sphagnum* plots, and this difference tended to be more pronounced in the moss removal subplots. There were no other effects of any other factor or combination of factors on resin-sorbed NH_4^+ (Table S4; Figure S6).

4 | DISCUSSION

Climate change-driven treeline shifts are effectuated through seedling establishment above the current treeline where mosses cover up to 100% of the ground. Our findings showed that positive effects of warming and precipitation on *B. pubescens* establishment (survival and growth) were always weaker or even reversed in the presence of mosses and that the strength of these moss-mediated effects can differ between moss species. *P. sylvestris* was in some cases promoted by higher precipitation and was not very responsive to warming, and the responses to precipitation were modified

TABLE 4 Results of linear mixed effects models for soil temperature (T) and moisture measured at 5 cm depth below the surface of each of three moss species (*Hylocomium splendens*, *Pleurozium schreberi* and *Sphagnum* sp.) when present or removed, under experimentally warmed or ambient conditions, and at naturally low or high precipitation sites through 29 June–11 August (early season) and 12 August–24 September (late season) 2012

		Early season				Late season			
		Soil T		Soil moisture		Soil T		Soil moisture	
	df	χ^2	*p*	χ^2	*p*	χ^2	*p*	χ^2	*p*
Warming (W)	1	12.9	**<.001**	0.8	.36	4.5	**.035**	0.0	.92
Precipitation (P)	1	0.6	.44	6.4	**.012**	0.3	.58	4.6	**.03**
Moss removal (R)	1	24.2	**<.001**	74.4	**<.001**	6.1	**.014**	53.6	**<.001**
Moss species (Moss)	2	6.9	**.032**	84.4	**<.001**	7.4	**.025**	46.1	**<.001**
W × P	1	0.8	.36	0.0	.84	1.9	.16	0.0	.93
W × R	1	2.8	.093	1.2	.27	2.4	.12	0.4	.51
W × Moss	2	0.6	.75	3.8	.15	0.6	.74	1.9	.39
P × R	1	3.8	.051	6.6	**.010**	0.3	.59	4.7	**.030**
P × Moss	2	3.2	.20	3.4	.18	4.5	.10	0.6	.74
R × Moss	2	1.5	.47	1.5	.47	1.5	.47	1.6	.44
W × P × R	1	0.2	.65	1.6	.20	0.0	.95	2.0	.16
W × P × Moss	2	1.0	.62	0.6	.75	0.4	.82	0.4	.83
W × R × Moss	2	1.6	.44	0.1	.96	0.8	.66	0.0	.98
P × R × Moss	2	1.4	.50	0.0	.98	0.2	.90	0.3	.87
W × P × R × Moss	2	1.0	.62	0.7	.72	0.1	.97	0.7	.69

Note: Significant *p*-values ($p < .05$) in bold and trends ($p < .1$) in italics, $n = 4$. Early season soil moisture data were log transformed prior to analysis.

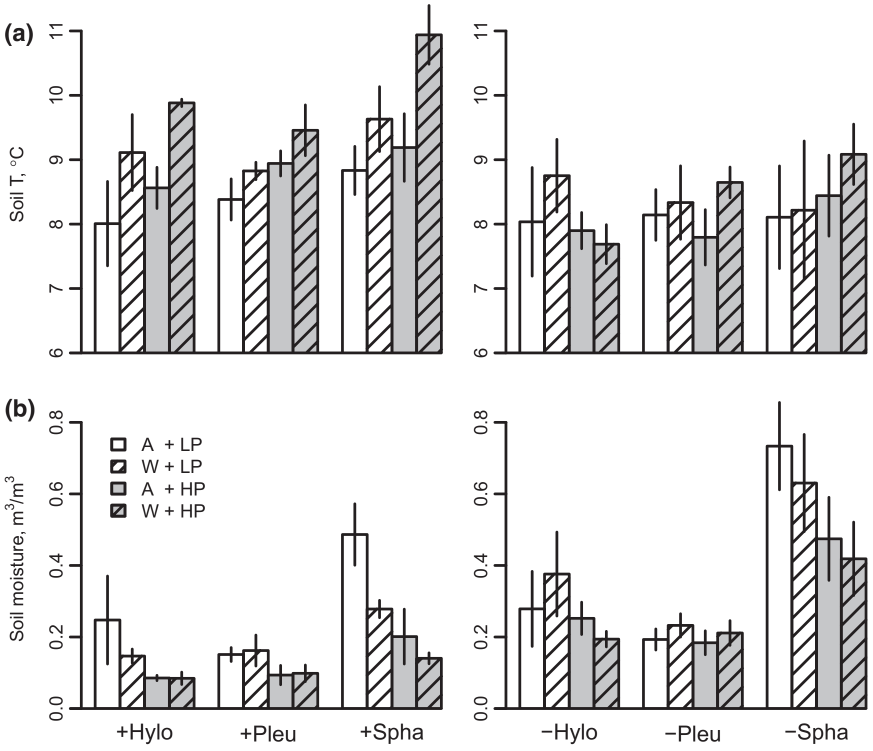


FIGURE 4 Average daily mean soil temperature (T; a) and volumetric soil moisture content (b) associated with each of three moss species (Hylo, *Hylocomium splendens*; Pleu, *Pleurozium schreberi*; Spha, *Sphagnum* spp.) when present (+) or removed (−), under experimentally warmed (W, hatched bars) or ambient conditions (A, open bars), and at naturally low precipitation (LP, white bars) or high precipitation (HP, grey bars) sites. Sensors were placed at 5 cm below the moss or soil surface and logged hourly through 29 June–11 august 2012. Bars are means ± *SE* ($n = 4$). See Table 4 for statistics

by species identity. The strong dominance of mosses in tundra can thus have hitherto unrecognized consequences for treeline responses to climate change. Below, we discuss these findings to provide insights about how mosses modify climate-change effects on tree seedling establishment and, potentially, treeline expansion.

4.1 | Interactive effects of warming and moisture

There were surprisingly few effects of warming on seedling establishment and consequently we did not find support for our first hypothesis that positive effects of warming would be more pronounced at high precipitation sites. Limitation of moisture leading to stagnant or negative responses in seedlings has previously been observed as a consequence of warming (Lazarus et al., 2018). This could suggest that warming by 0.8°C as was imposed in our experiment did not increase water stress in seedlings. This is further supported by the fact that soil moisture was also not affected by the presence of OTCs. Another interesting finding was that soil moisture was higher at low precipitation sites, which could reflect that mosses in low precipitation areas grow in locally wetter places to stay within their environmental niche. However, it was in particular areas where mosses were present that soil moisture was found to be higher at low precipitation sites. It is possible that moss morphology under different growth conditions caused a more compact moss carpet in the layer of moss under low precipitation, which would increase soil moisture (Bergamini & Peintinger, 2002).

4.2 | Moss presence moderates seedling response to climate

For *B. pubescens*, we found some support for our second hypothesis that presence of mosses would decrease positive responses to climate treatments. As such, warming increased *B. pubescens* growth only when *Sphagnum* was removed, not when *Sphagnum* was present (note that this effect could not be tested for the feather mosses). It was not clear whether this increased growth was a direct consequence of the effect of *Sphagnum* moss on temperature. Temperatures at 5 cm depth were increased by the OTCs but the temperature increase was larger when *Sphagnum* was present, not when removed as we had expected. This means that the greater growth response of *B. pubescens* seedlings to warming when mosses were absent, occurred despite the warming effect of the OTCs being less pronounced. Although tundra mosses are generally considered to respond negatively to warming (Elmendorf et al., 2012), the growth of *Sphagnum* and some feather mosses have shown strong positive responses to warming, which in some cases may supress and even cause smothering of small-statured vascular plants (Dorrepaal, Aerts, Cornelissen, Van Logtestijn, & Callaghan, 2006; Keuper et al., 2011; Lang et al., 2012). It is therefore likely that *B. pubescens* seedlings benefitted more from warming in the absence of *Sphagnum* because of these mosses being more competitive against seedlings at higher temperatures.

We found that higher precipitation increased survival of *B. pubescens* only when moss cover was removed. This was likely not due to more favourable soil moisture conditions, as soil moisture availability was already higher in the moss removal plots due to the more compact substrate. Rather, removing mosses could have alleviated competition from mosses growing better at higher precipitation (Busby, Bliss, & Hamilton, 1978; Stuiver et al., 2014; Zackrisson, Dahlberg, Norberg, Nilsson, & Jäderlund, 1998). Although moss competition seems to pose a stronger control than soil moisture on seedling survival, soil moisture is crucial for seedling establishment (Gill, Campbell, & Karlinsey, 2015; Tingstad, Olsen, Klanderud, Vandvik, & Ohlson, 2015). This was seen in our experiment by the large difference in survival between the moist *Sphagnum* plots and the dry feather moss plots and between feather moss plots with and without mosses, particularly for *B. pubescens*. *B. pubescens* has a higher optimum for soil moisture than does *P. sylvestris* (Sutinen, Teirilä, Pänttäjä, & Sutinen, 2002). In accordance, we did not find such modifications of moss presence on climate treatments on *P. sylvestris*. Our results show that presence of mosses not only has large (and mostly negative) effects on tree seedling establishment by providing a poorer quality substrate for early seedling establishment relative to the underlying soil, but also that mosses can alter *B. pubescens* seedling responses to climate through a combination of competition and effects on the abiotic environment.

4.3 | Moss species differ in their climate moderating effects

In accordance with our third hypothesis, moss species differed in how they modified climate responses of seedlings. Presence of *Pleurozium* and *Hylocomium* shifted the warming response of *B. pubescens* survival from positive to neutral and from negative to positive respectively. In agreement with our expectation, survival responses to warming thus changed in the presence of the two feather moss species, while this was not the case for *Sphagnum*. However, rather than enhancing experimental soil warming, removal of mosses had no effect on the warming intensity. On the one hand, the positive change in warming response of the seedlings with removal of *Pleurozium*, as expected, could instead be due to alleviation of competition when these mosses were absent rather than a direct temperature response. On the other hand, the change to a positive warming response in *B. pubescens* survival in the presence of *Hylocomium*, could be a direct warming response. *B. pubescens* seedlings have previously been shown in a climate chamber experiment to respond more positively to warming when growing in *H. splendens* (Lett et al., 2017). In that study, N availability was higher in *H. splendens* compared to other tundra moss species, including the ones in this study. Similarly, seedlings in boreal forest grew better in feather mosses than in *Sphagnum* unless nitrogen was added, suggesting that nutrient availability plays an important role for seedlings growing in these mosses (Pacé, Fenton, Paré, & Bergeron, 2018). Nitrogen availability in our field study was also higher in *Hylocomium* and *Pleurozium* plots than in *Sphagnum* plots, and partly explains the species differences that we found. Importantly, the presence of living mosses led to opposite warming effects than the underlying soil of the same mosses, although the warming effects on soil temperatures and nutrients were the same with and without mosses present. This denotes that mosses affect seedlings directly through their presence and not only indirectly through their effects on soil properties (Gornall, Woodin, Jónsdóttir, & van der Wal, 2011).

We found further support for our third hypothesis where moss species identity affected the extent to which *P. sylvestris* survival was enhanced by higher precipitation. Precipitation promoted

P. sylvestris survival the most when growing in *Sphagnum*, which has by far the highest moisture holding capacity of the three mosses (Elumeeva et al., 2011) and also the highest moisture content in our experiment. This was surprising as *P. sylvestris* at alpine treelines are more dominant at drier continental sites (Houston Durrant & Caudullo, 2017). This suggests that different life stages have different environmental filters and highlights that *P. sylvestris* at the early seedling stage is sensitive to low soil moisture.

4.4 | The role of mosses for seedling establishment at the treeline in a changing climate

Absence of mosses benefitted seedling survival more than either the experimental increase in temperature of approx. 1°C or the variation in precipitation between sites, and presence of mosses sometimes weakened some effects of the climate. These climate-modifying effects of the moss layer were both abiotic (through impacting nutrient conditions) and biotic (through increased competition). Previously it has been shown that soil properties (Ford & HilleRisLambers, 2020) and vascular plants such as shrubs (Grau et al., 2012; Milbau, Shevtsova, Osler, Mooshammer, & Graae, 2013; Tingstad et al., 2015) can mitigate climate-change impacts on seedling performance. Furthermore, competitive effects of vascular treeline vegetation (Bansal, Reinhardt, & Germino, 2011) can be more severe for tree seedlings than the direct effect of temperature or precipitation (Tingstad et al., 2015). Here we demonstrate that even small plants, such as mosses, that dwell at the bottom of the tundra vegetation, can have strong impacts on tree seedling survival and growth, or their responses to climate. As almost half of global treelines show no responses to climate warming (Harsch et al., 2009), the limited response of the seedlings to our climate treatments may provide a possible reason for this unresponsiveness.

The moss species included in this study are very common boreal and tundra species, and we therefore suggest that the effects on tree seedlings that we found can likely be translated to treelines more generally. Importantly, the abundance and species composition of mosses themselves at the treeline are highly responsive to environmental changes. Moss responses are still understudied in comparison to those of vascular plants (Elmendorf et al., 2012). Factors such as climate warming and herbivory from rodents and reindeer show large, often negative, effects on the abundance and species composition of mosses throughout the tundra biome (Elmendorf et al., 2012; Johnson et al., 2011; Olofsson et al., 2014; Yu, Epstein, Engstrom, & Walker, 2017) and thereby likely favour (Nystuen, Evju, Rusch, Graae, & Eide, 2014) or alter seedling establishment. Our study shows that these environmental effects on moss communities can potentially have cascading effects on the alpine treeline, both through the direct effects of mosses on seedling establishment and via the ability to modify seedling responses to climate. Improved understanding of moss responses to climate and environmental change is therefore needed in order to more fully predict their impact on tree seedling establishment and to guide management of for example, reindeer husbandry.

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AUTHOR CONTRIBUTION

E.D., D.A.W. and M.-C.N. designed and established the field experiment. S.L., E.D., D.A.W. and M.-C.N. designed the study. S.L., L.M.T., E.J.K. and E.D. performed fieldwork. S.L., L.M.T. and A.M. carried out laboratory work. S.L., L.M.T. and J.O. analysed the data. S.L. wrote the manuscript with contributions from all authors.

DATA AVAILABILITY STATEMENT

The data used in this article are available on figshare: https://doi.org/10.6084/m9.figshare.12527984.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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