Bryophyte community responses to long-term warming manipulations vary greatly between contrasting tundra habitats

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Abstract

Bryophytes are a diverse group of plants, both taxonomically and functionally. Although they are a major vegetation component in many tundra habitats and affect ecosystem function in various ways, they have not received full attention in studies on responses of tundra plant communities to climate warming.

Here we compared bryophyte community structure, taxonomic composition, diversity and bryophyte functional group (BFG) composition among five contrasting tundra habitats across Arctic bioclimatic sub-zones and how those communities responded to long-term (decadal) experimental warming. We further explored how selected functional traits of the dominating bryophyte species responded to warming.

Bryophyte cover and layer depth declined in response warming in only one of the habitats, the oro-Arctic *Betula nana* heath (BH) in Iceland, while increasing or unaffected in the other four habitats that all lacked erect-growing and warming-responsive deciduous shrubs. Warming also affected both taxonomic and BFG composition in BH and increased bryophyte diversity, while communities in the other habitats were not affected except in a high-Arctic moist snowbed in Svalbard. Shoot annual growth increased in the warmed plots in BH and tended to increase in the high-Arctic *Cassiope* heath in Svalbard, apparently due to shoot

etiolation in response to increased shrub shading. Nitrogen fixation by bacteria associated with the most abundant bryophyte species was at lower rates in the warmed plots than in controls in all habitats and water holding capacity (only measured in the two Icelandic habitats) was not affected by warming despite reduced moss colony density.

We conclude that an extensive and deep bryophyte layer generally enhances tundra plant community resistance to warming in tundra habitats. However, in habitats with warming-responsive erect deciduous shrubs, warming intensifies bryophyte-shrub interactions causing a decline in bryophyte cover and layer depth, which may further accelerate community change with implications for the soil environment and ecosystem processes.

Key words: bryophyte community composition, bryophyte layer depth, bryophyte functional groups, bryophyte diversity, water holding capacity, nitrogen fixation, high Arctic, sub-Arctic, oro-Arctic, Iceland, Svalbard

Introduction

Bryophytes are a major vegetation component in many habitats, particularly in the Arctic tundra (Berner, 2024; Longton, 1984). They play a key role in nutrient and carbon cycling both directly and indirectly by shaping the soil environment, thus increasing ecosystem stability and resilience (e.g. Turetsky et al., 2012). Bryophytes are a diverse group of plants, both taxonomically and functionally and bryophyte community composition may therefore strongly affect overall tundra plant community dynamics and ecosystem processes as well as how they respond to environmental changes. However, because bryophytes have often been neglected in ecological studies, we have limited understanding of how bryophytes may impact plant community and ecosystem responses to climate warming in contrasting tundra habitats.

As all green plants, bryophytes sequester atmospheric carbon through photosynthesis but being mostly non-vascular and poikilohydric their tissue composition, physiology and nutrient acquisition differ widely from vascular plants (e.g. Turetsky, 2003) and those differences result in a relatively recalcitrant litter (Lang et al., 2009). Bryophytes also provide habitats for diverse microbes, protists, micro- and meso-invertebrates, the bryosphere, that may take part in nutrient and carbon cycling (Grau-Andrés et al., 2022; Klarenberg et al., 2021; Lindo & Gonzalez, 2010; Papinot Lecomte et al., 2026). A good example is nitrogen fixation by bryophyte-associated cyanobacteria (Rousk, 2022). In moss-rich ecosystems, where bryophytes form a continuous ground layer, they efficiently absorb precipitation and atmospheric wet deposited nutrient ions (Armitage et al., 2012; Jónsdóttir et al., 1995; Koranda et al., 2023) and provide an insulating layer that shapes the soil microclimate in various Arctic and alpine habitats with consequences for soil microbial activity and nutrient

cycling (Gornall et al., 2007; Jaroszynska et al., 2023; Koranda et al., 2023). The insulating capacity of the bryophyte layer depends on various bryophyte traits related to morphology and water retention as well as the layer depth (mat thickness) (Gornall et al., 2007; Schuuring et al., 2024; Soudzilovskaia et al., 2013). Bryophytes interact both directly and indirectly with vascular plants in tundra habitats where they either facilitate or negatively affect seedling establishment (Jónsdóttir, 1995; Klanderud & Totland, 2004; Soudzilovskaia et al., 2011) and plant growth (Gornall et al., 2011), largely depending on the moss layer depth. Similarly, vascular plants may either facilitate or negatively affect bryophytes in various ways depending on the functionality of the bryophyte and vascular plant species. For instance, shading by shrubs may favour certain bryophyte species due to more favourable moisture conditions in the understory, while negatively affecting others through light competition (Alatalo et al., 2020; Jägerbrand et al., 2012; Pajunen et al., 2011; van Wijk et al., 2004).

The bryophyte component of tundra plant communities may vary in diversity from being dominated by one or a few species to a high evenness and species richness of over ten species per square meter. However, when assessing plant community composition in general and in Arctic tundra in particular, bryophytes are frequently treated as only one or a few units due to difficulties in species identification in the field. This is unfortunate because bryophyte floras are relatively rich at northern latitudes (Geffert et al., 2013; Mateo et al., 2016) and bryophytes outnumber vascular plant species in many regions such as Iceland and Svalbard.

High species diversity usually also reflects functional variability, which is still an understudied, but fast-growing field of research among bryophytes (Coe et al., 2024;

Cornelissen et al., 2007). A few functional trait studies on bryophytes sampled from Arctic and alpine tundra reveal large differences between species in important bryophyte traits such as decomposition rates, nutrient contents (Lang et al., 2009; van Zuijlen, Klanderud, et al., 2022), association with nitrogen fixing bacteria (Rousk, 2022; Rzepczynska et al., 2022; Stuart et al., 2021), water holding capacity (WHC) (Elumeeva et al., 2011; Roos et al., 2019; van Zuijlen, Klanderud, et al., 2022; Volkova et al., 2023) and other traits related to thermal conductivity (Soudzilovskaia et al., 2013). Because of the important role that bryophytes play in ecosystem functioning, there is an urgency to better understand how both taxonomic and functional diversity is affected by climate change, particularly at northern latitudes where climate is warming almost four times faster than the global average (Rantanen et al., 2022). One way to encourage higher bryophyte resolution in plant community analyses is to apply bryophyte functional groups (BFGs) where species that share similar functional traits are grouped together. Assessment of BFG community composition may also be useful to provide first insights into the functional characteristics of the communities. Several classifications have been suggested and based on previous attempts Lett et al. (2022) recently identified twelve BFGs to be applied to tundra communities, a classification that is still under evaluation.

Experimental studies in the tundra have demonstrated a general decline in bryophyte cover in response to long-term climate warming across tundra sites (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012) and similar trends have been detected as a response to ambient warming (Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe, et al., 2012). However, bryophyte cover responses to experimental and ambient warming vary between sites and habitat types, which may reflect either the functional variability among dominating

bryophyte species or indirect responses through vascular plant interaction (Alatalo et al., 2020; Jónsdóttir et al., 2005; Lang et al., 2012; van Wijk et al., 2004; van Zuijlen, Asplund, et al., 2022). For instance, some tundra bryophytes decline in response to increased shading caused by warming induced increase in shrub canopy height and litter deposition (Alatalo et al. 2020). Cover is, however, only one (two dimensional) aspect of bryophyte abundance. To assess how warming affects the capacity of the bryophyte layer to absorb precipitation and atmospheric deposition, as well as its insulating capacity, we also need to know how the third dimension, the bryophyte layer depth (mat thickness), is affected by warming. So far, that is rarely assessed.

Climate change is generally assumed to affect bryophytes and vascular plants differently due to the differences in morphology and physiology. He et al., (2016) argued that bryophyte diversity would decline in response to warming climate primarily due to a relatively low temperature optima for photosynthesis in many species and a narrow temperature ranges for net photosynthetic gain, which would in turn alter ecosystem structure and function. Furthermore, a recent modelling study indicated a slow expansion of bryophyte distribution ranges despite high wind dispersal capacities, predicting that bryophytes in general might not be able to track fast climate changes (Zanatta et al., 2020). The model predicted that Arctic and alpine bryophyte species will experience the highest range loss. Due to the challenge of bryophyte species identification only a few site-specific studies on the effects of climate warming on plant community diversity are available where bryophytes are included (Alatalo et al., 2020; Jägerbrand et al., 2006; Jónsdóttir et al., 2005; Lang et al., 2012; van Zuijlen, Asplund, et al., 2022). Although warming responses vary between bryophyte taxonomic groups, those studies showed a general decline in bryophyte

cover and a decline or no change in species diversity. The mechanisms behind are poorly understood but one might be the indirect warming effect through bryophyte-shrub interactions as suggested by some of those papers. However, all those studies are either from low-Arctic, sub-Arctic or alpine sites leaving a knowledge gap for the high-Arctic. The mechanisms may also be through direct effects of warming resulting in loss of species with low temperature optima or through some other bryophyte functional traits.

Bryophyte trait responses to warming may vary considerable between species as was demonstrated in a laboratory study of species-specific trait responses to temperature gradients: *Sphagnum* species increased shoot growth in response to temperature, which was partly attributed to increasing nitrogen fixation rates by associated bacteria (Rzepczynska et al., 2022), while other species, including *Racomitrium* species, showed limited shoot growth responses to temperature increase. However, for poikilohydric organisms like bryophytes, moisture regimes may modulate certain intraspecific trait responses to experimental warming as for example nitrogen fixation by bryophyte associated bacteria, one of the most studied bryophyte traits (Rousk, 2022). Most bryophyte species, including bryophytes in tundra ecosystems, are associated with nitrogen fixing bacteria, mainly cyanobacteria, although to a highly variable degree (Rousk, 2022; Stuart et al., 2021), and it has been estimated that the nitrogen input associated with mosses in moss-rich Arctic tundra may match or exceed input through nitrogen deposition (Ramm et al., 2022). Although nitrogen fixation is generally positively related to temperature when moisture is constantly kept at high levels (Rzepczynska et al., 2022) moisture availability varies greatly in time and space in nature, which may affect how this trait responds to climate warming (Lett et al., 2024). Water holding capacity is another commonly studied

bryophyte trait and at a colony level it is usually positively related to colony density (Elumeeva et al., 2011; Volkova et al., 2023). The effects of climate on water holding capacity have mainly been evaluated at the community level (as community weighted means) where it increased along an elevation gradient in alpine tundra (Roos et al., 2019) and decreased in response to simulated warming within the same region (van Zuijlen, Klanderud, et al., 2022). In both studies community level trait variability was mainly explained by species turnover rather than intraspecific trait variability, indicating low bryophyte trait plasticity.

In this paper we compile data on bryophyte community structure, composition, diversity and function from long-term (decades) warming experiments in contrasting tundra habitats across Arctic bioclimatic sub-zones to explore whether the above general findings apply to those habitats, aiming at increasing our understanding of how climate warming affects tundra ecosystems. Specifically, we hypothesize that 1) both bryophyte cover and layer depth in Arctic tundra decreases in response to warming, particularly in habitats with substantial shrub abundance, 2) those structural responses are reflected by a shift in bryophyte community composition and diversity as well as 3) bryophyte functional group composition and diversity. Furthermore, we expect 4) experimental warming to affect functional traits of the dominating bryophyte species such that growth of individual shoots increases, while nitrogen fixation by associated bacteria, water holding capacity and colony density decrease. To test the hypotheses, we compared the effect of warming treatments in two habitats in Iceland, one within the sub-Arctic and another within sub-Arctic-alpine (oro-Arctic), and three habitats in high Arctic Svalbard.

Methods

Research sites and study design

Warming experiments were established in contrasting habitats at two sites in Iceland, Thingvellir in 1995 and Audkúluheidi in 1996, and a few years later, in 2002, in three different habitats in Endalen, Svalbard (Figure 1). Both regions have experience ambient warming; an average increase of 1°C per century in Iceland (Bjornsson et al., 2008) and 0.32 °C per decade in Svalbard (Nordli et al., 2020). We followed the protocols of the International Tundra Experient (ITEX) (Henry et al., 2022) and simulated climate warming by year-round application of transparent open top chambers (OTCs) (Hollister et al., 2023).

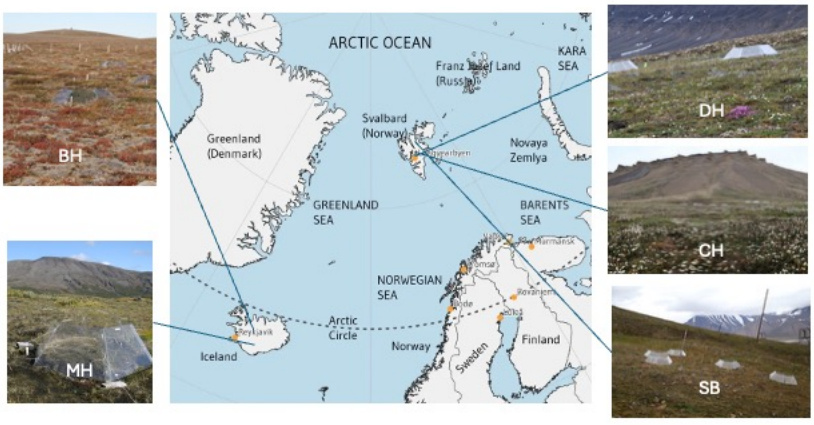

Figure 1. The geographical position of the five studied tundra habitats. BH = *Betula nana* heath in the Icelandic highlands (480 m above sea level) – oro-Arcitc; MH = *Racomitrium lanuginosum* moss heath in the Icelandic sub-Arctic (120 m above sea level); DH = *Dryas octopetal* heath in high Arctic Svalbard; CH = *Cassiope tetragona* heath in high Arctic Svalbard; SB = snowbed in the high Arctic Svalbard. The Icelandic sites, BH and MH, were established in 1996 and 1995, respectively. The Svalbard sites, DH, CH and SB, were all established in 2002. Map credit: Arto Vitikka, Arctic Centre, University of Lapland.

Audkúluheidi comprises rangelands in the northwestern highlands of Iceland that have been heavily utilised for livestock grazing, mainly sheep, and until 1980s also by horses (Jónsdóttir

et al., 2005). The bedrock is basalt covered with loose glacial deposits, and the soils are classified as well-drained Brown Andosols. Mean annual temperature was 0.7 ± 0.3 °C and mean annual precipitation 357 ± 14 mm for the period 1996–2017 (Kolka weather station, Icelandic Meteorological Office). In terms of Arctic bioclimatic sub-zones (Walker et al., 2009), this area is classified as sub-Arctic alpine or oro-Arctic with climate conditions resembling the low Arctic. The research site (65°26'N, 20°25'W, 480 m elevation) is located within a levelled mesic habitat (a zonal habitat sensu Walker et al. 2009), dominated within a moss rich *Betula nana* dwarf shrub heath with 25% vascular plant cover, 20% lichen and 70% bryophyte cover (Jónsdóttir et al. 2005). Other common species are the evergreen dwarf shrub *Empetrum nigrum,* the moss *Racomitrium lanuginosum* and the lichen *Cetraria islandica*. This habitat will be referred to here as *Betula* heath (BH). Ten pairs of 0.75 x 0.75 m plots were marked in 1996 and within each pair one plot was randomly assigned to a warming treatment. The OTCs increased summer temperatures at the cryptogam layer surfaces by 0.7-1.0°C but did not affect soil temperatures (Jónsdóttir et al. 2005). To prevent disturbance from the sheep the experimental plots were fenced (additional plots established to control for the sheep exclusion effect, not included here).

The Thingvellir research site is located on an 8000-year-old post-glacial basaltic lava field within Thingvellir National Park in southwestern Iceland (64°28'N, 21°08'W) at 120 m elevation, slightly below the treeline of the sub-Arctic mountain birch forest. Livestock grazing has been prevented within the park since its establishment in 1928. The soils are shallow, classified as Brown Andosols with high organic matter content (Jónsdóttir et al., 2005). Mean annual temperature was 4.1 ± 0.3 °C and mean annual precipitation 1242 ± 37 mm for the period 1996–2017 (Thingvellir weather station, Icelandic Meteorological Office).

221 The vegetation is characterised by open *Racomitrium lanuginosum* moss heath and patches
222 of *Salix* dwarf shrubs and mountain birch (*Betula pubescence*). The research site is located
223 within a levelled area dominated by the moss heath with more than 90% moss cover, sparse
224 cover of vascular plants (5-6%), most commonly the sedge *Carex bigelowii*, the grass *Festuca*
225 *richardsonii*, and the forb *Galium boreale* (Jónsdóttir et al., 2005). This habitat will be
226 referred to here as moss heath (MH). Ten pairs of 0.75 x 0.75 m plots were marked in 1995
227 and within each pair one plot was randomly assigned to a warming treatment. The OTCs
228 increased summer surface temperatures by 1-2 °C and tended to decrease soil
229 temperatures (Jónsdóttir et al. 2005).

230 The three high-Arctic habitats in Svalbard were all located on a south-east facing slope in
231 the valley Endalen (78°11'N, 15°45'E), 10 km east of Svalbard Airport, all within the Arctic
232 bioclimatic sub-zone C (Walker et al., 2009). The soils are Cryosols with a thin organic layer
233 on top of inorganic sediments (Jones et al., 2010). Mean annual temperature for 1981–2010
234 at Svalbard Airport was −5.2 °C and mean annual precipitation was 191 mm (Førland et al.,
235 2011). The habitats in the area are strongly shaped by topography and snow conditions in
236 winter (Jónsdóttir et al., 2023). The three studied habitats were (i) dry exposed ridges with
237 thin snow cover (∼10 cm) and early snowmelt in spring with vegetation characterised by the
238 prostrate evergreen dwarf shrub *Dryas octopetala*, (ii) mesic zonal habitats (*sensu* Walker et
239 al. 2009) in shallow depressions with deeper and later melting snow (12 -15 days later than
240 the ridges) and vegetation characterised by the evergreen erect dwarf shrub *Cassiope*
241 *tetragona*, and (iii) moist moss-rich snowbeds in deep depressions, with snow depth in
242 winter over 100 cm and snow melt typically 24-27 days later than on the ridges. The
243 habitats will be referred to here as Dryas heath (DH), Cassiope heath (CH) and snowbed

(SB), respectively. In DH other abundant vascular plants were *Salix polaris*, *Bistorta vivipara* and *Carex rupestris* (total vascular plant cover over 60%) and the most abundant bryophyte species was the moss *Sanionia uncinata* (bryophyte cover around 50%, lichen 5%). In CH other common vascular plant species were *Salix polaris*, *Bistorta vivipara* (total vascular plant cover over 70%) and the most abundant bryophytes were *Tomentypnum nitens* and *Sanionia uncinata* (bryophyte cover over 50%, lichen 7%). In SB the vascular plant cover was less than 50% with *Bistorta vivipara* and the grasses *Poa arctica* and *Festuca richardsonii* most common and *Tomentypnum nitens* and *Sanionia uncinata* as the most abundant bryophyte species (85% bryophyte cover). In each habitat ten 0.75x0.75 m plots were selected in 2002 and five of them were randomly assigned to a warming treatment. The OTCs increased July temperatures by 1.6°C across all habitats and tended to increase soil temperatures (Jónsdóttir et al. 2023).

Bryophyte community structure and composition and bryophyte functional groups

To test hypotheses 1 and 2 we used plant community composition data collected by the point intercept method at the beginning of the experiment and then at 3-7 years intervals. All species intercepted at 100 equally distributed points across the plots were recorded as well as litter and bare ground. If bryophytes or lichens were present in a point, they were only recoded once as “the last hit” in that point. The sum of all bryophyte (and lichen) records within a plot could, therefore, be translated into cover (one hit out of 100 = 1 % cover). All bryophytes (and lichens) were identified at the species or the genus level. In the latter case, the abundance was usually low and most likely only represented by a single species. We avoided disturbance of the bryophyte layer and, therefore, may have missed some liverwort species growing as single shoots within the layer. For those two reasons,

bryophyte species (taxonomic) richness and diversity estimates can be regarded as conservative.

The mean relative abundances of six major plant growth forms in control plots and warmed plots are shown in Figure S1 for all habitats at the start of the experiment and after 12-18 years of warming. More detailed account on overall plant community change is provided for the Svalbard sites by Jónsdóttir et al. (2023) and is being prepared for the two Icelandic sites.

Following the detailed point intercept analyses in 2014 and 2019 at the Icelandic sites and in 2015 at the Svalbard sites the bryophyte layer depth was estimated non-destructively in 25 evenly distributed points within each plot. After some trials the most accurate non-destructive method was to gently insert a split bamboo pin (grill pin) into the moss layer, until an increased resistance was sensed. That was assumed to by the moss-soil interface. The length of the inserted part of the pin provided an estimate of the bryophyte layer depth. The grill pin had the advantage over metal pins that it provided more resistance, which made it easier to determine the change in resistance when the moss-soil interface was reached.

To test hypothesis 3, each recorded bryophyte species (or genera) was assigned to one of the twelve bryophyte functional groups *sensu* Lett et al. (2022), (Table S1). Because lichens and biological soil crust (biocrust) are a part of the cryptogam layer we also report their abundance within each habitat, but do not include them in any statistical analyses.

Bryophyte trait measurements

To test hypothesis 4, we assessed warming responses of two traits of the dominating species in each habitat, annual shoot growth and potential nitrogen fixation rate, and in the two Icelandic habitats we also measured warming responses of the water holding capacity and colony density.

Annual shoot growth

We used two methods to measure the annual shoot growth, the shoot transplantation method and the less accurate cranked wire method as described in (Jónsdóttir et al., 1997). For the shoot transplantation in the Icelandic habitats, shoots of *Racomitrium lanuginosum*, were collected and trimmed to 30 mm lengths. Ten fresh trimmed shoots were weighed and gently fitted into a mesh bag of the same length. On 6th and 12th of June 2014 three mesh bags were transplanted into each experimental plot in a systematic way at BH and MH, respectively at. Five *a priory* fixed positions within the plot were numbered 1-5 and the mesh bags were transplanted into the first three, unless they did not fulfil the criterion of >3 cm bryophyte layer depth. Then the mesh bags were transplanted into positions 4 or 5. Cranked wires with fixed length of the upper vertical part were installed at the same positions, such that the 2 cm horizontal part was at the same level as the moss tips of the moss mat. In that way, each cranked wire provided a collective growth measure of several moss shoots. The mesh bags were collected by the end of June 2015 and the length of the vertical part of the cranked wire extending above the moss tips of the bryophyte layer measured. In the lab the length of the transplanted shoots within each mesh bag was measured individually and the dry weight of the pooled ten shoots measured.

In the Svalbard we used the same two methods as in Iceland with a slight modification of the transplant method The bryophyte layer at the *Dryas* heath (DH) was too shallow to allow application of those methods but in the other two habitats, CH and SB, shoots of *Sanionina uncinata* were collected from the respective habitat. Since this species is more delicate than *R. lanuginosum* and because the bryophyte layer was generally shallower, the shoots were trimmed to 20 mm lengths, and 15 trimmed shoots were fitted into each mesh bag. On 17 July 2014 three mesh bags were transplanted into each experimental plot within each habitat in the same systematic way as in Iceland but using the criterion of >2 cm bryophyte layer depth. The mesh bags were collected and the cranked wire measured on 4 August 2015, and the mesh bag shoots measured individually and weighed as described above.

N2-fixation

To measure nitrogen fixation capacities of the dominating bryophytes, we followed the procedure described in DeLuca et al., (2002) and Zackrisson et al., (2004). We collected 15 shoots of *Racomitrium lanuginosum* of 5 cm length per control plot and OTC in June, July (only controls) and August 2014 in each of the two habitats in Iceland and 15 shoots of *Sanionia uncinata* in early August 2013 in each of the Svalbard habitats. The 15 moss shoots were divided into three independent samples of 5 shoots each, placed in 20 ml vials, moistened with 2 ml of deionized water and sealed with a rubber septum. N_2-fixation rates were assessed by 24hr acetylene reduction assay (ARA) as described by Stuiver et al., (2015) and Gundale et al. (2012) in which 10% of the head space was removed and replaced with acetylene generated by mixing CaC_2 and water. The samples were incubated in a climate chamber for 24 hr at 13°C with a ratio of 21 hr day light to 4 hr dark. One set of 3 tubes was

332 employed as control and treated in the same manner except for the headspace substitution
333 to assess the endogenous moss ethylene production; and one set of 3 tubes with 2 ml of
334 deionized water and acetylene was used as blank samples to assess the concentration of
335 ethylene in the acetylene employed (Gentili et al., 2005). Each vial was analysed for
336 ethylene concentration by a Clarus 400 gas chromatograph (PerkinElmer Ltd., Beaconsfield,
337 UK) equipped with an automatic split/splitless injector and a flame ionization detector (FID),
338 and an Elite-Alumina column (30 m, 0.53 mm; PerkinElmer Ltd., Beaconsfield, UK). After
339 being analysed, moss samples were dried at 70°C for 48 hr and weighed. Ethylene values
340 were expressed as μmol g^{-1} day^{-1} using the universal law theoretical stoichiometric ratio of
341 acetylene to N (3:1) (DeLuca *et al*., 2002; Zackarisson *et al*., 2004).

342 Water holding capacity and colony density

343 Water holding capacity (WHC) was determined for *Racomitrium lanuginosum*, the
344 dominating species in the Icelandic habitats BH and MH. To get the most ecologically
345 relevant information we measured WHC of moss colonies (i.e. including external water;
346 following Elumeeva et al., (2011); Lett et al., 2022) of a standardised volume. In June 2020,
347 two moss cores were taken from each plot along a line running through the middle of the
348 plot, 20 cm from the opposite plot edges, following these rules: (i) select only healthy moss;
349 (ii) If dead moss shoots move to the side of line; (iii) if vascular plants are in the way, move
350 to the side of the line. A metal core of 5 cm diameter was gently inserted into the moss
351 layer and the moss shoots within that area carefully pulled out to make sure to get the full
352 length of all shoots. After measuring the length (depth) of the collected moss colony at four
353 sides it was trimmed to 5 cm length/depth providing a standard volume of 98.17 cm^3. Each
354 standardised colony was place in a pre-weighed plastic container, 5 cm in diameter, 7 cm

355 deep, with a mesh fixed at 2 cm from the bottom such that the uppermost shoot tips were
356 levelled with the rim of the container, allowing water drainage. The colonies were
357 moistened to field saturation by spraying with water (all excess water was poured off) and
358 weighed to measure the saturation weight, then dried at 70°C to assess their dry weight.
359 The WHC was calculated as the difference between saturated and dry weight, divided by dry
360 weight (g g^{-1}). Colony density was calculated as dry weight per volume (g cm^{-3}).

361 *Data analyses*

362 An overview of all data included in this paper and when collected in each habitat is provided
363 in Table S2.

364 To test whether warming affected bryophyte layer depth, cover, species richness, Shannon
365 diversity, shoot growth, shoot biomass, nitrogen fixation, water-holding capacity and colony
366 density (hypotheses 1,2 and 4), we fitted Bayesian generalized linear mixed models using
367 the R package MCMCglmm (Hadfield, 2010). Models were defined based on the design of
368 each response variable: layer depth was modelled across habitat × year × treatment, cover
369 across habitat × treatment, nitrogen fixation across habitat × treatment × month in Iceland
370 and habitat × treatment in Svalbard, and the remaining trait and diversity variables across
371 habitat × treatment. Random effects reflected the nested sampling structure of each
372 dataset and included plot, colony, and/or shoot identity as appropriate (e.g., plot for layer
373 depth, cover and nitrogen fixation; colony for water-holding capacity and colony density;
374 shoot and plot for shoot growth). Continuous (Gaussian, identity-link) responses (layer
375 depth, shoot growth, shoot and colony biomass, water-holding capacity and Shannon
376 diversity) were modelled on their measured scale, whereas count-based responses (cover

and species richness) were modelled with a Poisson family (log link) and back-transformed to the response scale for presentation. We used weakly informative priors and ran chains with sufficient iterations to achieve effective sample sizes (> 1000) for all parameters. Convergence was assessed visually from trace and density plots. Posterior summaries are reported as means with 95% credible intervals (CI). We evaluated warming effects by assessing whether credible intervals for control and OTC distributions overlapped and treated an effect as credible if intervals did not overlap.

To assess whether bryophyte cover and layer depth were related to vascular plant variables, we fitted ordinary least-squares linear regressions of cover and layers depth on canopy height, litter abundance, total shrub abundance, deciduous and evergreen shrub abundance, separately by habitat and survey year (hypothesis 1; means ±SD for vascular plant variable used in Table S3). Predictors were reduced by backward selection using Akaike's information criterion (AIC), retaining a variable only when its removal increased AIC by more than two (Burnham & Anderson, 2002). Regression fits are shown with 95% confidence bands; slopes, coefficients of determination (R^2) and p-values were extracted from the corresponding `lm` models.

To test whether warming shifted bryophyte species composition and functional-group composition (hypotheses 1 and 2), we used permutational multivariate analysis of variance (PERMANOVA) on Bray–Curtis dissimilarities with the adonis2 function in the vegan package (Oksanen, 2024), fitting year and treatment as marginal terms (by = "margin") with 10,000 permutations, separately for each habitat. Multivariate homogeneity of group dispersions was checked with betadisper for both treatment and year groupings. Where dispersion differed significantly between groups (e.g., for treatment in BH), this is noted as a caveat to

the corresponding PERMANOVA result. Compositional change was visualized per habitat using principal components analysis (PCA) for both species and functional group-based community composition.

Results

Bryophyte community structure

Bryophyte cover was above 40% on average in all habitats and reached over 97% in the *Racomitrium lanuginosum* moss heath (MH) (Figure 2). Cover declined in response to warming in the *Betula* heath (BH) in Iceland, although it was only significantly reduced in BH after 23 years of treatment (19% lower on average in warmed plots in 2019; Figure 2a). In contrast, cover significantly increased in response to warming in the *Cassiope tetragona* heath in Svalbard (CH, 35% higher on average in warmed plots) (Figure 2b). Cover did not differ between treatments in the other three studied habitats.

Bryophyte layer depth varied greatly between the habitats ranging from less than one cm in the *Dyas octopetala* heath (DH) to over 15 cm on average in the MH (Figure 2c and d). The bryophyte layer depth showed contrasting trend in warming responses among the habitats. It BH it declined by 2 cm on average in the warmed plots after 23 years of treatment (31% shallower than in control plots; Figure 1c) while it was not significantly affected in MH. In Svalbard, however, the moss depth increased in CH by 2 cm on average in response to warming (54% deeper in warmed plots than controls), while not depth was not affected by treatment in the other two habitats (Figure 2d).

Bryophyte community structure was negatively related to vascular plant variables in three of the studied habitats. In BH, bryophyte cover declined with litter abundance and bryophyte layer depth declined with shrub abundance in 2014 (Table S4) and deciduous shrub abundance in 2019 (Figure 3a and b, Table S4). In MH bryophyte cover declined with litter abundance both in 2014 and 2019 (Table S4; Figure 3c; relationships only shown for 2019) and a significant negative relationship was maintained, albeit less sharp, after removing the outlier in 2019 (p = 0.002). The only vascular plant relationship detected in the Svalbard habitats was a negative relationship between bryophyte layer depth and deciduous shrubs in CH, where depth declined even more sharply (higher slope value) than in BH (Figure 3d, Table S4).

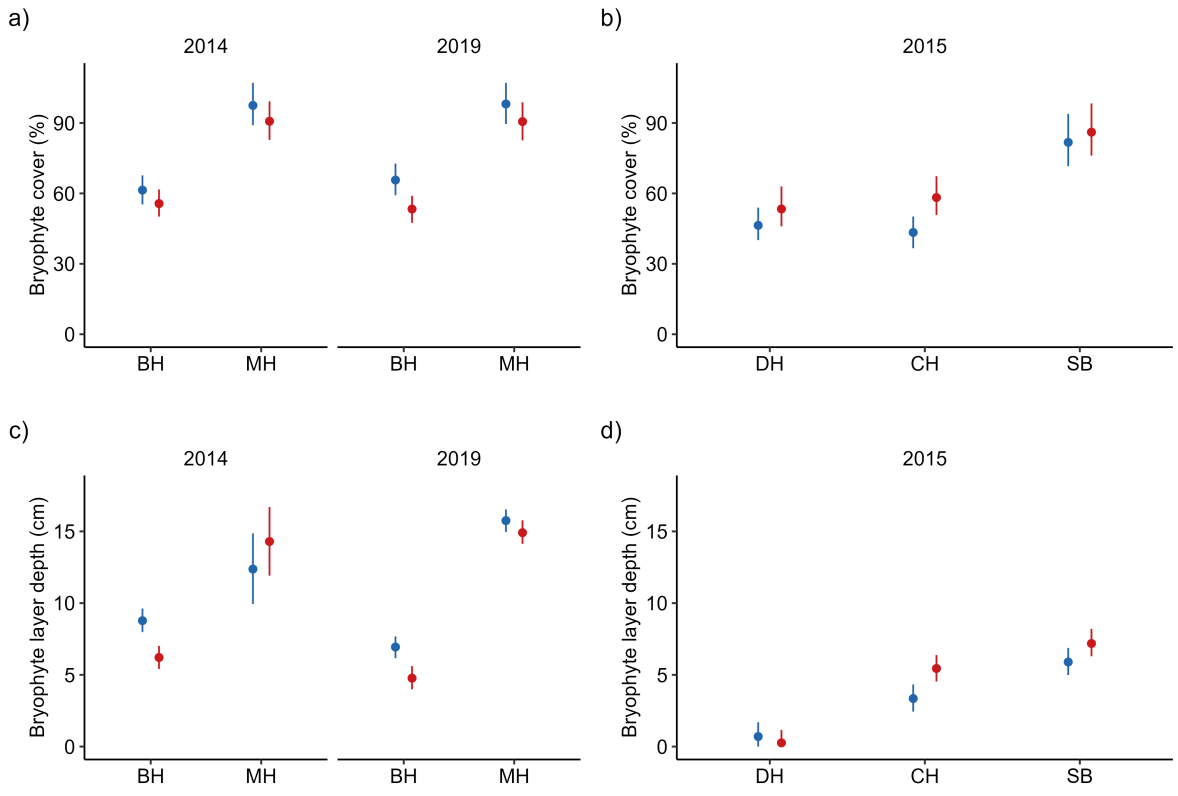

Figure 2. Effects of experimental warming on bryophyte community structure in different tundra habitats. Posterior mean and 95% credible intervals based on results from MCMCglmm models. Blue = control plots, Red = warmed plots. a) Bryophyte cover in the two Icelandic habitats, *Betula nana* heath (BH) and the *Racomitrium lanuginosum* moss heath (MH) in 2014 and 2019 (the two years of layer depth measurements). b) Bryophyte cover in the three high-Arctic Svalbard habitats, *Dryas* heath (DH), *Cassiope* heath (CH) and snowbed (SB) in 2015 (the final year of analysis). c) Bryophyte layer depth in the two Icelandic habitats. d) Bryophyte layer depth in the three Svalbard habitats.

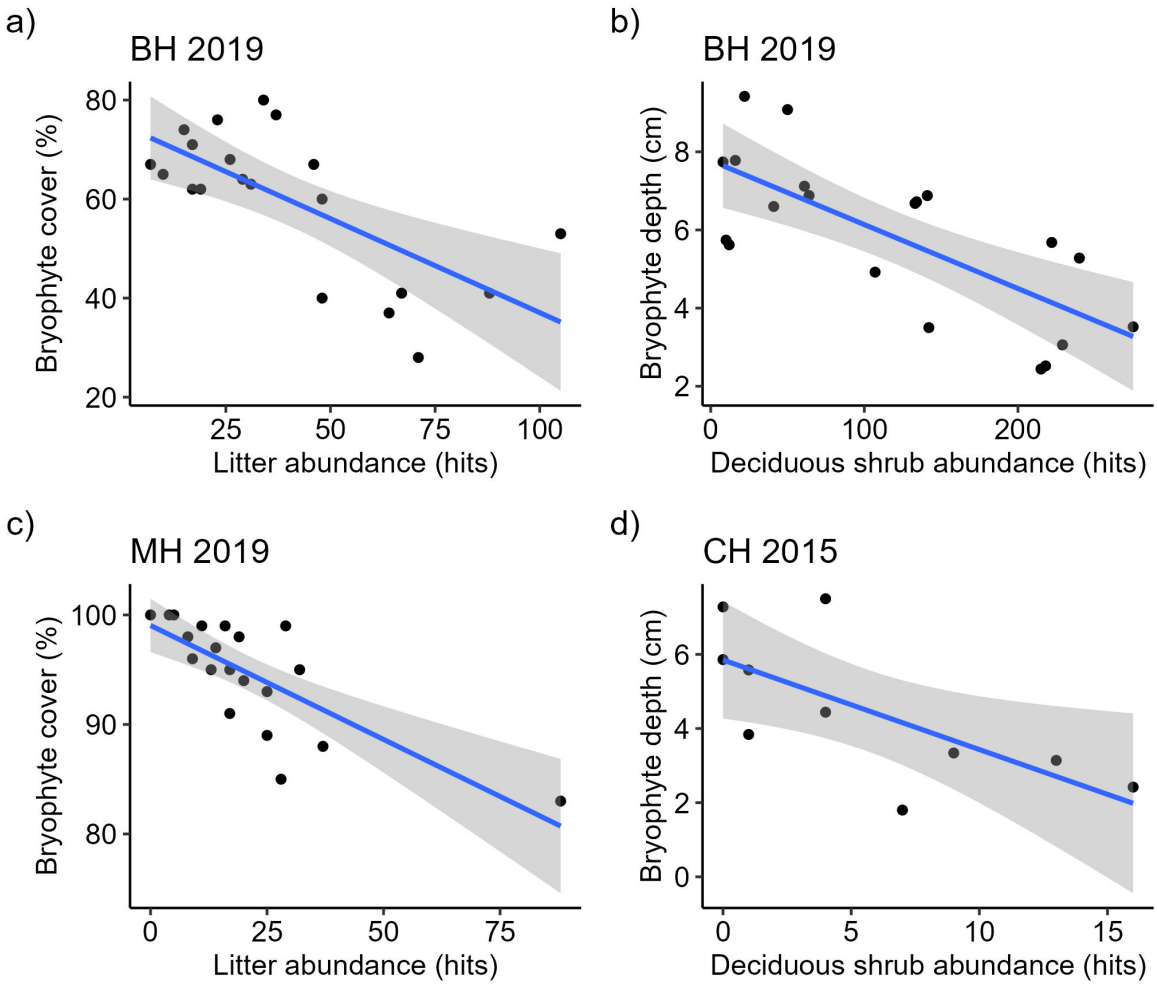

Figure 3. Significant relationships between bryophyte community structure and vascular plant variables. Lines show linear regression fits with 95% confidence bands. a) Bryophyte

445 cover and litter abundance in BH (slope = -0.38 ± 0.09, R^2 = 0.47, p < 0.001). b) Bryophyte
446 layer depth and deciduous shrub abundance in BH (slope = −0.016 ± 0.004, R^2 = 0.53, p <
447 0.001). c) bryophyte cover and litter abundance in MH (slope = −0.21 ± 0.04, R^2 = 0.58, p <
448 0.001). d) Bryophyte layer depth and deciduous shrub abundance in CH (slope = -0.296 ±
449 0.078, R^2 = 0.46, p < 0.01).

450 *Bryophyte community composition and diversity*

451 The bryophyte community in the *Racomitrium lanuginosum* moss heath (MH) in Iceland,
452 only composed of that single species (Table S1), did not change in response to warming. In
453 the *Betula* heath (BH) the first PCA ordination axis explained over 90% of the overall
454 variation in bryophyte community composition and both year and warming treatment
455 significantly contributed to that variation (Figure 4a; Table S5). The trajectories of the
456 treatment x year centroids differed greatly, which is related to the significant homogeneity
457 of group dispersion for treatment (Table S5). This may reflect that treatment differences
458 were more strongly driven by increased spread of the plots within the ordination space than
459 shifts in the group centroids. The bryophyte community composition in the *Dryas* (DH) and
460 *Cassiope* heaths (CH) in Svalbard shifted with time but were not affected by the warming
461 treatment (Figures 4b, c; Table S5). It should be noted that homogeneity of group dispersion
462 for year was significant in DH, indicating an increasing spread of the plots with time within
463 the ordination space. While community composition showed no temporal trend in the
464 snowbed habitat (SB) it was significantly affected by the warming treatment (Figure 4d;
465 Table S5).

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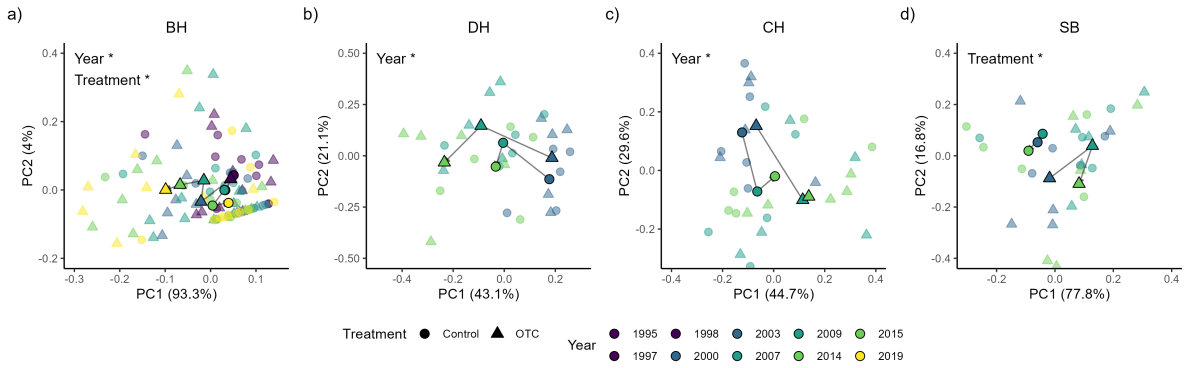
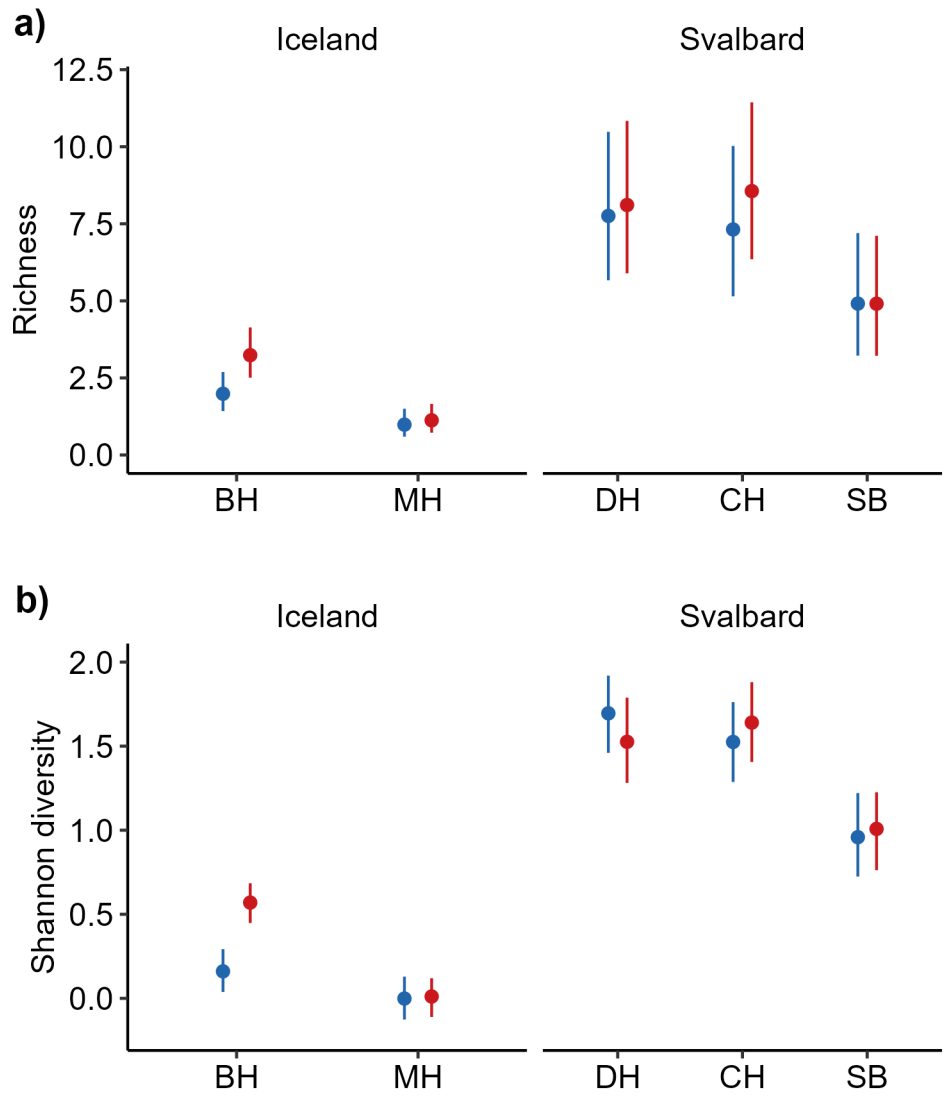


Figure 4. Principal component analysis (PCA) of bryophyte species composition in control (circles) and warmed (OTC, triangles) plots in four of the five studied habitats (the moss heath (MH) only had one species): a) *Betula* heath (BH) (Iceland) and the Svalbard habitats b) *Dryas* heath (DH), c) *Cassiope* heath (CH) and d) snowbed (SB). Points are individual plots coloured by survey year (see legend); large black-outlined symbols are treatment × year centroids, connected by arrows to show the direction of compositional change through time for each treatment. Significant terms from habitat-specific PERMANOVAs (Bray–Curtis dissimilarity; year and treatment as predictors; 10,000 permutations) are indicated in each panel (* $p < 0.05$). Full PERMANOVA results, including tests of multivariate dispersion homogeneity, are given in Table S5.

Species richness was in general lower in the two Icelandic habitats than the three Svalbard habitats, or only 1-4 species per plot compared with 3-11 in the Svalbard plots (Figure 5a). Warming did not significantly affect species richness in any of the habitats, but it tended to increase richness in warmed BH plots (Figure 5a). That increase was reflected in a significantly higher species diversity in warmed BH plots than controls (Figure 5b). Warming did not affect species diversity in any of the other habitats.



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486 **Figure 5**. Effects of experimental warming on bryophyte species richness and° Shannon
487 diversity in different tundra habitats in the final year of analyses. Posterior mean and 95%
488 credible intervals based on results from MCMCglmm models. Blue = control plots; red =
489 warmed plots. a) Species richness in the Icelandic habitats, *Betula nana* heath (BH) and
490 *Racomitrium lnuginosum* moss heath (MH) in 2019 after 23 years of warming and in the
491 three Svalbard habitats *Dryas* heath (DH), *Cassiope* heath (CH) and snowbed (SB) in 2015
492 after 13 years of warming. b) Shannon diversity in the two Icelandic habitats and the three
493 Svalbard habitats.

494 *Bryophyte functional group composition*

Eight of the twelve bryophyte functional groups (BFG) suggested by Lett et al. (2022) were represented in our study and their number varied from one group in the *Racomitrium lanuginosum* moss heath in Iceland (MH) to two in the *Betula nana* heath (BH), four in the snowbed (SB) and five in the *Dryas* (DH) and *Cassiope* heaths (CH) (Table S1). Ordination of the bryophyte community composition based on BFGs rather than species largely reflected the species-based ordination although with some interesting differences (Figure 6; Table S6). In BH the first axis also here explained the over 90% of the variation and both year and treatment were significant, with significant dispersion homogeneity for treatment (Figure 6a). In DH both treatment and year were significant with significant dispersion homogeneity for year (Figure 6b). Here the trajectories of the control plots and warmed plots were similar but more extended along the first axis for the warmed plots. In CH, year was significant but not treatment as for the species-base ordination (Figure 6c), while in the SB neither year or treatment were significant (Figure 6d), although treatment was close to significance (p=0.05339; Table S6).

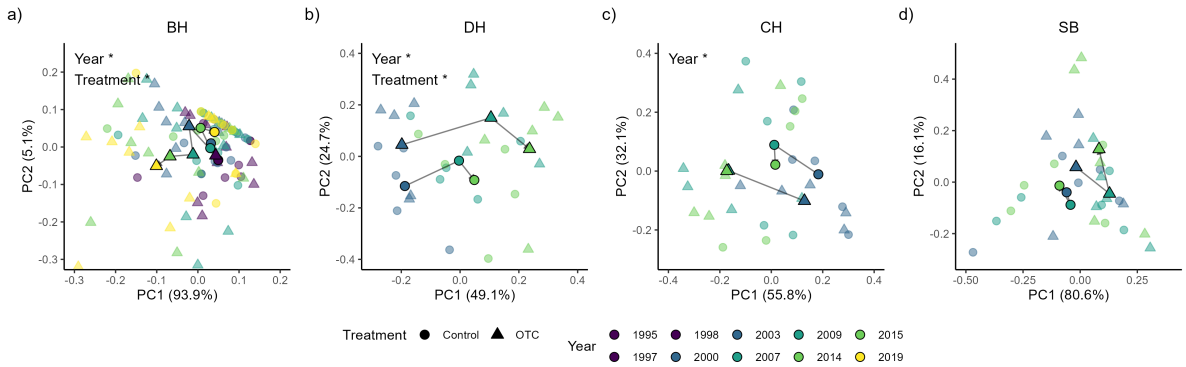

Figure 6. Bryophyte functional group (BFG) composition shown by principal component analysis (PCA) for four habitats (the moss heath (MH) was only composed of a single

species) where bryophyte taxa had been assigned to one of the twelve BFGs suggested by Lett et al., (2022): (a) *Betula* heath (BH) in Iceland and (b–d) the Svalbard habitats *Dryas* heath (DH), *Cassiope* heath (CH) and snowbed (SB). Individual plots are coloured by survey year, with control and warmed plots distinguished by shape (circles and triangles, respectively). Bold, outlined symbols mark the centroid of each treatment in each year; arrows trace these centroids chronologically, so their length and direction summarise how each treatment's functional composition shifted over the monitoring period. Asterisks report the terms retained as significant (* $p < 0.05$) in per-habitat PERMANOVA. Complete results are tabulated in table S6.

In the BH the cover of branched turf mosses (*BT*) tended to decline in response to warming and weft mosses (*We*) (mainly *Hylocomium splendens*) significantly increased (Figure 7; Figure S2). Two new BFGs established in the BH, short unbranched (*SU*) (*Pohlia* spp., *Tortula* spp.) and leafy liverwort (*LL*) (*Ptilidium ciliare*). No new BFG became established in the warmed plots of any of the other four habitats (Figure 7). In the DH *BT* mosses tended to decline in the warmed plots and *SU* mosses tended to increase, while no obvious abundance trends were detected in CH (Figure 7; Figure S2). In SB opposite trends were observed: *We*-mosses tended to decline and *BT* to increase in abundance in response to warming (Figure 7; Figure S2). Lichens were present in three of the habitats, BH, DH and CH and biocrust in two habitats, DH and CH. Interestingly, lichen cover decreased in response to warming in BH but increased in DH and CH, while biocrust decreased in both DH and CH (Figure 7).

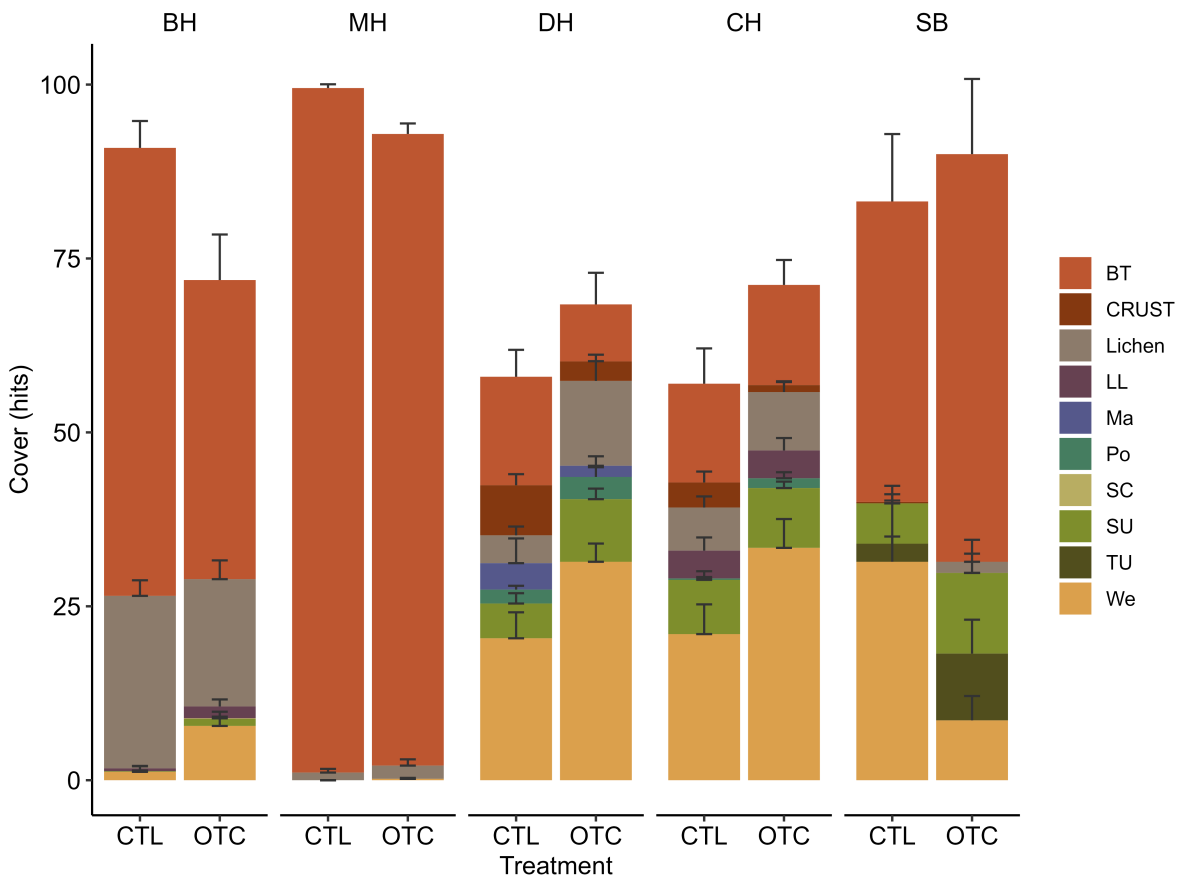

Figure 7. Effects of experimental warming on mean cover (+SE) of different bryophyte functional groups (BFG) in the last year of analysis (2019 for BH and MH, 2015 for DH, CH and SB). CTL = control plots; OTC = warmed plots. The cover of two other cryptogam groups, biocrust and lichens, is also shown within the stacked bars, which provides the average total cover of the cryptogam layer for each habitat and treatment. BT = branched turf; LL = leafy liverwort; Ma = mat; Po = Polytrichales; SC = small cushion; SU = short unbranched turf; TU = tall unbranched turf; We = weft. Also shown is the cover of lichen and biological soil crust (CRUST).

Bryophyte functional traits of the dominating species

Annual shoot growth of the dominating species within the Icelandic habitats, the *BT* moss *Racomitrium lanuginosum*, was on average between 6.5 mm (*Betula heath,* BH) and 6.9 mm

(moss heath, MH) in the control plots and it significantly increased in response to warming only in BH (39% increase) (Figure 8a). Annual shoot growth of the *We* moss *Sanionia uncinata* in control plots in the Svalbard habitats was on average 2.5 mm and 3.4 mm in the *Cassiope* heath (CH) and snowbed (SB), respectively, and tended to increase in response to warming only in CH (Figure 8). Interestingly, annual growth estimates using the less accurate cranked wire method showed similar patterns with significant warming effect only in BH (Figure S3). The total biomass of ten *R. lanuginosum* shoots in the two Icelandic habitats was almost six-fold greater than the 15 shoots of *S. uncinata* and was not affected by the warming treatment in any of the habitats (Figure 8b).

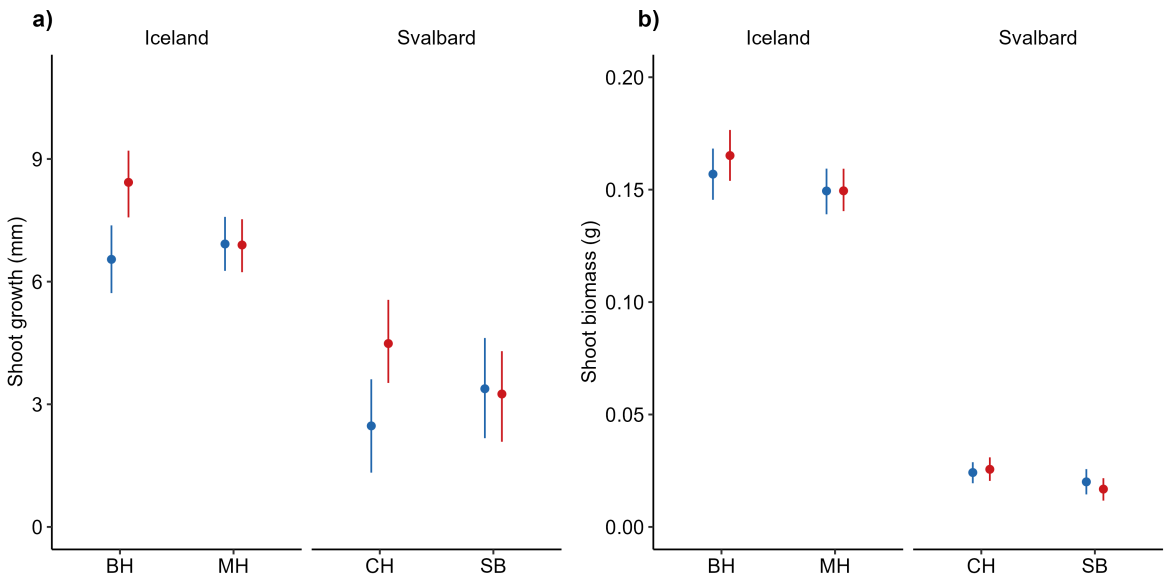

Figure 8. Effects of experimental warming on the annual shoot growth and shoot biomass of the dominating bryophyte species in different habitats. Posterior mean and 95% credible intervals based on results from MCMCglmm models. Blue = control plots; red = warmed plots. a) Annual shoot growth of *Racomitrium lanuginosum* in the two Icelandic habitats

Betula heath (BH) and moss heath (MH) and of *Sanionia uncinata* in two of the Svalbard sites, the *Dryas* heath (DH) and *Cassiope* heath (CH). b) shoot biomass.

Potentila nitrogen fixation rates in *Racomitrium lanuginosum* from the Icelandic habitats BH and MH were up to four times faster in June than in July and August and in both habitats the warming treatment decreased the fixation rates significantly in June (55-71% reduction) (Figure 9). The fixation rates in *Sanionia uncinata* in early August in the Svalbard habitats were about 14-fold faster than the highest rates in *R. lanuginosum*. Warming tended to reduce the rates in all habitats, but the reduction was only significant in the SB habitat (reduced by 84% on average).

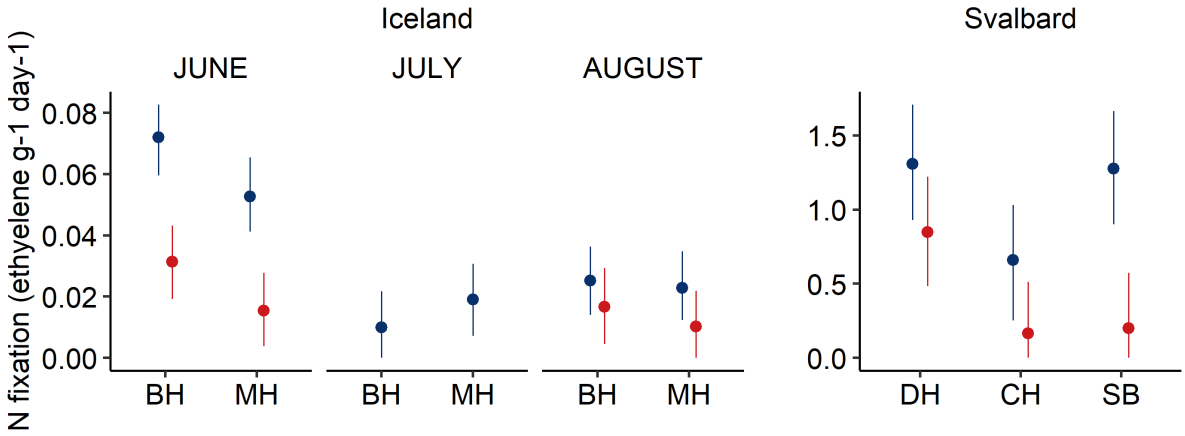

Figure 9. Effects of experimental warming on nitrogen fixation rates in dominating bryophyte species in different habitats. Posterior mean and 95% credible intervals based on results from MCMCglmm models. Blue = control plots; red = warmed plots A) Measurements in *Racomitrium lanuginosum* from control plots in the Icelandic habitats *Betula nana* heath (BH) and moss heath (MH) in June, July and August 2014 and warmed plots in June and August, B) measurements in *Sanionia uncinata* from control and warmed plots in the Svalbard habitats *Dryas* heath (DH), *Cassiope* heath (CH) and snowbed (SB) in early August 2013.

Water holding capacity of *R. lanuginosum* colonies in the control plots was lower in BH than in MH and it was not affected by the warming treatment (Figure 10a). Colony density was similar in the control plots of both habitats and was reduced by warming in the BH by 46% (Figure 10b).

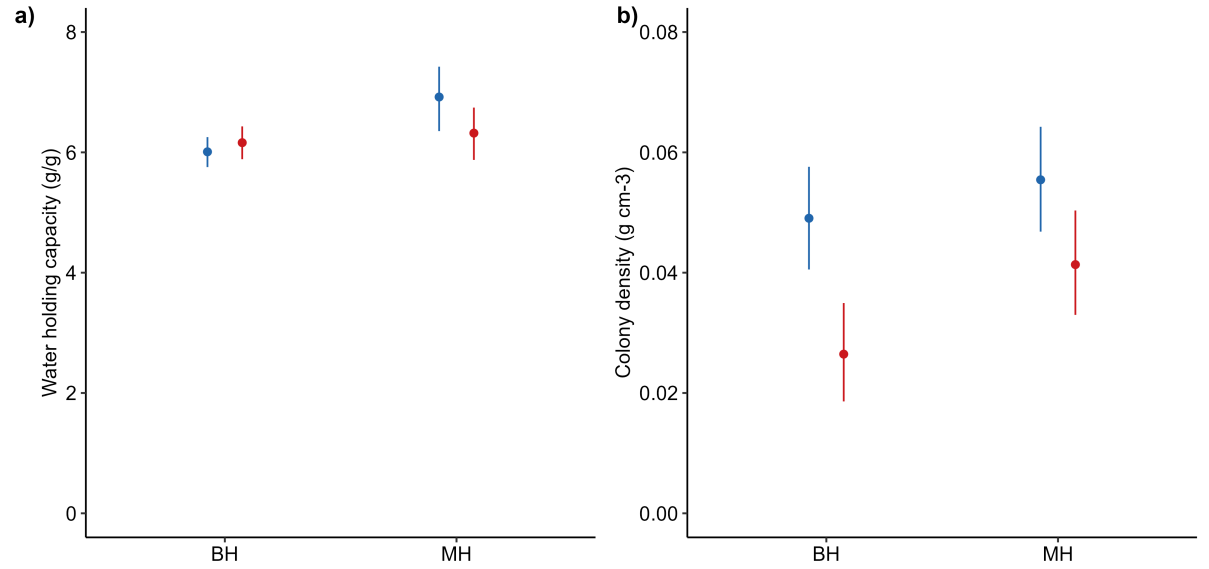

Figure 10. Effects of experimental warming on a) colony water holding capacity and b) colony density of *Racomitrium lanuginosum* in the two Icelandic habitats *Betula* heath (BH) and moss heath (MH) in Iceland. Posterior mean and 95% credible intervals based on results from MCMCglmm models. Blue = control plots; red = warmed plots.

Discussion

Our results revealed contrasting responses to experimental warming across the five studied tundra habitats. Warming decreased bryophyte cover and layer depth only in one habitat, the *Betula nana* heath (BH) in Iceland, leaving bryophyte communities of other habitats

595 either unaffected or with increased cover and layer depth (*Cassiope* heath, CH, in Svalbard).
596 The cover and layer depth responses were only partly reflected by shifts in bryophyte
597 community composition diversity. Shifts in bryophyte functional group (BFG) composition
598 largely mirrored shifts in taxonomic composition over time and in response to warming in all
599 habitats and the functional trait measurements of the dominating species provided some
600 insights into functional warming responses and how they may differ across contrasting
601 tundra habitats.

602 *Bryophyte community structure*

603 The decline in bryophyte cover that has been found in responses to long-term experimental
604 and ambient warming across the tundra (Elmendorf, Henry, Hollister, Björk, Bjorkman, et
605 al., 2012; Elmendorf, R Henry, & Hollister, 2012) and further demonstrated in site-specific
606 papers from low Arctic and alpine tundra (Alatalo et al., 2020; Lang et al., 2012; Sistla et al.,
607 2013; van Zuijlen, Asplund, et al., 2022) was not found in all the habitats studied here. Most
608 likely, the cover-decline in the oro-Arctic *Betula nana* heath (BH), was indirectly caused by
609 warming through interactions with shrubs, deciduous shrubs in particular, that increased in
610 abundance in response to warming (Jónsdóttir et al., 2005). This is supported by the
611 negative relationships between bryophyte cover and the abundance of deciduous shrubs
612 and vascular plant litter, where most of the deposited litter was composed of senescent
613 leaves from *Betula nana*. Similar negative bryophyte-deciduous shrub relationships have
614 been indicated in other studies from the low Arctic and alpine tundra (Alatalo et al., 2020;
615 Lang et al., 2012; Pajunen et al., 2011; van Wijk et al., 2004). Further support for shrubs
616 being the main driver of bryophyte cover decline in warmed plots in BH was provided by the
617 lack of direct treatment effect on bryophyte cover in the sub-Arctic shrub-free *Racomitrium*

618 *lanuginosum* moss heath in Iceland (MH) where moss cover was consistently high across
619 time and treatments (80-100%). Interestingly, even though cover was unaffected by the
620 warming treatment in the shrub-free MH a significant negative cover-vascular plant litter
621 relationship was detected. That litter originated primarily from the grass *Avenella flexuosa*
622 that had increased in abundance in a few of the warmed plots.

623 The lack of change and even a cover increase in response to warming in the three high-
624 Arctic habitats in Svalbard also contrasted with the expected bryophyte cover decline. Such
625 responses have also been reported for other high-Arctic communities, where cover
626 increased in both a sedge meadow and an evergreen (*Cassiope*) heath, similar to the CH in
627 Svalbard (Edwards & Henry, 2016; Hudson & Henry, 2010). Common to all those high-Arctic
628 communities is that the vascular plant component responded less strongly to the
629 experimental warming than reported from warmer sites and, overall, the plant communities
630 were more resistant to warming (Edwards & Henry, 2016; Hudson & Henry, 2010; Jónsdóttir
631 et al., 2023). In our study this was reflected by the absence of any significant bryophyte
632 cover relationships with vascular plant variables in the Svalbard habitats. In this context it is
633 important to note that the deciduous shrubs, where present, were rather prostrate a in all
634 those high-Arctic communities and, therefore, may not have been as competitive as the
635 more erect-growing deciduous shrubs in tundra habitats at warmer sites. On the opposite,
636 the only deciduous shrub species in the Svalbard habitats, the small prostrate *Salix polaris*,
637 tended to decline in response to experimental warming (Jónsdóttir et al., 2023).

638 Despite the strength of bryophyte impacts on vascular plants (specifically: seedling
639 establishment, growth and survival), as well as the soil environment through insulation is
640 strongly related to the depth of the bryophyte layer (Gornall et al., 2007; Jaroszynska et al.,

2023; Schuuring et al., 2024; Soudzilovskaia et al., 2013), experimental warming effects on bryophyte layer depth are rarely assessed. Here we demonstrate that in tundra habitats where bryophyte cover is affected by experimental warming, either positively (CH) or negatively (BH), the bryophyte layer depth responds in the same direction. Interestingly, there was a negative relationship between bryophyte layer depth and deciduous shrub abundance in CH. Most likely the causal relationship here is opposite to the negative relationship in found in BH: an increase in bryophyte layer depth by over 60% together with an increased vascular plant canopy height (Jónsdóttir et al. 2023) may have caused an increased shading of the small prostrate *S. polaris.* Even with the caveat in mind that the open top chambers may have reduced trampling by large herbivores (reindeer) in the high-Arctic Svalbard habitats (plots not fenced), our results strongly suggest a divergent response of bryophyte-rich tundra ecosystems to warming. In high-Arctic ecosystems and other tundra ecosystems lacking erect and responsive deciduous shrubs, bryophyte cover and layer depth may stay unchanged or even increase, thus further increasing the insulation of the soil environment, which contributes to slower ecosystem processes and overall community resistance to climate change. In contrast, tundra ecosystems at warmer sites with more responsive, erect deciduous shrubs the bryophyte cover and layer depth will decline, driven by the bryophyte-deciduous shrub interaction, and may eventually enter a positive feedback loop further accelerating ecosystem processes and warming-induced overall community change.

Bryophyte community composition and diversity

The community structural responses to climate warming were only partly reflected in community taxonomic composition over time and treatments. The community composition

of the BH shifted over time and was significantly affected by the warming treatment, similar to the findings of the few previous experimental studies assessing bryophyte community composition (Alatalo et al., 2020a; van Zuijlen, Asplund, et al., 2022). However, opposite to those studies, bryophyte diversity increased in the warmed plots in the BH. The explanation may be related to land use change (Jónsdóttir et al. 2005). BH is within a degraded rangeland and despite the increase in vascular plant abundance in response to warming the overall vegetation had not have fully recovered after 23 years of grazing protection and warming, which allowed new bryophyte species to establish and shading-tolerant species to increase in abundance, thus enhancing bryophyte diversity. This may also explain the significant treatment effect on the homogeneity of group dispersion reflecting increased plot differences within treatment. Community differences between treatments were mainly driven by a decline in the abundance of the branched turf moss (*BT*) *Racomitrium lanuginosum* and an increase in the abundance of more shading tolerant species, particularly the weft (*We*) moss *Hylocomium splendence*, in the warmed plots.

In the moist snowbed (SB) in Svalbard communities responded in a unique way, showing no shift in composition in the control plots over time while the warming treatment significantly shifted community composition, but without affecting bryophyte diversity. The DH and CH communities shifted over time while unaffected by the warming treatment despite the significant positive warming effects on bryophyte cover and layer depth in CH. In both habitats the community trajectories of the control and warmed plots were similar, and the warming treatment did not affect any of the diversity metrics. Interestingly, the community change in response to warming in the SB seemed to be driven by a decrease in the *We* moss *Sanionia uncinata* and an increase in more erect species such as the *BT* moss *Tomentypnum*

nitens, while no such warming trends were detected in the drier habitats. This may potentially be a consequence of an intensified bryophyte-bryophyte species competition without vascular plant interference in this moss-rich moist habitat.

BFG composition

The shifts in BFG community composition over time and in response to warming largely mirrored the shifts in species composition in the studied habitats and the differences in species diversity between habitats were also reflected by the number and abundance of BFGs. Overall, the *BT* group was most negatively affected by warming and *We* the most positively affected group, but the opposite trend was found in the snowbed (SB). Besides difference in morphology, other functional traits that have been documented so far for the *BT* and *We* groups do not seem to differ much, although water holding capacity tended to be higher in *We* mosses (Lett et al. 2022). Even though there were no significant effects of warming on the abundance of individual BFGs except for an increase in We in the BH, we detected a opposite trends in warming responses of BT and We between the snowbed on one hand and the other two Svalbard habitats on the other. The SB had the highest moisture levels of all studied habitats, which may have enhanced the competitiveness of the *BT* mosses in the SB warmed plots.

Although bryophytes were the focus of this study, it is interesting to note that other cryptogam groups responded differently to warming in the different habitats. Lichen cover decreased in the BH and increased in the high-Arctic DH and CH, while biological soil crust decreased in the same two habitats.

To our knowledge, this is the first study to assign the BFG classification by Lett et al. (2022) to bryophyte community data. Previous attempts to assign functional groups to bryophyte communities distinguished only between mosses and liverworts, *Sphagnum* mosses and other mosses and sometimes between acrocarp vs. pleurocarp mosses. *Sphagnum* mosses have been found to be more resistant to warming than non-*Sphagnum* mosses (Lang et al., 2012) and acrocarp mosses to be more negatively affected by warming than pleurocarp mosses, although that varied substantially (Elmendorf et al., 2012a; van Zuijlen et al., 2022). Our study shows that even though more detailed functional trait measurements for the twelve BFGs are needed for interpretations of the functional warming responses of the bryophyte communities, their application is useful in enhancing bryophyte resolution in future tundra plant community assessments and understanding bryophyte functional diversity.

Bryophyte functional traits

The few functional traits we measured in the dominating species provided some preliminary insight to functional responses of the bryophyte component to warmer climate and how they may differ between tundra habitats.

Generally, bryophyte shoot growth rate is enhanced by increasing temperature when moisture levels are kept constant up to an optimum, although growth rates vary substantially among species (Furness & Grime, 1982; Rzepczynska et al., 2022). However, bryophyte shoot growth in natural environments is also strongly affected by moisture regimes and nutrient availability (nitrogen deposition, N_2-fixation etc.) and it is therefore important to assess growth responses to climate warming *in situ*. Our growth

730 measurements showed large difference in annual shoot growth between the two species
731 where *Rachomitrium lanuginosum* annual shoot growth in the two Icelandic habitats was 2-
732 3 times greater than in *Sanionia uncinata* in the Svalbard sites. The two species belonged to
733 different BFGs and this difference is most likely more related to inherent species differences
734 than climatic conditions. The warming treatment affected annual shoot growth only in the
735 BH where it was on average 30% greater than in the controls. However, since warming did
736 not affect annual growth of *R. lanuginosum* in the "unshaded" MH and shoot biomass was
737 not affected in any of the Icelandic habitats, increased annual shoot growth in warmed BH
738 was most likely a result of an etiolation, which is a common shading response in many moss
739 species. That may also have been the case in CH where annual shoot growth tended to
740 increase in the warmed plots and where vascular canopy hight increased (Jónsdóttir et al.
741 2023). Such etiolation in response to warming was also indicated in a warming experiment
742 in an alpine *Dryas* heath by a higher specific shoot length (van Zuijlen et al, 2022).

743 The potential nitrogen fixation rates in *R. lanuginosum* in the two Icelandic habitats were at
744 low levels as was also found for this species in the study by Rzepczynska et al. (2022) in
745 comparison with nine other species from sub-Arctic sites. The decline in nitrogen fixation
746 over time in the deep layers of *R. lanuginosum* in both the Icelandic habitats most likely
747 reflects seasonal changes in moisture regimes as the uppermost moss segments, containing
748 most of the N_2-fixing bacteria (Papinot Lecomte et al., 2026), gradually dry out. The nitrogen
749 fixation rates in *S. uncinata* in the three high-Arctic Svalbard habitats in early August were
750 much faster than in *R. lanuginosum*. While this suggests a strong difference in bryophyte-
751 contributed ecosystem nitrogen input, the difference between the species may have been
752 somewhat exaggerated by the relatively larger shoot proportion that did not host any N_2-

753 fixing bacteria in *R. lanuginosum*. In a study of nitrogen fixation potentials in 34 bryophyte
754 species sampled from various Alaskan sites, nitrogen fixation rates in R. *lanuginosum* were
755 the second fastest and fixation rates of S. uncinate were quite low (Stuart et al., 2021). This
756 discrepancy may either be caused by differences in environmental conditions at the time of
757 sampling or due to methodological differences (acetylene reduction assay and $^{15}N_2$
758 incubation, respectively) or a combination of both.

759 The decrease in nitrogen fixation in response to experimental warming in our study
760 (significantly so in the two Icelandic habitats in June and the snowbed in Svalbard) agrees
761 with negative response to the warming treatment in previous experimental studies in the
762 tundra (Permin et al., 2022; Sorensen et al., 2012) and has been attributed to dryer
763 conditions under warming. Indeed, both moss species and precipitation may modulate the
764 effects of long-term experimental warming on bryophyte-associated nitrogen fixation (e.g.
765 Lett et al., 2024). However, reduction in nitrogen fixation may also reflect warming induced
766 shifts in the moss-associated bacterial communities towards less efficient N_2-fixing bacteria
767 as was the case in the experimental plots in BH (Klarenberg et al., 2021). Reduced nitrogen
768 input through N_2- fixation by bryophyte associated bacteria in response to climate warming
769 may have consequences for the ecosystem nutrient availability unless compensated by
770 faster ecosystem nitrogen cycling.

771 The lack of warming effects on the capacity of the uppermost five cm of the *R. lanuginosum*
772 layer to retain moisture in the two Icelandic habitats, here expresses as colony water
773 holding capacity (WHC), was surprising and contradicts results from other warming
774 experiments (van Zuijlen et al., 2022). Even more surprising was the decline in colony
775 density in response to warming (only significant in the BH) without a decrease in WHC, but

776 previous studies have demonstrated positive relationships between WHC and colony
777 density (Elumeeva et al., 2011; Volkova et al., 2023). Apparently, the WHC-temperature
778 relationship may be complicated under field conditions. For instance, Roos et al. (2019)
779 found decreasing WHC with decreasing temperatures along an elevation gradient in an
780 alpine tundra.

781 *Conclusions*

782 All five tundra habitats had relatively high cover of bryophytes but differed in moss layer
783 depth, bryophyte species composition, diversity and bryophyte functional group
784 composition and in deciduous shrub abundance. All those aspects may have influenced how
785 the bryophyte communities responded to simulated climate warming although bryophyte
786 cover and layer depth and the presence of erect deciduous shrubs seemed to play a key
787 role. Bryophyte cover and layer depth in habitats lacking erect deciduous shrubs most likely
788 contributed to overall community resistance to warming, while interaction with the
789 warming-responsive erect deciduous shrubs resulted in bryophyte cover and layer depth
790 decline, which in turn may have accelerated ecosystem processes and overall community
791 change. Finally, the BFG classification and the trait measurements of the dominating species
792 provided some understanding of the complex mechanisms behind bryophyte community
793 responses to warming, or the lack of responses. The high bryophyte community diversity in
794 the high-Arctic habitats may have contributed to their warming resistance although the
795 single-species sub-Arctic moss heath community was also highly resistant.

796 This study highlights the important role of bryophytes in tundra communities, how that role
797 is shaped by habitat differences across bioclimatic sub-zones and how it is modulated by

warming climate. It also emphasises the need for further bryophyte focused studies to better understand tundra ecosystem functioning as well as their response to climate change.

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References

Alatalo, J. M., Jägerbrand, A. K., Erfanian, M. B., Chen, S., Sun, S. Q., & Molau, U. (2020). Bryophyte cover and richness decline after 18 years of experimental warming in alpine Sweden. *AoB PLANTS*, *12*(6). https://doi.org/10.1093/AOBPLA/PLAA061

Armitage, H. F., Britton, A. J., van der Wal, R., Pearce, I. S. K., Thompson, D. B. A., & Woodin, S. J. (2012). Nitrogen deposition enhances moss growth, but leads to an overall decline in habitat condition of mountain moss-sedge heath. *Global Change Biology*, *18*(1), 290–300. https://doi.org/10.1111/j.1365-2486.2011.02493.x

Berner, L. (2024). *the arctic Plant aboveground Biomass Synthesis Dataset*. https://doi.org/10.1038/s41597-024-03139-w

Bjornsson, H., Sveinbjornsdottir, A., Danielsdottir, A., Snorrason, A., Sigurðsson, B., Sveinbjornsson E, Viggosson G, Sigurjonsson J, Baldursson, S., Þorvaldsdottir, S., & Jonsson, T. (2008). *Hnattrænar loftslagsbreytingar og áhrif þeirra á Íslandi.* https://doi.org/ISBN 978-9979-839-28-6

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical informationtheoretic approach* (2nd ed.). Springer-Verlag.

Coe, K., Carter, B., Slate, M., & Stanton, D. (2024). Moss functional trait ecology: Trends, gaps, and biases in the current literature. *American Journal of Botany*, *111*(2), e16288. https://doi.org/10.1002/AJB2.16288

Cornelissen, J. H. C., Lang, S. I., Soudzilovskaia, N. A., & During, H. J. (2007). Comparative cryptogam ecology: A review of bryophyte and lichen traits that drive biogeochemistry. *Annals of Botany*, *99*(5), 987–1001. https://doi.org/10.1093/aob/mcm030

DeLuca, T. H., Zackrisson, O., Nilsson, M. C., & Sellstedt, A. (2002). Quantifying nitrogen-fixation in feather moss carpets of boreal forests. *Nature*, *419*(6910), 917–920. https://doi.org/10.1038/nature01051

Edwards, M., & Henry, G. H. R. (2016). The effects of long-term experimental warming on the structure of three High Arctic plant communities. *Journal of Vegetation Science*, *27*(5), 904–913. https://doi.org/10.1111/jvs.12417

Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Björk, R. G., Bjorkman, A. D., Callaghan, T. V., Collier, L. S., Cooper, E. J., Cornelissen, J. H. C., Day, T. A., Fosaa, A. M., Gould, W. A., Grétarsdóttir, J., Harte, J., Hermanutz, L., Hik, D. S., Hofgaard, A., Jarrad, F., Jónsdóttir, I. S., … Wookey, P. A. (2012). Global assessment of experimental climate warming on tundra vegetation: Heterogeneity over space and time. In *Ecology Letters* (Vol. 15, Number 2, pp. 164–175). https://doi.org/10.1111/j.1461-0248.2011.01716.x

Elmendorf, S. C., Henry, G. H. R., Hollister, R. D., Björk, R. G., Boulanger-Lapointe, N., Cooper, E. J., Cornelissen, J. H. C., Day, T. A., Dorrepaal, E., Elumeeva, T. G., Gill, M., Gould, W. A., Harte, J., Hik, D. S., Hofgaard, A., Johnson, D. R., Johnstone, J. F., Jónsdóttir, I. S., Jorgenson, J. C., … Wipf, S. (2012). Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change*, *2*(6), 453–457. https://doi.org/10.1038/nclimate1465

Elumeeva, T. G., Soudzilovskaia, N. A., During, H. J., & Cornelissen, J. H. (2011). The importance of colony structure versus shoot morphology for the water balance of 22 subarctic bryophyte species. *Journal of Vegetation Science*, *22*(1), 152–164. https://doi.org/10.1111/j.1654-1103.2010.01237.x

Førland, E. J., Benestad, R., Hanssen-Bauer, I., Haugen, J. E., & Skaugen, T. E. (2011). Temperature and Precipitation Development at Svalbard 1900–2100. *Advances in Meteorology*, *2011*, 1–14. https://doi.org/10.1155/2011/893790

Furness, S. B., & Grime, J. P. (1982). Growth Rate and Temperature Responses in Bryophytes: II. A Comparative Study of Species of Contrasted Ecology. *Source: Journal of Ecology*, *70*(2), 525–536. https://www.jstor.org/stable/2259920

Geffert, J. L., Frahm, J. P., Barthlott, W., & Mutke, J. (2013). Global moss diversity: Spatial and taxonomic patterns of species richness. *Journal of Bryology*, *35*(1), 1–11. https://doi.org/10.1179/1743282012Y.0000000038

869 Gentili, F., Nilsson, M. C., Zackrisson, O., DeLuca, T. H., & Sellstedt, A. (2005). Physiological
870 and molecular diversity of feather moss associative N2-fixing cyanobacteria. *Journal of*
871 *Experimental Botany*, *56*(422), 3121–3127. https://doi.org/10.1093/JXB/ERI309
872 Gornall, J. L., Jónsdóttir, I. S., Woodin, S. J., & Van Der Wal, R. (2007). Arctic mosses govern
873 below-ground environment and ecosystem processes. *Oecologia*, *153*(4), 931–941.
874 https://doi.org/10.1007/s00442-007-0785-0
875 Gornall, J. L., Woodin, S. J., Jónsdóttir, I. S., & van der Wal, R. (2011). Balancing positive and
876 negative plant interactions: How mosses structure vascular plant communities.
877 *Oecologia*, *166*(3), 769–782. https://doi.org/10.1007/s00442-011-1911-6
878 Grau-Andrés, R., Thieffry, S., Tian, S., Wardle, D. A., & Kardol, P. (2022). Responses of
879 bryosphere fauna to drought across a boreal forest chronosequence. *Oecologia*, *200*(1–
880 2), 231–245. https://doi.org/10.1007/S00442-022-05255-Z/FIGURES/6
881 Gundale, M. J., Wardle, D. A., & Nilsson, M. C. (2012). The effect of altered macroclimate on
882 N-fixation by boreal feather mosses. *Biology Letters*, *8*(5), 805.
883 https://doi.org/10.1098/RSBL.2012.0429
884 Hadfield, J. D. (2010). MCMC Methods for Multi-Response Generalized Linear Mixed
885 Models: The MCMCglmm R Package. *Journal of Statistical Software*, *33*(2), 1–22.
886 https://doi.org/10.18637/JSS.V033.I02
887 He, X., He, K. S., & Hyvönen, J. (2016). Will bryophytes survive in a warming world?
888 *Perspectives in Plant Ecology, Evolution and Systematics*, *19*, 49–60.
889 https://doi.org/10.1016/J.PPEES.2016.02.005
890 Henry, G. H. R., Hollister, R. D., Klanderud, K., Björk, R. G., Bjorkman, A. D., Elphinstone, C., J,
891 I. S., Molau, U., Petraglia, A., Oberbauer, S. F., Rixen, C., & Wookey, P. A. (2022). *The*
892 *International Tundra Experiment (ITEX): 571*(October), 550–571.
893 Hollister, R. D., Elphinstone, C., Henry, G. H. R., Bjorkman, A. D., Klanderud, K., Björk, R. G.,
894 Björkman, M. P., Bokhorst, S., Carbognani, M., Cooper, E. J., Dorrepaal, E., Elmendorf,
895 S. C., Fetcher, N., Gallois, E. C., Guoðmundsson, J., Healey, N. C., Jónsdóttir, I. S.,
896 Klarenberg, I. J., Oberbauer, S. F., … Wookey, P. A. (2023). A review of open top
897 chamber (OTC) performance across the ITEX Network. *Arctic Science*, *9*(2), 331–344.
898 https://doi.org/10.1139/as-2022-0030
899 Hudson, J. M. G., & Henry, G. H. R. (2010). High Arctic plant community resists 15 years of
900 experimental warming. *Journal of Ecology*, *98*(5), 1035–1041.
901 https://doi.org/10.1111/j.1365-2745.2010.01690.x
902 Jägerbrand, A. K., Kudo, G., Alatalo, J. M., & Molau, U. (2012). Effects of neighboring
903 vascular plants on the abundance of bryophytes in different vegetation types. *Polar*
904 *Science*, *6*(2), 200–208. https://doi.org/10.1016/j.polar.2012.02.002
905 Jägerbrand, A. K., Lindblad, K. E. M., Björk, R. G., Alatalo, J. M., & Molau, U. (2006).
906 Bryophyte and lichen diversity under simulated environmental change compared with
907 observed variation in unmanipulated alpine tundra. *Biodiversity and Conservation*,
908 *15*(14), 4453–4475. https://doi.org/10.1007/S10531-005-5098-1/METRICS
909 Jaroszynska, F., Althuizen, I., Helen Halbritter, A., Klanderud, K., Lee, H., Telford, R. J., &
910 Vandvik, V. (2023). *Bryophytes dominate plant regulation of soil microclimate in alpine*
911 *grasslands*. https://doi.org/10.1111/oik.10091
912 Jones, A., Stolbovov, V., Tarnocai, C., Broll, G., Spaargaren, O., & Montanarella, L. (2010).
913 *Soil Atlas of the Northern Circumpolar Region* (P. O. of the E. Union, Ed.).
914 Jónsdóttir, I. S. (1995). Importance of sexual reproduction in Arctic clonal plants and their
915 evolutionary potential. . In T. V. Callaghan, W. C. Oechel, T. Gilmanow, J. I. Holten, U.

916 Molau, B. Maxwell, B. Sveinbjörnsson, & M. Tyson (Eds.), *Global change and Arctic*
917 *terrestrial ecosystems. Proceedings, nternational conference, 21-26 August 1993,*
918 *Oppdal, Norway, Ecosystem report 10.* (pp. 81–88). Commission of the European
919 Communities Ecosystems Research Report, Brussels.
920 Jónsdóttir, I. S., Callaghan, T. V., & Lee, J. A. (1995). Fate of added nitrogen in a moss-sedge
921 Arctic community and effects of increased nitrogen deposition. *Science of The Total*
922 *Environment*, *160–161*(C), 677–685. https://doi.org/10.1016/0048-9697(95)04402-M
923 Jónsdóttir, I. S., Crittenden, P., & Jägerbrand, A. (1997). Measuring growth rate in
924 bryophytes and lichens . *Summary Document of 8th Annual ITEX Workshop*, 10–15.
925 https://www.diva-portal.org/smash/get/diva2:1217789/FULLTEXT01.pdf
926 Jónsdóttir, I. S., Halbritter, A. H., Christiansen, C. T., Althuizen, I. H. J., Haugum, S. V., Henn, J.
927 J., Björnsdóttir, K., Maitner, B. S., Malhi, Y., Michaletz, S. T., Roos, R. E., Klanderud, K.,
928 Lee, H., Enquist, B. J., & Vandvik, V. (2023). Intraspecific trait variability is a key feature
929 underlying high Arctic plant community resistance to climate warming. *Ecological*
930 *Monographs*, *93*(1), 1–21. https://doi.org/10.1002/ecm.1555
931 Jónsdóttir, I. S., Magnússon, B., Gudmundsson, J., Elmarsdóttir, Á., & Hjartarson, H. (2005).
932 Variable sensitivity of plant communities in Iceland to experimental warming. *Global*
933 *Change Biology*, *11*(4), 553–563. https://doi.org/10.1111/j.1365-2486.2005.00928.x
934 Klanderud, K., & Totland, O. (2004). Habitat dependent nurse effects of the dwarf-shrub
935 Dryas octopetala on alpine and arctic plant community structure. *Ecoscience*, *11*(4),
936 410–420.
937 http://gateway.webofknowledge.com/gateway/Gateway.cgi?GWVersion=2&SrcA
938 uth=mekentosj&SrcApp=Papers&DestLinkType=FullRecord&DestApp=
939 WOS&KeyUT=000226278100008
940 Klarenberg, I. J., Keuschnig, C., Russi Colmenares, A. J., Warshan, D., Jungblut, A. D.,
941 Jónsdóttir, I. S., & Vilhelmsson, O. (2021). Long-term warming effects on the
942 microbiome and nifH gene abundance of a common moss species in sub-Arctic tundra.
943 *New Phytologist*, 1–13. https://doi.org/10.1111/nph.17837
944 Koranda, M., Rinnan, R., & Michelsen, A. (2023). Close coupling of plant functional types
945 with soil microbial community composition drives soil carbon and nutrient cycling in
946 tundra heath. *Plant and Soil*, *488*(1–2), 551–572. https://doi.org/10.1007/S11104-023-
947 05993-W/FIGURES/5
948 Lang, S. I., Cornelissen, J. H. C., Klahn, T., van Logtestijn, R. S. P., Broekman, R., Schweikert,
949 W., & Aerts, R. (2009). An experimental comparison of chemical traits and litter
950 decomposition rates in a diverse range of subarctic bryophyte, lichen and vascular
951 plant species. *Journal of Ecology*, *97*(5), 886–900. https://doi.org/10.1111/j.1365-
952 2745.2009.01538.x
953 Lang, S. I., Cornelissen, J. H. C., Shaver, G. R., Ahrens, M., Callaghan, T. V., Molau, U., Ter
954 Braak, C. J. F., Hölzer, A., & Aerts, R. (2012). Arctic warming on two continents has
955 consistent negative effects on lichen diversity and mixed effects on bryophyte diversity.
956 *Global Change Biology*, *18*(3), 1096–1107. https://doi.org/10.1111/J.1365-
957 2486.2011.02570.X
958 Lett, S., Christiansen, C. T., Dorrepaal, E., & Michelsen, A. (2024). Moss species and
959 precipitation mediate experimental warming stimulation of growing season N2 fixation
960 in subarctic tundra. *Global Change Biology*, *30*(7), e17401.
961 https://doi.org/10.1111/GCB.17401

962 Lett, S., Jónsdóttir, I. S., Becker-Scarpitta, A., Christiansen, C. T., During, H., Ekelund, F.,
963 Henry, G. H. R., Lang, S. I., Michelsen, A., Rousk, K., Alatalo, J. M., Betway, K. R., Rui, S.
964 B., Callaghan, T., Carbognani, M., Cooper, E. J., Cornelissen, J. H. C., Dorrepaal, E.,
965 Egelkraut, D., … Zuijlen, K. van. (2022). Can bryophyte groups increase functional
966 resolution in tundra ecosystems? *Arctic Science*, *8*(3), 609–637.
967 https://doi.org/10.1139/as-2020-0057
968 Lindo, Z., & Gonzalez, A. (2010). The bryosphere: An integral and influential component of
969 the Earth's biosphere. *Ecosystems*, *13*(4), 612–627. https://doi.org/10.1007/s10021-
970 010-9336-3
971 Longton, R. (1984). The role of bryophytes in terrestrial ecosystems. *The Journal of the*
972 *Hattori Botanical Laboratory*, *55*, 147–163.
973 Mateo, R. G., Broennimann, O., Normand, S., Petitpierre, B., Araújo, M. B., Svenning, J.-C.,
974 Baselga, A., Fernández-González, F., Gómez-Rubio, V., Muñoz, J., Suarez, G. M., Luoto,
975 M., Guisan, A., & Vanderpoorten, A. (2016). The mossy north: an inverse latitudinal
976 diversity gradient in European bryophytes. *Nature Publishing Group*, *4000*.
977 https://doi.org/10.1038/srep25546
978 Nordli, Ø., Wyszyński, P., Gjelten, H. M., Isaksen, K., Łupikasza, E., Niedźwiedź, T., &
979 Przybylak, R. (2020). Revisiting the extended svalbard airport monthly temperature
980 series, and the compiled corresponding daily series 1898–2018. *Polar Research*, *39*, 1–
981 15. https://doi.org/10.33265/polar.v39.3614
982 Oksanen, J. et al., (2024). *vegan: Community Ecology Package (Version (Version 2.6-6.1)*
983 *[Computer software]*. https://cran.r-project.org/web/packages/vegan/index.html
984 Pajunen, A. M., Oksanen, J., & Virtanen, R. (2011). Impact of shrub canopies on understorey
985 vegetation in western Eurasian tundra. *Journal of Vegetation Science*, *22*(5), 837–846.
986 https://doi.org/10.1111/J.1654-1103.2011.01285.X
987 Papinot Lecomte, B., Pálsson, S., Vilhelmsson, O. Þ., & Jónsdóttír, I. S. (2026). What is hiding
988 within the moss? Assessing the impact of sheep grazing on bryosphere diversity in
989 Icelandic tundra. *Community Ecology*. https://doi.org/10.1007/S42974-026-00329-X
990 Permin, A., Michelsen, A., & Rousk, K. (2022). Direct and indirect effects of warming on moss
991 abundance and associated nitrogen fixation in subarctic ecosystems. *Plant and Soil*,
992 *471*(1–2), 343–358. https://doi.org/10.1007/S11104-021-05245-9/FIGURES/6
993 Ramm, E., Liu, C., Ambus, P., Butterbach-Bahl, K., Hu, B., Martikainen, P. J., Marushchak, M.
994 E., Mueller, C. W., Rennenberg, H., Schloter, M., Siljanen, H. M. P., Voigt, C., Werner, C.,
995 Biasi, C., & Dannenmann, M. (2022). A review of the importance of mineral nitrogen
996 cycling in the plant-soil-microbe system of permafrost-affected soils—changing the
997 paradigm. *Environmental Research Letters*, *17*(1), 013004.
998 https://doi.org/10.1088/1748-9326/AC417E
999 Rantanen, M., Karpechko, A. Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K.,
1000 Vihma, T., & Laaksonen, A. (2022). The Arctic has warmed nearly four times faster than
1001 the globe since 1979. *Communications Earth and Environment*, *3*(1), 1–10.
1002 https://doi.org/10.1038/s43247-022-00498-3
1003 Roos, R. E., van Zuijlen, K., Birkemoe, T., Klanderud, K., Lang, S. I., Bokhorst, S., Wardle, D. A.,
1004 & Asplund, J. (2019). Contrasting drivers of community-level trait variation for vascular
1005 plants, lichens and bryophytes across an elevational gradient. *Functional Ecology*,
1006 *33*(12), 2430–2446. https://doi.org/10.1111/1365-2435.13454
1007 Rousk, K. (2022). Biotic and abiotic controls of nitrogen fixation in cyanobacteria–moss
1008 associations. *New Phytologist*, *235*(4), 1330–1335. https://doi.org/10.1111/NPH.18264

Rzepczynska, A. M., Michelsen, A., Olsen, M. A. N., & Lett, S. (2022). Bryophyte species differ widely in their growth and N2-fixation responses to temperature. *Arctic Science*, *8*(4), 1236–1251. https://doi.org/10.1139/AS-2021-0053/SUPPL_FILE/AS-2021-0053_SUPPLA.DOCX

Schuuring, S., Halvorsen, R., Bronken Eidesen, P., Niittynen, P., Kemppinen, J., & Lang, S. I. (2024). High Arctic Vegetation Communities With a Thick Moss Layer Slow Active Layer Thaw. *Journal of Geophysical Research: Biogeosciences*, *129*(8), e2023JG007880. https://doi.org/10.1029/2023JG007880

Sistla, S. A., Moore, J. C., Simpson, R. T., Gough, L., Shaver, G. R., & Schimel, J. P. (2013). Long-term warming restructures Arctic tundra without changing net soil carbon storage. *Nature*, *497*(7451), 615–618. https://doi.org/10.1038/nature12129

Sorensen, P. L., Lett, S., & Michelsen, A. (2012). Moss-specific changes in nitrogen fixation following two decades of warming, shading, and fertilizer addition. *Plant Ecology*, *213*(4), 695–706. https://doi.org/10.1007/s11258-012-0034-4

Soudzilovskaia, N. A., Bodegom, P. M., & Cornelissen, J. H. C. (2013). Dominant bryophyte control over high-latitude soil temperature fluctuations predicted by heat transfer traits, field moisture regime and laws of thermal insulation. *Functional Ecology*, *27*(6), 1442–1454. https://doi.org/10.1111/1365-2435.12127

Soudzilovskaia, N. A., Graae, B. J., Douma, J. C., Grau, O., Milbau, A., Shevtsova, A., Wolters, L., & Cornelissen, J. H. C. (2011). How do bryophytes govern generative recruitment of vascular plants? *New Phytologist*, *190*, 1019–1031. https://doi.org/10.1111/j.1469-8137.2011.03644.x

Stuart, J. E. M., Holland-Moritz, H., Lewis, L. R., Jean, M., Miller, S. N., McDaniel, S. F., Fierer, N., Ponciano, J. M., & Mack, M. C. (2021). Host Identity as a Driver of Moss-Associated N2 Fixation Rates in Alaska. *Ecosystems*, *24*(3), 530–547. https://doi.org/10.1007/S10021-020-00534-3/FIGURES/4

Stuiver, B. M., Gundale, M. J., Wardle, D. A., & Nilsson, M. C. (2015). Nitrogen fixation rates associated with the feather mosses Pleurozium schreberi and Hylocomium splendens during forest stand development following clear-cutting. *Forest Ecology and Management*, *347*, 130–139. https://doi.org/10.1016/J.FORECO.2015.03.017

Turetsky, M. R. (2003). The Role of Bryophytes in Carbon and Nitrogen Cycling. In *Source: The Bryologist* (Vol. 106, Number 3).

Turetsky, M. R., Bond-Lamberty, B., Euskirchen, E., Talbot, J., Frolking, S., McGuire, A. D., & Tuittila, E. S. (2012). The resilience and functional role of moss in boreal and arctic ecosystems. *New Phytologist*, *196*(1), 49–67. https://doi.org/10.1111/j.1469-8137.2012.04254.x

van Wijk, M. T., Clemmensen, K. E., Shaver, G. R., Williams, M., Callaghan, T. V, Chapin, F. S., Cornelissen, J. H. C., Gough, L., Hobbie, S. E., Jonasson, S., Lee, J. A., Michelsen, A., Press, M. C., Richardson, S. J., & Rueth, H. (2004). Long-term ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, Northern Sweden: generalizations and differences in ecosystem and plant type responses to global change. *Global Change Biology*, *10*(1), 105–123. https://doi.org/10.1111/j.1365-2486.2003.00719.x

van Zuijlen, K., Asplund, J., Sundsbø, S., Dahle, O. S., & Klanderud, K. (2022). Ambient and experimental warming effects on an alpine bryophyte community. *Arctic Science*, *8*(3), 831–842. https://doi.org/10.1139/AS-2020-0047/SUPPL_FILE/AS-2020-0047SUPPLA.DOCX

van Zuijlen, K., Klanderud, K., Dahle, O. S., Hasvik, Å., Knutsen, M. S., Olsen, S. L., Sundsbø, S., & Asplund, J. (2022). Community-level functional traits of alpine vascular plants, bryophytes, and lichens after long-term experimental warming1. *Arctic Science*, *8*(3), 843–857. https://doi.org/10.1139/AS-2020-0007

Volkova, I. I., Volkov, I. V., Morozova, Y. A., Nikitkin, V. A., Vishnyakova, E. K., & Mironycheva-Tokareva, N. P. (2023). Water Holding Capacity of Some Bryophyta Species from Tundra and North Taiga of the West Siberia. *Water 2023, Vol. 15, Page 2626*, *15*(14), 2626. https://doi.org/10.3390/W15142626

Walker, D. A., Raynolds, M. K., Daniëls, F. J. A., Einarsson, E., Elvebakk, A., Gould, W. A., Katenin, A. E., Kholod, S. S., Markon, C. J., Melnikov, E. S., Moskalenko, N. G., Talbot, S. S., & Yurtsev, B. A. (2009). The Circumpolar Arctic vegetation map. *Dx.Doi.Org*, *16*(3), 267. https://doi.org/10.1658/1100-9233(2005)016[0267:TCAVM]2.0.CO;2

Zackrisson, O., DeLuca, T. H., Nilsson, M. C., Sellstedt, A., & Berglund, L. M. (2004). NITROGEN FIXATION INCREASES WITH SUCCESSIONAL AGE IN BOREAL FORESTS. *Ecology*, *85*(12), 3327–3334. https://doi.org/10.1890/04-0461

Zanatta, F., Engler, R., Collart, F., Broennimann, O., Mateo, R. G., Papp, B., Muñoz, J., Baurain, D., Guisan, A., & Vanderpoorten, A. (2020). Bryophytes are predicted to lag behind future climate change despite their high dispersal capacities. *Nature Communications*, *11*(1). https://doi.org/10.1038/s41467-020-19410-8

Supporting information

Content:

Figures:

Tables:

Table S5. Results of Permanova's of the effect of treatment and year on bryophyte species composition in five different in four of the five studied tundra habitats.

Table S6. Results of Permanova's of the effect of treatment and year on bryophyte functional group composition in the five studied tundra habitats.

Supporting figures

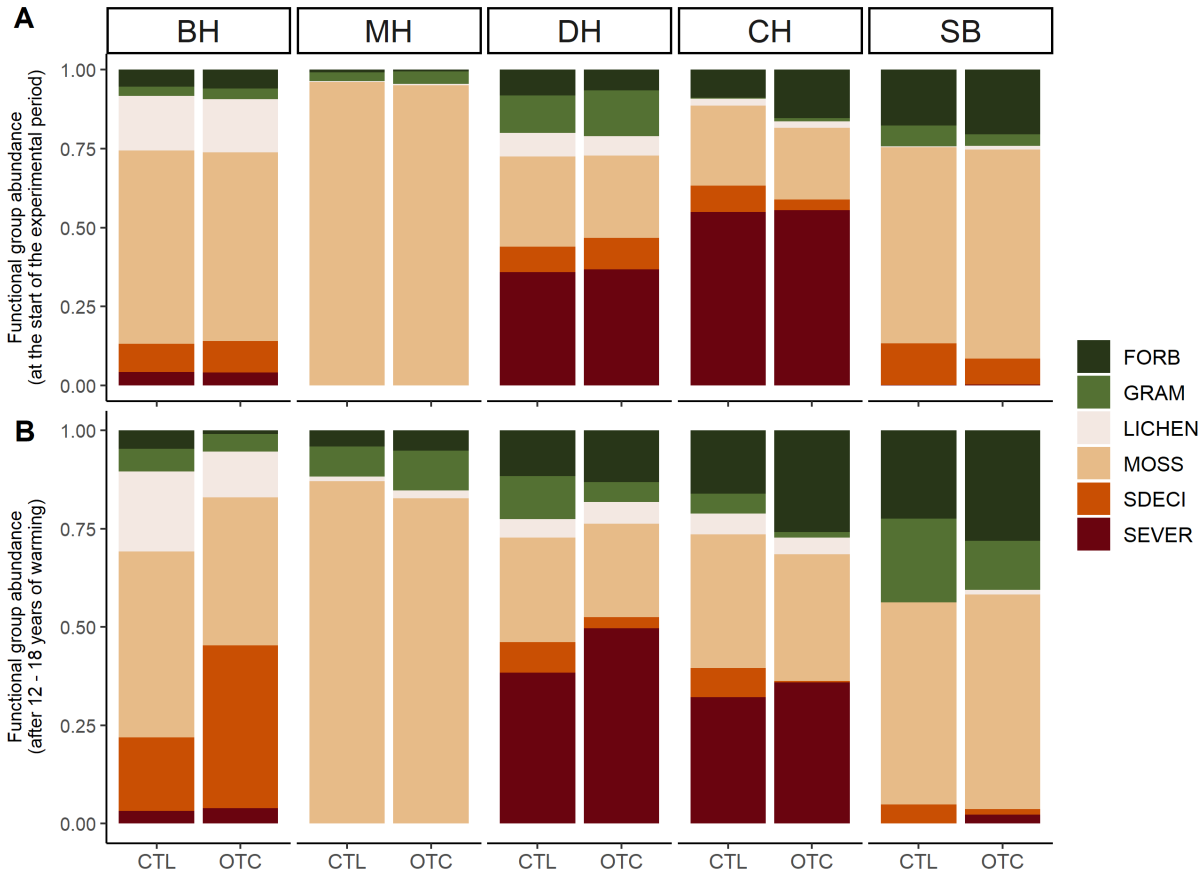

Figure S1. The relative abundance (point intercept hits) of major growth forms (functional groups) within the control (CTL) and experimentally warmed plots (OTC) at the five studied habitats. A) at the start of the experiment and B) after 12-18 years of experimental warming. BM = *Betula nana* heath in the Icelandic highlands, 480 m above sea level; (oro-Arctic); MH = *Racomitrium lanuginosum* moss heath at 120 m altitude in Iceland (sub-Arctic); DH = *Dryas octopetala* heath in high Arctic Svalbard; CH = *Cassiope tetragona* heath in high Arctic Svalbard; SB = snowbed in high Arctic Svalbard. The Icelandic sites, BH and MH, were established in 1996 and 1995, respectively. The Svalbard sites, DH, CH and SB, were all established in 2002. Treatments: CTL = control/ambient temperatures; OTC = experimentally warmed plots. Growth forms: FORBS = herbs other than graminoids; GRAM = graminoids: LICHEN = lichens; MOSS = bryophytes: SDECI = deciduous dwarf-shrubs; SEVER = evergreen dwarf-shrubs. (Data from BH and MH: Jónsdóttir et al. 2005, Jónsdóttir et al., in preparation. Data from DH, CH and SB: Jónsdóttir et al. 2023). Figure credits: Katrín Björnsdóttir.

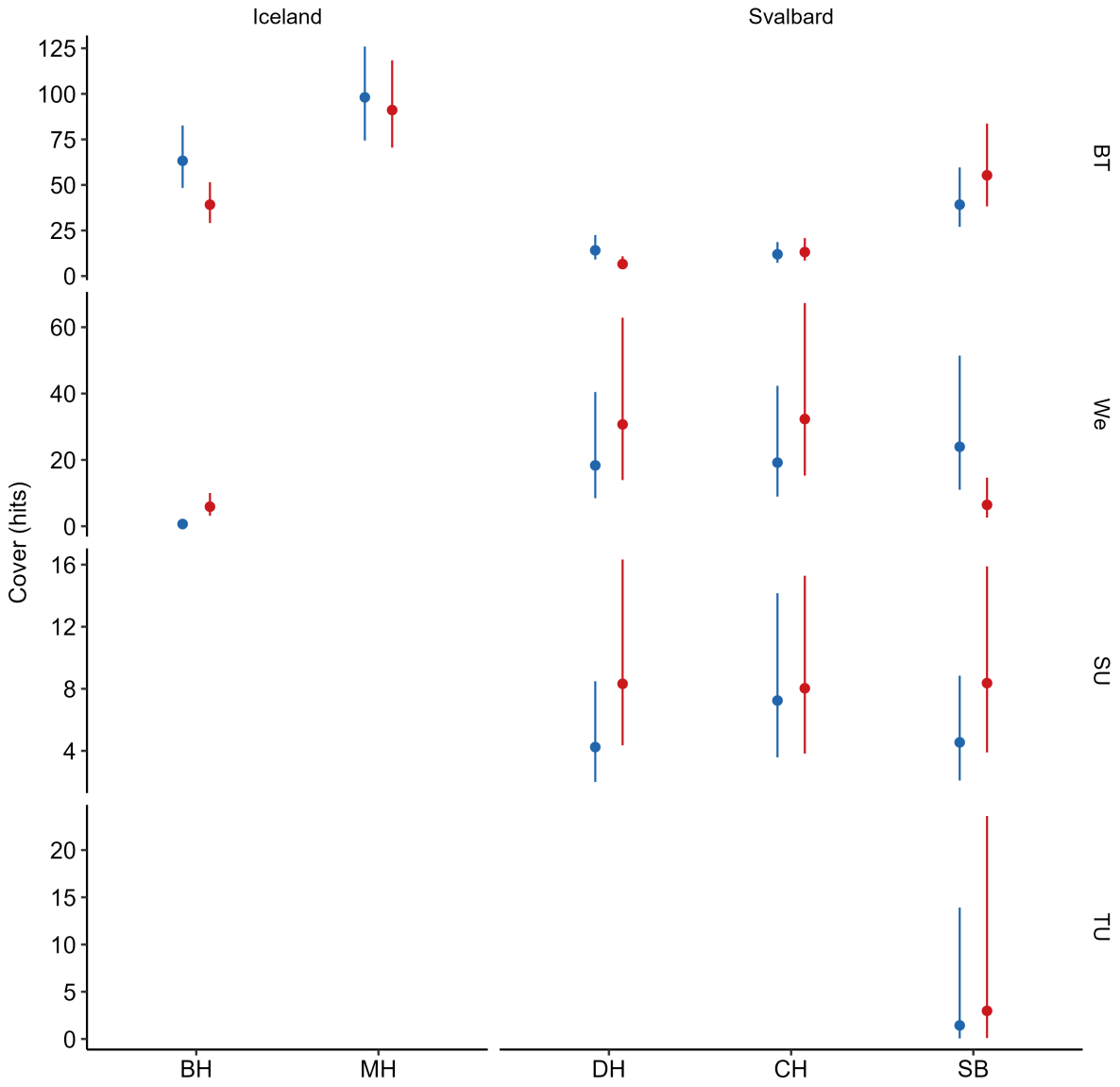

Figure S2. Effects of experimental warming on the cover of the most abundant bryophyte functional groups (BFGs) in the final year of analyses in the five studied tundra habitats. BT=branched turf; We=weft; SU= short unbranched; TU=tall unbranched. Posterior mean and 95% credible intervals based on results from MCMCglmm models. Blue = control plots; red = warmed plots.

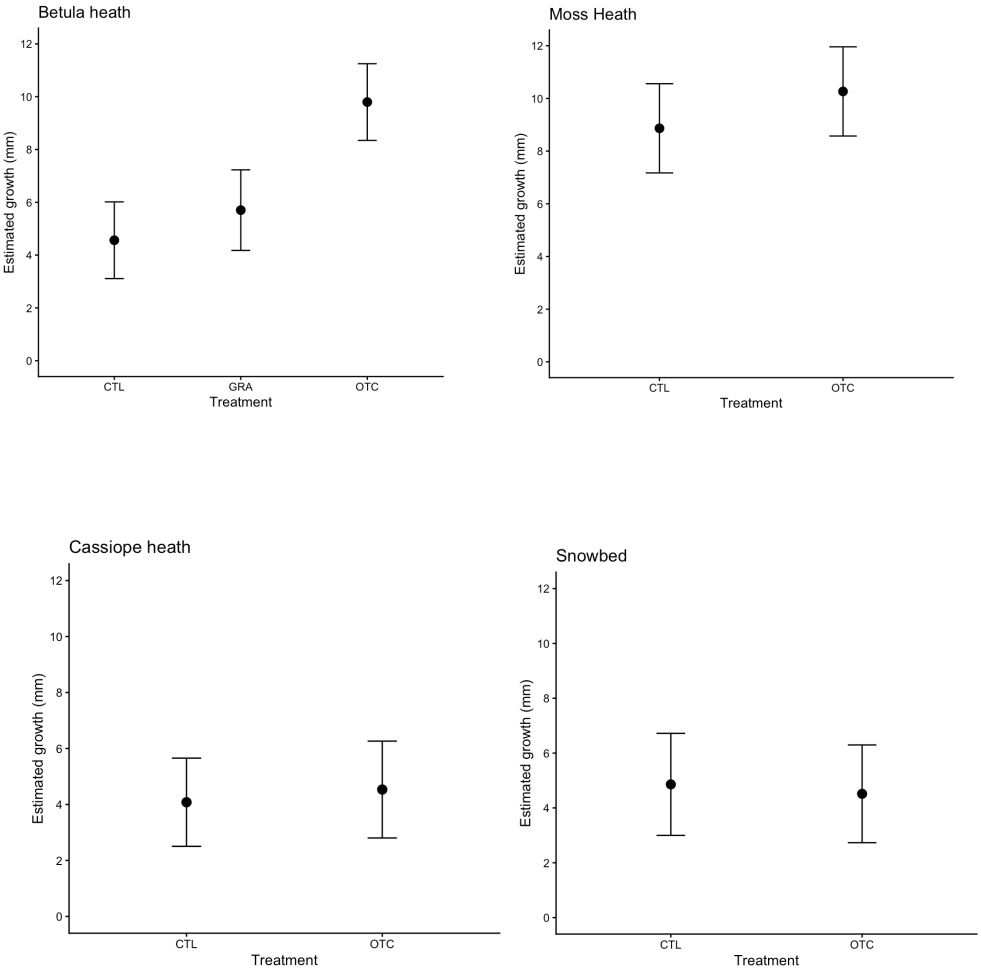

Figure S3. Annual moss growth in four of the studied habitats using cranked wire. The method measures the growth of a collection of moss shoots, (rather than a single shoot) as extension above the horizontal part of the cranked wire one year after installation. The treatment GRA (=grazed) in the *Betula* heath was not considered further in this study. Statistical evaluation: mixed effect model (lmer) with Treatment as a fixed factor and Plot as random (3 measurements per plot).
Betula heath: Contrast estimate (CTL – OTC) = -5.23 ± 1.02 (SE), ***p* <0.0001**
Moss heath: Contrast estimate (CTL – OTC) = -1.4 ± 1.12 (SE), *p*= 0.2118
Cassiope heath: Contrast estimate (CTL – OTC) = -0.453 ± 1.19 (SE), *p*= 0.7042
Snowbed: Contrast estimate (CTL – OTC) = 0.344 ± 1.31 (SE), *p*=0.7934

Supporting Tables

Table S1. Bryophyte taxa recorded in the plant community analyses in the five habitats and their bryophyte functional groups (BFG) *sensu* Lett et al. (2022). BH = *Betula nana* heath in Iceland; MH = moss heath in Iceland; DH = *Dryas* heath in Svalbard; CH = *Cassiope* heath in Svalbard; SB = snowbed in Iceland.

Species	BFG*	BH	MH	DH	CH	SB
Aulacomnium turgidum (Wahlenb.) Schwägr.	SU			X	X	X
Bryum sp.	SU			X	X	X
Campylium stellatum (Hedw.) Lange & C.E.O.Jensen	TU					X
Dicranoweisia crispula (Hedw.) Milde	SC	X				
Dicranum sp.	SU	X		X	X	X
Distichium sp.	SU			X		X
Ditrichum sp.	SU			X		X
Encalypta sp.	SU					X
Hylocomium splendens (Hedw.) Schimp.	We	X		X	X	
Hypnum bambergeri Schimp.	Ma	X				
Hypnum revolutum (Mitt.) Lindb.	Ma			X		
Meesia uliginosa Hedw.	SC				X	
Oncophorus wahlenbergii Brid.	SC					X
Orthotrichum sp.	SC			X	X	
Pohlia sp.	SU	X		X	X	X
Polytrichum alpinum Hedw.	Po	X				
Polytrichum sp.	Po			X	X	
Ptilidium ciliare (L.) Hampe	LL	X			X	
Racomitrium cansecence (Hedw.) Brid.	BT			X	X	
Racomitrium ericoides (Brid.) Brid.	BT	X				
Racomitrium lanuginosum (Hedw.) Brid.	BT	X	X	X	X	
Racomitrium sp.	BT	X				
Sanionia uncinata (Hedw.) Loeske	We	X		X	X	X
Tomentypnum nitens (Hedw.) Loeske	BT	X		X	X	X
Tortula sp.	SU			X		
Leafy liverwort, unidentified	LL			X	X	X

*LL = leafy liverwort; Po = Polytrichales; SC = small cushion; SU = short unbranched turf; TU = tall unbranched turf; We = weft; Ma = mat; BT = branched turf.

Table S2. Overview of the raw data used in this paper and when collected at the five tundra habitats

	Iceland		**Svalbard**		
	***Betula* heath**	**Moss heath**	***Dryas* heath**	***Cassiope* heath**	**Snowbed**
Point-intercept data	1997, 2000, 2007, 2015, 2019	1995, 1998, 2000, 2007, 2014, 2019	2003, 2009, 2015	2003, 2009, 2015	2003, 2009, 2015
Bryophyte layer depth	2014, 2019	2014, 2019	2015	2015	2015
Annul shoot growth	2014-2015	2014-2015	2014-2015	2014-2015	2014-2015
N_2 fixation	2014, June, July, August	2014, June, July, August	2013 early August	2013 early August	2013 early August
Water holding capacity and colony density	2020	2020			

Table S3. The vascular plant variables (mean ± SD) used in regression analysis for bryophyte cover and layer depth.

Locatio	Habitat	Year	Treatment	Canopy height (cm)	Deciduous shrub abundance (hits)	Evergreen shrub abundance (hits)	Shrub abundance (hits)	Litter abundance (hits)
Iceland	BH	2019	CTL	2.19 ± 1.75	42.60 ± 40.91	17.10 ± 16.68	59.70 ± 56.85	26.30 ± 17.85
Iceland	BH	2019	OTC	13.53 ± 5.01	191.40 ± 57.09	32.40 ± 18.61	223.80 ± 65.96	53.90 ± 28.14
Iceland	MH	2019	CTL	0.55 ± 0.38	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	11.40 ± 8.40
Iceland	MH	2019	OTC	0.82 ± 0.73	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	30.30 ± 21.51
Svalbard	DH	2015	CTL	1.13 ± 0.18	13.00 ± 6.00	68.00 ± 18.21	81.00 ± 21.01	63.00 ± 7.35
Svalbard	DH	2015	OTC	1.73 ± 0.60	6.80 ± 4.76	112.20 ± 20.61	119.00 ± 23.39	75.60 ± 6.66
Svalbard	CH	2015	CTL	1.29 ± 0.55	9.20 ± 5.76	43.60 ± 41.20	52.80 ± 44.80	67.40 ± 5.86
Svalbard	CH	2015	OTC	2.17 ± 1.48	1.80 ± 2.05	66.40 ± 100.33	68.20 ± 101.51	59.80 ± 14.20
Svalbard	SB	2015	CTL	1.09 ± 0.56	6.40 ± 5.22	0.00 ± 0.00	6.40 ± 5.22	40.80 ± 14.70
Svalbard	SB	2015	OTC	1.26 ± 0.14	3.40 ± 1.14	2.40 ± 4.34	5.80 ± 4.76	38.40 ± 23.48

Table S4. Multiple regression models for effects of vascular plant variables on moss cover and moss depth in the five studied tundra habitats. BH=*Betula* heath; MH= moss heath; DH=*Dryas* heath; CH=*Cassiope* heath; SB snowbed. Data for warmed and ambient plots are combined. Significant predictors are shown in bold.

		Predictors	*Estimates*	*SE*	*CI*	*Statistic*	*p*
Bryophyte cover	BH 2014	Intercept	73.14	4.38	63.79 – 82.48	16.68	**<0.001**
		Litter abundance	-1.27	0.34	-2.00 – -0.54	-3.69	**0.002**
		Canopy height	1.37	0.90	-0.54 – 3.29	1.53	0.147
		Shrub abundance	1.42	0.84	-0.37 – 3.20	1.69	0.111
		Deciduous shrub abundance	-1.46	0.87	-3.32 – 0.40	-1.68	0.114
		Observations	20				
		R2 / R2 adjusted	0.697 / 0.617				
Bryophyte cover	BH 2019	Intercept	78.57	4.66	68.65 – 88.50	16.88	**<0.001**
		Litter abundance	-0.50	0.21	-0.95 – -0.04	-2.34	**0.033**
		Canopy height	2.87	1.78	-0.93 – 6.68	1.61	0.128
		Shrub abundance	0.37	0.25	-0.17 – 0.91	1.46	0.164
		Deciduous shrub abundance	-0.63	0.35	-1.39 – 0.12	-1.79	0.094
		Observations	20				
		R^2 / R^2 adjusted	0.618 / 0.516				
Bryophyte cover	MH 2014	Intercept	99.01	1.21	96.46 – 101.56	81.93	**<0.001**
		Litter abundance	-0.64	0.13	-0.92 – -0.37	-4.93	**<0.001**
		Canopy height	1.67	1.24	-0.95 – 4.29	1.35	0.196
		Observations	20				
		R2 / R2 adjusted	0.624 / 0.580				
Bryophyte cover	MH 2019	Intercept	98.65	1.23	96.05 – 101.24	80.18	**<0.001**
		Canopy height	1.89	1.95	-2.21 – 6.00	0.97	0.344
		Litter abundance	-0.25	0.06	-0.38 – -0.12	-4.11	**0.001**
		Observations	20				
		R^2 / R^2 adjusted	0.600 / 0.553				
Bryophyte cover	MH 2019	Intercept	99.99	1.84	96.10 – 103.88	54.45	**<0.001**

			1.04	2.13	-3.49 – 5.56	0.49	0.634
Without outlier (litter abundance 88)		Canopy height					
		Litter abundance	-0.30	0.08	-0.48 – -0.13	-3.73	**0.002**
		Observations	19				
		R^2 / R^2 adjusted	0.468 / 0.401				
Bryophyte cover	DH 2015	Intercept	13.29	47.88	-109.78 – 136.37	0.28	0.792
	Model NS	Canopy height	-16.41	15.94	-57.37 – 24.56	-1.03	0.350
		Litter abundance	1.01	0.84	-1.16 – 3.18	1.20	0.283
		Deciduous shrub abundance	-0.36	0.94	-2.76 – 2.05	-0.38	0.720
		Shrub abundance	-0.06	0.23	-0.65 – 0.53	-0.27	0.797
		Observations	10				
		R^2 / R^2 adjusted	0.268 / -0.317				
Bryophyte cover	CH 2015	Intercept	44.06	26.66	-24.48 – 112.61	1.65	0.159
	Model NS	Canopy height	9.28	4.58	-2.49 – 21.05	2.03	0.099
		Litter abundance	0.03	0.40	-1.01 – 1.07	0.07	0.946
		Deciduous shrub abundance	-0.90	0.56	-2.35 – 0.55	-1.60	0.171
		Shrub abundance	-0.10	0.10	-0.35 – 0.15	-1.04	0.345
		Observations	10				
		R^2 / R^2 adjusted	0.702 / 0.463				
Bryophyte cover	SB 2015	Intercept)	112.41	28.39	39.42 – 185.39	3.96	**0.011**
	Model NS	Canopy height	-17.09	13.05	-50.63 – 16.46	-1.31	0.247
		Litter abundance	-0.03	0.25	-0.67 – 0.61	-0.13	0.900
		Shrub abundance	-1.38	1.50	-5.23 – 2.46	-0.92	0.398
		Evergreen shrub abundance	1.61	1.72	-2.82 – 6.04	0.93	0.394
		Observations	10				
		R^2 / R^2 adjusted	0.309 / -0.244				

Bryophyte depth	BH 2014	Intercept	11.42	0.64	10.05 – 12.79	17.77	**<0.001**
		Litter abundance	-0.10	0.05	-0.21 – 0.01	-2.00	0.064
		Canopy height	0.14	0.13	-0.14 – 0.42	1.08	0.298
		Shrub abundance	-0.27	0.12	-0.53 – -0.01	-2.21	**0.043**
		Deciduous shrub abundance	0.23	0.13	-0.04 – 0.50	1.81	0.091
		Observations	20				
		R^2 / R^2 adjusted	0.786 / 0.729				
Bryophyte depth	BH 2019	Intercept	8.33	0.61	7.02 – 9.63	13.57	**<0.001**
		Litter abundance	-0.06	0.03	-0.12 – 0.00	-2.04	0.059
		Canopy height	0.50	0.24	-0.00 – 1.00	2.13	0.050
		Shrub abundance	0.06	0.03	-0.01 – 0.13	1.87	0.081
		Deciduous shrub abundance	-0.11	0.05	-0.21 – -0.01	-2.38	**0.031**
		Observations	20				
		R^2 / R^2 adjusted	0.647 / 0.553				
Bryophyte depth	MH 2014	Intercept	13.26	0.76	11.65 – 14.87	17.33	**<0.001**
		Litter abundance	0.19	0.08	0.02 – 0.37	2.33	**0.032**
		Canopy height	-2.00	0.79	-3.66 – -0.34	-2.54	**0.021**
		Observations	20				
		R^2 / R^2 adjusted	0.306 / 0.225				
Bryophyte depth	MH 2019	Intercept	15.66	0.68	14.23 – 17.09	23.12	**<0.001**
	Model NS	Litter abundance	0.05	0.03	-0.03 – 0.12	1.36	0.191
		Canopy height	-1.86	1.07	-4.12 – 0.40	-1.74	0.100
		Observations	20				
		R^2 / R^2 adjusted	0.152 / 0.052				
Bryophyte depth	DH 2015	Intercept	1.99	0.62	0.52 – 3.45	3.21	0.015
	Model NS	Canopy height	-0.45	0.34	-1.24 – 0.35	-1.33	0.226
		Deciduous shrub abundance	-0.05	0.03	-0.12 – 0.02	-1.76	0.121
		Observations	10				
		R^2 / R^2 adjusted	0.380 / 0.203				

Bryophyte depth	CH 2015	Intercept	5.85	0.69	4.27 – 7.43	8.54	**<0.001**
		Deciduous shrub abundance	-0.24	0.09	-0.45 – -0.04	-2.71	**0.027**
		Observations	10				
		R^2 / R^2 adjusted	0.478 / 0.413				
Bryophyte depth	CH 2015	Intercept	9.3	2.39	3.16 – 15.44	3.89	**0.012**
	Model NS	Litter abundance	-0.04	0.02	-0.09 – 0.02	-1.84	0.126
		Canopy height	-1.24	1.1	-4.06 – 1.59	-1.13	0.311
		Shrub abundance	0.26	0.1	0.01 – 0.52	2.69	**0.043**
		Deciduous shrub abundance	-0.34	0.15	-0.72 – 0.03	-2.37	0.064
		Observations	10				
		R^2 / R^2 adjusted	0.715 / 0.487				

Table S5. Results of Permanova's of the effect of treatment and year on bryophyte species composition in five different in four of the five studied tundra habitats – the moss heath (MH) only had a single species. BH=*Betula* heath; DH=*Dryas* heath; CH=*Cassiope* heath; SB snowbed.. Significant predictors are shown in bold. Homogeneity of multivariate dispersions (betadisper) was tested before PERMANOVA analysis; p-values > 0.05 indicate equal variance assumption is met.

Habitat		DF	Sum of Squares	R2	F	P	Homogeneity P
BH	**Year**	1	0.1888	**0.05455**	6.0345	**0.006799**	0.052
	Treatment	1	0.2372	**0.06855**	7.5825	**0.001200**	**0.002**
	Residual	97	3.0350	0.87690			
DH	**Year**	1	0.7944	**0.19941**	7.2216	**9.999e-05**	**0.006**
	Treatment	1	0.2193	0.05504	1.9933	0.07369	0.419
	Residual	27	2.9700	0.74555			
CH	**Year**	1	0.6185	**0.16792**	5.7978	**9.999e-05**	0.378
	Treatment	1	0.1846	0.05011	1.7303	0.121	0.809
	Residual	27	2.8801	0.78197			
SB	Year	1	0.11593	0.04222	1.3287	0.2538	0.692
	Treatment	1	0.27445	**0.09994**	3.1456	**0.0435**	0.374
	Residual	27	2.35571	0.85784			

Table S6. Results of Permanova's of the effect of treatment and year on bryophyte functional group composition in the five studied tundra habitats. BH=*Betula* heath; MH= moss heath; DH=*Dryas* heath; CH=*Cassiope* heath; SB snowbed. Significant predictors are shown in bold.

Habitat		DF	Sum of Squares	R2	F	P	Homogeneity
BH	**Year**	1	0.1847	**0.05642**	6.3154	**0.006399**	0.069
	Treatment	1	0.2519	**0.07965**	8.6133	**0.0015**	**0.002**
	Residual	99	2.8364	0.86662			
DH	**Year**	1	0.66193	**0.22791**	8.8774	**9.999e-05**	**0.013**
	Treatment	1	0.22917	**0.07891**	3.0734	**0.0215**	0.452
	Residual	27	2.0132	0.69318			
CH	**Year**	1	0.41935	**0.16146**	5.5757	**0.0014**	0.104
	Treatment	1	0.14719	0.05667	1.957	0.1204	0.616
	Residual	27	2.03069	0.78187			
SB	Year	1	0.03081	0.01255	0.3823	0.71463	0.642
	Treatment	1	0.24869	0.10127	3.0855	0.05339	0.289
	Residual	27	2.17614	0.88618			