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RESEARCH ARTICLE

Moss species and precipitation mediate experimental warming stimulation of growing season N_2 fixation in subarctic tundra

Signe Lett[1,2] | Casper T. Christiansen[1,2] | Ellen Dorrepaal[3] | Anders Michelsen[1,2]

[1]Terrestrial Ecology Section, Department of Biology, University of Copenhagen, Copenhagen, Denmark

[2]Center for Permafrost (CENPERM), University of Copenhagen, Copenhagen, Denmark

[3]Climate Impacts Research Centre, Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden

Correspondence
Signe Lett, Terrestrial Ecology Section, Department of Biology, University of Copenhagen, DK-2100 Copenhagen, Denmark.
Email: signe.lett@bio.ku.dk; signelett@gmail.com

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Abstract

Climate change in high latitude regions leads to both higher temperatures and more precipitation but their combined effects on terrestrial ecosystem processes are poorly understood. In nitrogen (N) limited and often moss-dominated tundra and boreal ecosystems, moss-associated N_2 fixation is an important process that provides new N. We tested whether high mean annual precipitation enhanced experimental warming effects on growing season N_2 fixation in three common arctic-boreal moss species adapted to different moisture conditions and evaluated their N contribution to the landscape level. We measured in situ N_2 fixation rates in *Hylocomium splendens*, *Pleurozium schreberi* and *Sphagnum* spp. from June to September in subarctic tundra in Sweden. We exposed mosses occurring along a natural precipitation gradient (mean annual precipitation: 571–1155 mm) to 8 years of experimental summer warming using open-top chambers before our measurements. We modelled species-specific seasonal N input to the ecosystem at the colony and landscape level. Higher mean annual precipitation clearly increased N_2 fixation, especially during peak growing season and in feather mosses. For *Sphagnum*-associated N_2 fixation, high mean annual precipitation reversed a small negative warming response. By contrast, in the dry-adapted feather moss species higher mean annual precipitation led to negative warming effects. Modelled total growing season N inputs for *Sphagnum* spp. colonies were two to three times that of feather mosses at an area basis. However, at the landscape level where feather mosses were more abundant, they contributed 50% more N than *Sphagnum*. The discrepancy between modelled estimates of species-specific N input via N_2 fixation at the moss core versus ecosystem scale, exemplify how moss cover is essential for evaluating impact of altered N_2 fixation. Importantly, combined effects of warming and higher mean annual precipitation may not lead to similar responses across moss species, which could affect moss fitness and their abilities to buffer environmental changes.

KEYWORDS
alpine ecosystem, arctic-boreal bryophytes, *Hylocomium splendens*, landscape scale, moisture, *Pleurozium schreberi*, *Sphagnum*, temperature

1 | INTRODUCTION

Plant primary production in boreal, subarctic and arctic ecosystems is generally N limited (Du et al., 2020), as anthropogenic N deposition is low and low temperatures restrict microbial N recycling (Li et al., 2020; Nadelhoffer et al., 1992; Salazar et al., 2020). Consequently, N input via biological fixation by moss-associated bacteria can amount to quantities close to annual tundra plant requirements (Rousk et al., 2016; Rousk, Sorensen, & Michelsen, 2017) and is therefore a key component in the N budget of arctic ecosystems (DeLuca et al., 2002; Rousk et al., 2015; Stewart et al., 2011). As N_2 fixation is a moisture and temperature sensitive process, N_2 fixation rates can be expected to increase with projected increases in precipitation and temperatures in cold ecosystems (Bintanja & Andry, 2017; IPCC, 2021). However, higher temperatures can reduce moisture availability, which may instead hamper moss-associated N_2 fixation (Deslippe et al., 2005; Sorensen et al., 2012). Moss species differ in their sensitivity to changes in temperature and moisture (Furness & Grime, 1982; Stuiver et al., 2014) Their associated N_2 fixation might therefore respond differently to the expected changes in climate (Bintanja & Andry, 2017). A crucial prerequisite for quantifying changes in large-scale ecosystem N input via mosses in a future climate is therefore to understand how the combined, and likely interacting, effects of changes in temperature and precipitation depend on moss characteristics, but so far this has not been accomplished in situ.

Biological N_2 fixation rates are theoretically directly enhanced by warming and the temperature optimum for nitrogenase, the enzyme fixing N, varies and can be as high as 40°C (Stal, 2017; Zielke et al., 2002). However, in situ, higher temperatures are often associated with drier conditions and the availability of moisture is a prerequisite for N_2 fixation (Reed et al., 2011). As a result, ecosystems subjected to experimental warming or peak growing season conditions often show decreased or stagnant N_2 fixation rates (Gundale et al., 2009; Sorensen et al., 2012). Alleviating water stress by short-term experimental water addition alone can increase moss N_2 fixation rates more than warming of 1–2°C alone (Rousk et al., 2018) and tissue moisture content sometimes influences warming responses in moss-associated N_2 fixation in vitro (Rousk, Pedersen, et al., 2017). However, projecting the effects of future climate change requires studies that include climate factors such as temperature and precipitation separately and in combination (Dormann & Woodin, 2002). Furthermore, seasonal variation in climate and moss moisture status throughout the season may affect the susceptibility to changes in temperature and precipitation over time. How realistic precipitation scenarios modify warming impacts on moss-associated N_2 fixation input is not known.

Mosses are poikilohydric plants, which means that they cannot actively regulate their tissue water content. However, moss species vary in their sensitivity to drought and in the functional traits that determine their tissue moisture content. As a consequence, they also differ in their preferred habitat (Elumeeva et al., 2011; Lett et al., 2022). As moisture is a prerequisite for N_2 fixation, warming may promote N_2 fixation more in species that can maintain a higher moisture content than in species that easily dry out (Stewart et al., 2011; Stuart, Holland-Moritz, et al., 2020). Conversely, however, such moss species that have a higher water holding capacity may be less affected by changes in precipitation than species that dry out faster. Although it is well recognised that moss moisture is essential for N_2 fixation, we do not know how the interacting effect of warming and precipitation regime affects N_2 fixation rates across moss species in their natural habitats across the tundra landscape.

Contribution of moss-associated N_2 fixation to the ecosystem N input depends on species-specific fixation rates, moss species dominance in the ecosystem and likely the seasonal variation in climate (Lett & Michelsen, 2014; Rousk et al., 2015; Stuart, Holland-Moritz, et al., 2020). While species-specific in situ N_2 fixation rates are relatively easy to obtain, moisture and temperature conditions in the moss layer may change across the growing season and point measurements of N_2 fixation might not fully describe N_2 fixation cumulative rates. Further, species-specific cover estimates at a scale larger than the plot or site scale are few and difficult to obtain as mosses are difficult to identify to species and notoriously overlooked (but see Rzepczynska et al., 2022). Modelled rates combined with high temporal resolution field microclimate data can resolve this issue and provide estimates of seasonal N input. Combined with species distribution data, seasonal N_2 fixation estimates would yield meaningful estimates of N_2 fixation across time and space in heterogeneous tundra ecosystems. Species-specific N_2 fixation rates and temperature sensitivity could in principle be incorporated into functional models such as dynamic vegetation models where mosses currently due to lack of data are rarely included even as a separate functional group (Lett et al., 2022; Porada et al., 2023; St. Martin & Mallik, 2017).

The aim of this study was to investigate the combined, and likely interacting, effects of warming, variation in precipitation, and differences in moss species identity and characteristics on N_2-fixation associated to moss colonies in tundra. We hypothesised that because N_2 fixation rates are highly moisture and temperature-dependent (1) higher mean annual precipitation will amplify experimental warming-induced increases in N_2 fixation rates. We further hypothesised that (2) the positive effect of high mean annual precipitation on the effect of experimental warming will be more pronounced in species known to have lower moss moisture holding capacity and under dry conditions, that is during warm, peak growing season periods. To test our hypotheses, we measured in situ N_2 fixation at the colony scale throughout the growing season in three common, dominant arctic—boreal moss species, that is *H. splendens*, *P. schreberi* and *Sphagnum* spp. At the each of eight sites distributed along a gradient of mean annual precipitation in subarctic Sweden, alpine tundra patches dominated by one of each of the moss species were subjected to eight summers of experimental warming before our measurement, using open-top chambers (Lett et al., 2020). We also measured moss microclimatic conditions in the experiment input to model species- and climate-specific N_2 fixation. We modelled colony scale N_2 fixation input and combined these with literature cover estimates

for the species to evaluate the potential impacts of our results at the landscape scale. Investigating the interacting effects of moisture and temperature in important arctic-boreal moss species will improve understanding of moss functioning and predictions of input of N into heterogeneous tundra landscape under realistic future climate scenarios.

2 | MATERIALS AND METHODS

2.1 | Site description and experimental design

The study took place above the natural subarctic-alpine treeline (570–755 m asl.) in Northern Sweden (N68°18′–68°31′, E18°12′–18°54′). The study included eight sites distributed along a 35 km-long precipitation gradient in the Torneträsk catchment area (Figure S1). Mean annual precipitation varied from 571 mm $year^{-1}$ at the driest site close to Paddus sites to 1155 mm $year^{-1}$ at the wettest site westwards towards the Norwegian boarder (gridded data 4 × 4 km pixels, Swedish Meteorological and Hydrological Institute, SMHI, 1961–1990, Table 1). Rainfall during the measurement period in 2018 (June–September) was 287 mm at Abisko meteorological station (dry end of gradient) and 857.5 mm at Katterjåkk meteorological station (wet end of gradient, SMHI, Figure S2). Mean annual precipitation correlated with number of days with rain events measured at each site in 2014 ($p = .038$, $R^2 = .53$, Figure S3). Approximately 50% of the annual precipitation falls as snow (SMHI) and annual N deposition is <1 kg ha^{-1} $year^{-1}$ for this area (Ferm et al., 2019). Local site vegetation varied but was typical treeless tundra-heath, with the presence of dwarf shrubs such as *Empetrum hermaphroditum* Hagerup, *Betula nana* L. and *Salix* spp. and a high dominance of bryophytes (Table 1; Lett et al., 2020).

At each site in 2011, six plots were established in patches dominated by one of three dominant moss species, *Hylocomium splendens* (Hedw.) Schimp., *Pleurozium schreberi* (Brid.) Mitt. and *Sphagnum* spp. (including *S. capillifolium* (Ehrh.) Hedw. and *S. fuscum* (Schimp.)). For each moss species, one plot was left as control, and one was subjected to experimental warming each year from late June until late September (8 years before the start of this study). Plots were passively warmed through hexagonal Perspex open-top chambers, OTCs (MacroLife, Arla plast, Sweden), which is a standardised method to simulate climate warming across tundra ecosystems (Hollister et al., 2022; Marion et al., 1997). The chambers were 40 cm tall and covered a hexagonal area of 2.35 m^2 (diameter of 165 cm × 180 cm, and 0.95 m^2 exposed area in the centre). Control plots had the same shape and dimensions as the warmed plots. One half of each hexagonal plot had all moss biomass removed manually at the initiation of the experiment, while the other half of each plot was left untouched. For our current study, we ignored the plot halves without mosses and only included plot halves with an intact

TABLE 1 Site conditions at the eight sites in the mean annual precipitation gradient (modified from Lett et al., 2020).

Site name	Precipitiation[a] (mm $year^{-1}$)	Elevation (m a.s.l.)	Aspect	Vascular plant cover[b] (%)	Dominant vascular plants[b]
Jieprenjåkk 2	571	750	S	182	*Salix* sp., *Empetrum hermaphroditum*, *Betula nana*, *V. myrtillus*, *Eleocharis uniglumis*, *Equisitum palustre*
Paddus 1	653	775	N	176	*E. hermaphroditum*, *Andromeda polifolia*, *Vaccinium uliginosum*, *Pedicularis flammea*, *Calamagrostis stricta*, *Festuca ovina*
Paddus 2	653	705	N	194	*E. hermaphroditum*, *Vaccinium vitis-idaea*, *B. nana*, *Salix* sp., *Equisitum arvense*, *Pedicularis lapponica*, *Lycopodium annotinum*, *Carex stricta*
Jieprenjåkk 1	755	740	S	187	*Salix* sp., *Empetrum hermaphroditum*, *Vaccinium myrtillus*, *Carex* sp., *Festuca ovina*, *Equisitum pratense*
Pålnoviken 2	811	660	S	171	*E. hermaphroditum*, *B. nana*, *V. myrtillus*, *Rubus chamaemorus*, *Cornus suecica*, *Equisitum sylvaticum*, *F. ovina*
Pålnoviken 1	1090	750	E	191	*Salix lanata*, *V. uliginosum*, *E. hermaphroditum*, *Bartsia alpina*, *P. lapponica*, *Festuca vivipara*, *Carex* sp.
Katterjåkk	1155	550	NW	184	*E. hermaphroditum*, *V. myrtillus*, *B. nana*, *Cornus suecica*, *Rubus chamaemorus*, *P. lapponica*, *Carex nigra*
Vassijaure	1155	570	N	171	*E. hermaphroditum*, *V. uliginosum*, *V. myrtillus*, *A. polifolia*, *R. chamaemorus*, *C. suecica*, *Deschampsia flexuosa*, *Carex* sp.

[a]Mean annual precipitation (1961–1991), gridded data Swedish Meteorological and Hydrological Institute 4 × 4 km pixels.
[b]Point intercept measurement from July 2014.

moss carpet. The used plot halves with mosses are onwards referred to as 'plots'. In this way, each site represented a level of mean annual precipitation in the gradient and included a full set of combination of moss species and warming treatment. This setup resulted in a total of 48 plots for this study. For more detailed descriptions of the sites, see Lett et al. (2020).

2.2 | Estimation of N_2 fixation in situ

On the first sampling date in June 2018, a moss core of 5 cm diameter was taken to a depth of 6 cm in each plot. For *Sphagnum* spp., the core usually only consisted of living moss, whereas for *H. splendens* and *P. schreberi*, the bottom 1–2 cm was organic soil. In warmed plots, moss cores were taken within the centre of the plot, to make sure they were not rain sheltered by the sides of the OTCs. Each core was placed in an open nylon mesh bag (50 µm mesh size; Sintab, Sweden) and placed in the hole of its original position in the moss layer between measurements (following Sorensen et al., 2012). The mesh 'bags' thus enabled repeated handling of the small moss cores for N_2 fixation measurements, while allowing for natural contact and moisture exchange with the surrounding moss carpet as well as exposure to natural light and temperature in between measurements.

To determine N_2 fixation, we used the acetylene reduction assay (Stewart et al., 1967). This method estimates the activity of the enzyme nitrogenase, which is responsible for the process of N_2 fixation. Like atmospheric nitrogen (N_2), acetylene (C_2H_2) has a triple bond. Nitrogenase can therefore also reduce acetylene to ethylene (C_2H_4), and even small changes in concentration of both gasses can be analysed via simple gas chromatography. In addition to being relatively inexpensive, this non-destructive method is preferred for repeated measurements over time on the same moss colony as in this study (Lett & Michelsen, 2014; Saiz et al., 2019). Substrate-specific conversion factors between ethylene production and N_2 fixation allows for calculating N_2 fixation in the samples (see below).

At all sites, in situ acetylene reduction assays (ARA) were performed five times during the growing season 2018 (14 June–21 September), except at two of the low precipitation sites, which could not be visited during the first sampling campaign in June due to exceptionally bad weather. As the eight sites are distributed over a large area, they were usually visited sequentially in a random order within 4–6 days, although one July campaign was spread over 10 days. At each sampling time, the mesh bags containing moss cores were incubated individually with approx. Ten per cent acetylene in transparent PVC jars (0.5 L) placed for 2 h inside the plot they belonged to during incubation. Acetylene was developed inside the jar from calcium carbide by adding water with a syringe through a rubber septum in the lid. Through the rubber septum, we also took gas samples with a syringe at three time points in duplicates, which we transferred to evacuated 5.9 mL vials (Exetainers® Labco, Ceredigion, UK). Vials were stored for a maximum of 2 months until analysis for acetylene and ethylene production on a gas chromatograph (SRI 310C, FID, SIR Instruments, California).

Temperature in the moss core was measured before and after each incubation with a handheld thermometer and averaged to estimate mean incubation temperature at 3 cm depth. Before each incubation, mosses were weighed on a field scale to later determine gravimetric moisture content.

2.3 | Climate chamber incubations for converting from ethylene production to N_2 fixation

Nitrogenase can reduce acetylene instead of N_2, at a theoretical conversion factor of 4.0 mol C_2H_2 per mol N_2 reduced at acetylene-saturated conditions (Mulholland et al., 2004). However, this conversion factor can depend on the microbial community present within the moss shoots (Leppänen et al., 2013; Moisander et al., 1996). To determine the conversion factor between ARA and actual N_2 fixation for our three moss species, all 48 moss cores were brought to Copenhagen after the last field sampling. Moss cores were transported in individual specimen cups that kept field moisture conditions and were acclimatised under controlled conditions in climate-regulated growth chambers for 3 days at 7°C and ~300 µmol m^{-2} s^{-1} photosynthetic active radiation, a daylength of 18 and 6 h darkness. After acclimatisation, mosses were incubated to determine N_2 fixation, first with ARA and then by labelling with $^{15}N_2$. Before $^{15}N_2$ incubations, a smaller subsample representing the whole depth of the moss core was taken from each moss core to determine their natural abundance of ^{15}N. For ARA and $^{15}N_2$ incubations, mosses placed in transparent polypropylene specimen cups (162 mL) were incubated at the same conditions as during acclimatisation. With a syringe, 10 mL of air was replaced with either acetylene (Air Liquide) or N_2 (>99.9% N_2, of which 99.2% was $^{15}N_2$; Eurisotop, Saint Aubin, France). For ARA and the $^{15}N_2$ labelling, incubation times were 3 and 23 h, respectively, with lights off for 45 min and 6 h (25% of the time), respectively. The longer incubation time for $^{15}N_2$ labelling was chosen to ensure sufficient $^{15}N_2$ labelling.

2.4 | Chemical analyses of moss tissue

After climate chamber incubations, natural abundance and ^{15}N subcores were divided into three horizontal layers for chemical analyses and biomass determination. For feather mosses (*H. splendens* and *P. schreberi*), these layers were the green top 2 cm (moss shoot), the brown layer and the soil. For *Sphagnum*, this was the 0–1 cm (capitula), the 1–2 cm and the 2–6 cm layers (unless there was a distinct soil layer in which case an extra layer was included). The reason for the extra top layer in *Sphagnum* was that the capitula of *Sphagnum* mosses create a dense surface, through which light will not penetrate. N_2 fixation and the factors affecting it are therefore likely primarily present in the moss shoot or capitula. Finally, all fractions of moss cores were freeze-dried, weighed and homogenised.

To determine core ^{15}N enrichment and shoot $\delta^{13}C$, subsamples of homogenised moss and soil material were weighed into tin capsules

and analysed with an Eurovector elemental analyser (Eurovector, Redevalle, Italy) coupled to an Isoprime isotope ratio mass spectrometer (Elementar, Cheadle Hulme, UK). Total core ^{15}N uptake was then calculated as weighted means across all fractions of each core, except the soil fraction. While the soil fraction had very low incorporation of ^{15}N, this fraction was also the heaviest (Table S1). This caused core ^{15}N uptake to be very variable. Shoot $\delta^{13}C$ was measured to provide a time-integrated measure of moss production in relation to site water availability. Moss $\delta^{13}C$ gives an indication of past moisture conditions as wetter relative to drier shoots will be more strongly CO_2 limited due to slower diffusion of CO_2 in water than in air. In moist mosses, Rubisco will therefore discriminate less against the rarer ^{13}C isotope and have higher $\delta^{13}C$ values (Deane-Coe et al., 2015).

2.5 | Plot-scale environmental measurements

Temperature and volumetric water content (VWC) were measured in all plots at 5 cm depth from the moss surface using 5TM sensors and logged every hour throughout the full period of measurements with EM50 data loggers (Decagon Devices Inc., WA, USA). Volumetric moisture content measurements are useful for continuous moisture measurements but are sensitive to type of substrate. Comparison of VWC between soils or other substrates such as different moss species may therefore be biased (Cobos, 2010). Logged volumetric moisture measurements were therefore calibrated for each moss species. Three separate moss cores belonging to each of the three species (for *Sphagnum* spp., we used *S. fuscum*) were fully water-saturated and weighed repeatedly while drying. With a 5TM sensor, we simultaneously measured VWC for each moss species. Species-specific relationships between the two variables were used to calculate volumetric moisture content from logged field volumetric moisture content.

2.6 | Data analysis and statistics

All data processing, analyses and visualisations were performed in R version 4.2.0 (R Core Team, 2022). For each core at each measurement time, ethylene production rate ($\mu mol\, m^{-2}\, h^{-1}$) was calculated by fitting linear curves through three time points using the R package HMR (Pedersen, 2020). Field N_2 fixation rates were calculated from the linear relationship between ethylene production and ^{15}N incorporation of the moss cores during climate chamber incubation. A linear model linking ethylene production, ^{15}N uptake and moss species showed that moss species did not influence this relationship significantly and was left out of the model.

Effects of warming treatment, precipitation regime, moss species and measurement date on ethylene production, calculated N_2 fixation rates and incubation temperature and core moisture, and daily means of logged subsurface temperature and moisture were analysed with mixed effects models using the *nlme* package (Pinheiro et al., 2018). Fixed factors in the model were 'mean annual precipitation' and 'date', as continuous variables, and 'warming' and 'moss species' as categorical variables, and all their interactions. Date was included as an orthogonal quadratic polynomial term. 'Plot' was set as a random factor to take the repeated measurements on moss cores through time into account. 'Plot' was further nested in 'site' to take the nested design of the experiment into account. Moss chemical data were analysed with similar models but without plot as random effect. To specifically test the effect of moisture and temperature for each species, N_2 fixation rates were also analysed with mixed effects models with 'incubation temperature', 'moss core moisture content' and 'moss species' and the interaction term 'incubation temperature'×'moss core moisture content' as predictors. To aid understanding of the many levels of interactions in the experimental design, effects on N_2 fixation of significant factors and interactions were visualised by graphing model predictions and 95% CI without data points using the *ggeffects* package (Lüdecke, 2018). Prior to all mixed effect model analyses, data were checked for normality and homoscedasticity and data were natural log (ethylene production, N_2 fixation, incubation core moisture and moss density) or square root (incubation core temperature and logged moss temperature and moisture) transformed if necessary.

2.7 | Species-specific seasonal N input through N_2 fixation at the landscape scale

To quantify the input of N of the three moss species to the ecosystem at the colony scale over the course a growing season, we estimated overall growing season (mid-June to mid-September) N_2 fixation using separate hierarchical generalised additive models (HGAMs) for each moss species and plot-scale logged temperature and moisture data. Each HGAM included incubation temperature, soil moisture and day of year as smoothing variables with thin plate regression splines (TPRS), and each model was fitted using the *mgcv* package. Uncertainties around the conversion factors were not considered in the HGAMs. To get as many observation points as possible and obtain reasonable model fits, we pooled data for each moss species across sites and warming treatments. We included day of year in the models to account for seasonal effects that were otherwise not directly accounted for by microclimate, such as changes in surrounding plant community phenology. For integrating to the full growing season period (mid-June to mid-September), we used daily means of continuous plot-scale soil temperature and moisture data (converted from volumetric to gravimetric, see above) for each moss species in experimentally warmed and control plots separately and for sites of low (571–775 $mm\, year^{-1}$) and high (881–1155 $mm\, year^{-1}$) mean annual precipitation.

N_2 fixation was measured on mono-specific moss cores. Therefore, input of N of the three moss species to the ecosystem reflects the species response to the climate treatments at the plot scale, assuming 100% moss cover. To estimate species' individual contribution in a heterogeneous tundra landscape, estimated species-specific seasonal

N input was combined with species-specific moss cover. Estimated moss species-specific seasonal N input was modelled using plot-scale N_2 fixation rate measurements, logger moisture and temperature data, and day of year. We used moss cover estimates from Rzepczynska et al. (2022). These were 14% for *P. schreberi*, 4% for *H. splendens* and <0.5% *Sphagnum* and represented a 3 km^2 heath landscape at the wet end of our gradient (300 2×2 m^2 transect plots).

3 | RESULTS

3.1 | Growing season soil climate

Experimental warming increased temperature more strongly in the early growing season, here by ~2.5°C while the effect of OTCs had mostly disappeared by early September (Table 2, Figure 1a). The specific warming intensity varied between sites and moss species in non-straightforward ways. The warming intensity decreased slightly (<0.05°C) with increasing mean annual precipitation. Date was the strongest predictor of temperature at −5 cm depth (Table 2; Figure 1a). Soil moisture at −5 cm was very variable between sites, but *Sphagnum* spp. was the wettest of the three species throughout the whole period. Experimental warming decreased soil moisture at −5 cm but predominantly in *Sphagnum* spp. and here more pronounced at high mean annual precipitation and early in the season (Table 2; Figure 1b).

TABLE 2 Results of mixed effect models for daily averages of temperature and moisture (gravimetric) 5 cm below the moss surface and logged hourly.

		Temperature		Moisture	
	df	χ^2	*p*	χ^2	*p*
Precipitation (*P*)	1	15.1	**<.001**	37.3	**<.001**
Warming (*W*)	1	17.8	**<.001**	44.8	**<.001**
Moss species (MS)	2	3.3	.19	29443.0	**<.001**
Date[a] (*D*)	2	3563.6	**<.001**	23.8	**<.001**
P×*W*	1	1.2	.28	66.2	**<.001**
P×MS	2	74.9	**<.001**	147.3	**<.001**
W×MS	2	1.7	.43	656.2	**<.001**
P×*D*	2	49.6	**<.001**	12.4	**.002**
W×*D*	2	19.7	**<.001**	9.1	**.011**
MS×*D*	4	26.3	**<.001**	53.6	**<.001**
P×*W*×MS	2	11.4	**.003**	310.0	**<.001**
P×*W*×*D*	2	0.3	.87	0.2	.91
P×MS×*D*	4	7.5	.11	3.9	.42
W×MS×*D*	4	12.1	**.017**	76.5	**<.001**
P×*W*×MS×*D*	4	4.7	.32	11.5	**.022**

Note: Degrees of freedom (df), chi-squared (χ^2) and *p*-values are given. Bold values are significant at $p < .05$. Temperature and moisture data were square root transformed prior to analyses.

[a]Date is included as an orthogonal, quadratic polynomial.

3.2 | Microclimate in mosses during incubations

Temperature measured in the moss cores during incubations was the same across moss species and not affected by OTCs (Table S2). Incubation temperature peaked at the end of July at 25.0±1.0°C during an unusually warm period and was lowest, 12.8±0.3 and 11.3±0.6°C, in the beginning and the end of the growing season (Figure S4a; Table S2). Incubation temperature also depended somewhat on mean annual precipitation regime although this effect differed between the measurement rounds, and the pattern was not consistent (Figure S4a; Table S2).

Gravimetric water content in the moss cores was three times higher in *Sphagnum* than the two feather mosses and varied during the season (Figure S4b; Table S2). For all species, water content was lower during July and August than in spring and autumn, but water content in the pleurocarpous mosses decreased earlier and more pronounced than in *Sphagnum* spp. (Figure S4b; Table S2, period × moss species interaction). At the beginning of the growing season, moss cores at the low end of the mean annual precipitation gradient had on average higher moisture content than those at sites with higher mean annual precipitation (Figure S4b; Table S2, interaction mean annual precipitation × period) even though the actual precipitation in the month of June was three times higher at the high than at the low end of the gradient (Figure S2). In the second half of the growing season, gravimetric water content of the moss cores increased along the precipitation gradient. Across all measurement times, water content was negatively correlated with incubation temperature (Figure 2, $p < .001$, $R^2 = .77$).

3.3 | Conversion of ethylene production to $^{15}N_2$ uptake

Ethylene production of the harvested cores incubating at 7°C in climate chambers was within the range of measured field ARA activity at the beginning and the end of the growing season (Figure S5). Nitrogen fixation, measured as $^{15}N_2$, and ethylene production were significantly correlated ($R^2 = .75$, $p < .001$, Figure S6). The regression slope, that is the average conversion factor of μmol ethylene produced per μmol N taken up for each core, was 1.6±0.13 and did not differ between the moss species (Figure S6).

3.4 | Microclimate effects on N_2 fixation

Moss core moisture content and incubation temperature both predicted N_2 fixation rates and interacted so that the effect of core moisture content depended on the effect of incubation temperature and the effect of incubation temperature depended on soil moisture content (Figure 2; Table 3). Nitrogen fixation rates peaked at approx. 20°C for all species while the moisture content associated with the highest N_2 fixation rates was around 5 and 10 g water g^{-1} moss biomass for feather mosses and *Sphagnum*, respectively (Figure 2).

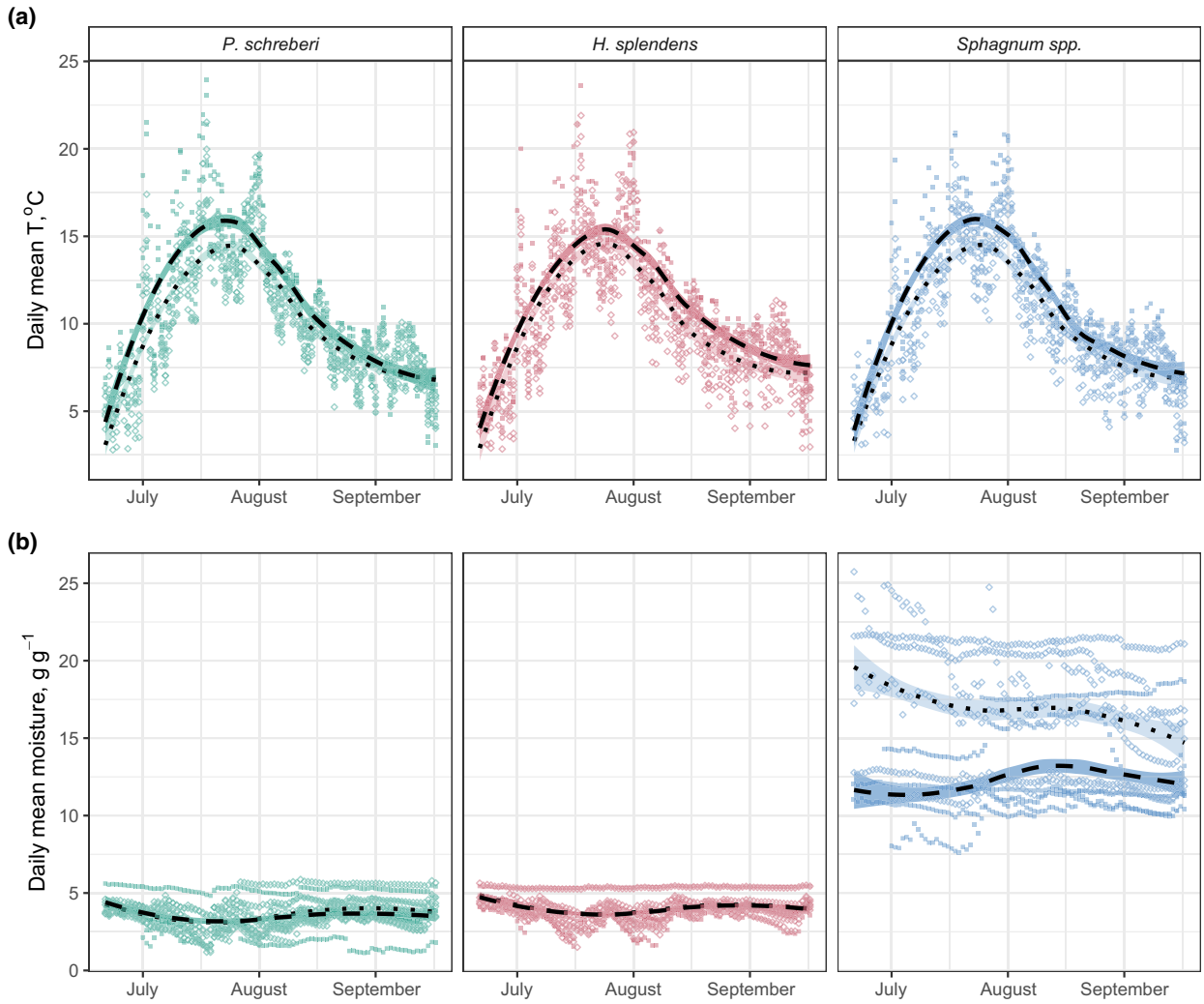

FIGURE 1 Logged daily mean temperature (a) and gravimetric moisture content (b) in 5 cm below the moss surface of three moss species *Hylocomium splendens* (red), *Pleurozium schreberi* (green) and *Sphagnum* sp. (blue) at eight sites along a mean annual precipitation gradient (not shown) subjected to experimental warming using open-top chambers (dashed, darker shades and filled squares) or left unmanipulated (dotted, lighter shades and open diamonds). Lines represent loess smooth relations (in R) and shadows show 0.95 confidence intervals. Some sites and moss species combinations have missing data due to malfunctioning sensors (9 out 48 sensors are missing, two to four per species). See Table 2 for statistics.

3.5 | Climate treatment effects on N_2 fixation

The effect of experimental warming on N_2-fixation depended on mean annual precipitation in a different way for the three moss species (mean annual precipitation × warming × moss species interaction, Table 4; Table S3). For *H. splendens* and *P. schreberi*, no effect of warming at low mean annual precipitation turned into a negative effect at high mean annual precipitation, while for *Sphagnum* spp., high mean annual precipitation regime reversed a slightly negative warming effect to a slightly positive one (Figure 3a; Figure S7). Irrespective of warming treatments, site mean annual precipitation was important for N_2 fixation rates, but this effect depended strongly on measurement period (mean annual precipitation × period interaction, Table 4), because site mean annual precipitation only increased N_2 fixation rates in early August (Figure 3b). Interestingly, this was not during the warmest measurement conditions in July (Figure S4a).

Site mean annual precipitation also increased N_2 fixation more in *H. splendens* than in *Sphagnum* spp. and *P. schreberi* (Figure 3a; Table 4, mean annual precipitation × moss species interaction).

3.6 | N_2 fixation—Moss species-specific seasonal patterns

Moss species differed in their N_2 fixation rates and *Sphagnum* spp. generally had the highest fixation rates (Figure 3a and c, Table 4). Measurement period was a strong overall predictor for N_2 fixation rates, which were generally highest in July and August (Figure 3b). This pattern was largely driven by *Sphagnum* spp., which peaked in N_2 fixation in early August, whereas feathermoss N_2 fixation rates varied less across the season (Table 4, significant moss species × period interaction).

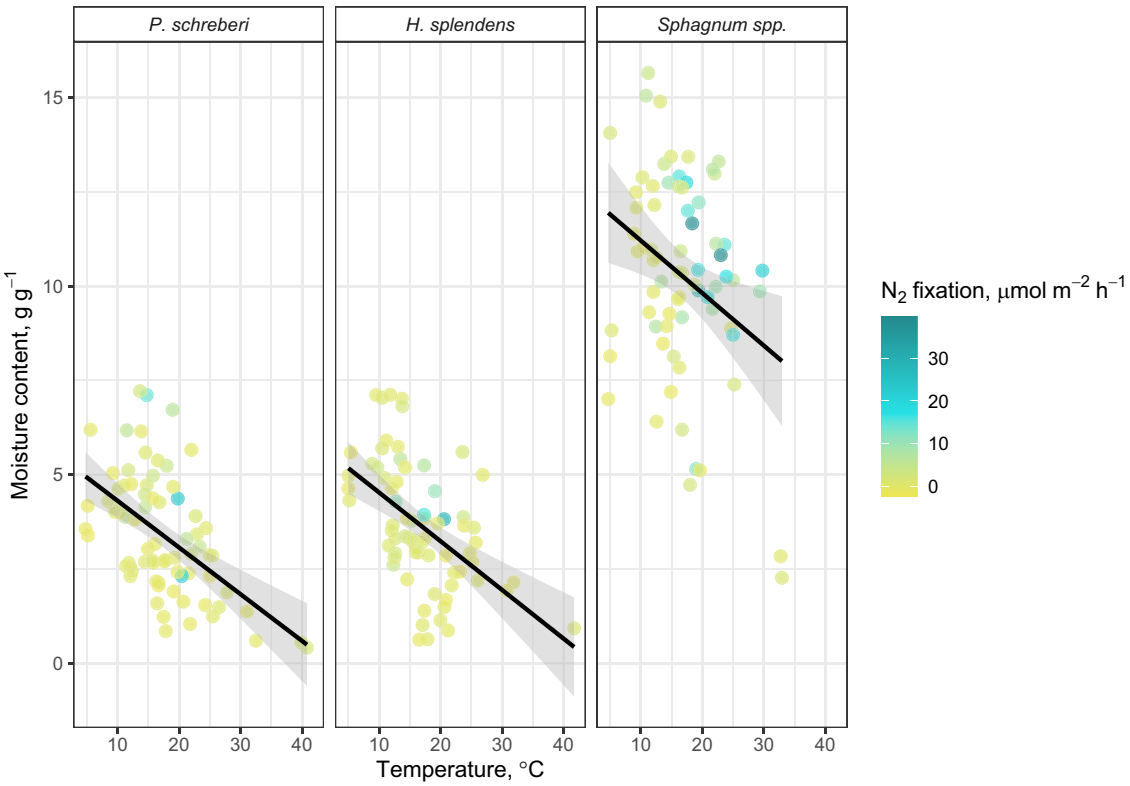

FIGURE 2 Relationship between N_2 fixation, incubation core moisture content and incubation temperature in three moss species *Pleurozium schreberi*, *Hylocomium splendens* and *Sphagnum* spp. measured five times in the same moss colonies in the period from 14 June to 21 September along a mean annual precipitation gradient. Each point represents a measurement. For statistics, see Table 3.

TABLE 3 Results of linear mixed effects model for N_2 fixation rates (µmol m^{-2} h^{-1}) predicted by measured incubation temperature and moss cores moisture content and moss species.

	df	χ^2	*p*
Incubation temperature (*T*)	1	27.9	**<.001**
Moisture content (Moist)	1	25.7	**<.001**
Moss species (MS)	2	1.7	.42
T×Moist	1	30.8	**<.001**

Note: Degrees of freedom (df), chi-squared (χ^2) and *p*-values are given. Bold values are significant at $p < .05$. N_2 fixation data were log-transformed prior to analysis.

3.7 | Moss density and shoot $\delta^{13}C$

Top layer (green part of the moss shoots) $\delta^{13}C$, which reflect past moisture conditions in the moss tissue during moss carbon acquisition (Deane-Coe et al., 2015; Rzepczynska et al., 2022), was generally decreased by warming (Figure 4b; Table S4). *Sphagnum* spp. had the highest $\delta^{13}C$ values, with most values above −30‰, whereas almost all values for feather mosses were below −30‰ (Figure 4a; Table S4). The density of the top layer of the moss core was highest in *Sphagnum* spp. and warming decreased density in all moss species (Figure 4b; Table S4). In the top layer, density was explained by $\delta^{13}C$ (Figure 4c). Top layer $\delta^{13}C$ predicted average N_2 fixation across

TABLE 4 Results of linear mixed effects model (type II sums of squares) for N_2 fixation (µmol m^{-2} h^{-1}).

	df	χ^2	*p*
Precipitation (*P*)	1	1.7	.19
Warming (*W*)	1	0.7	.41
Moss species (MS)	2	38.6	**<.001**
Date[a] (*D*)	2	20.5	**<.001**
P×*W*	1	0.4	.51
P×MS	2	6.3	**.043**
W×MS	2	0.4	.84
P×*D*	2	9.5	**.009**
W×*D*	2	0.4	.82
MS×*D*	4	34.5	**<.001**
P×*W*×MS	2	6.3	**.044**
P×*W*×*D*	2	0.1	.95
P×MS×*D*	4	1.3	.86
W×MS×*D*	4	2.2	.70
P×*W*×MS×*D*	4	1.3	.85

Note: Degrees of freedom (df), chi-squared (χ^2) and *p*-values are given. Bold values are significant at $p < .05$. Data were natural log-transformed prior to analysis. The model intercept was 0.18 and variance of the nested random effects were as follows: Site: 0.20 and Site/plot: 0.071.

[a] Date is included as an orthogonal, quadratic polynomial.

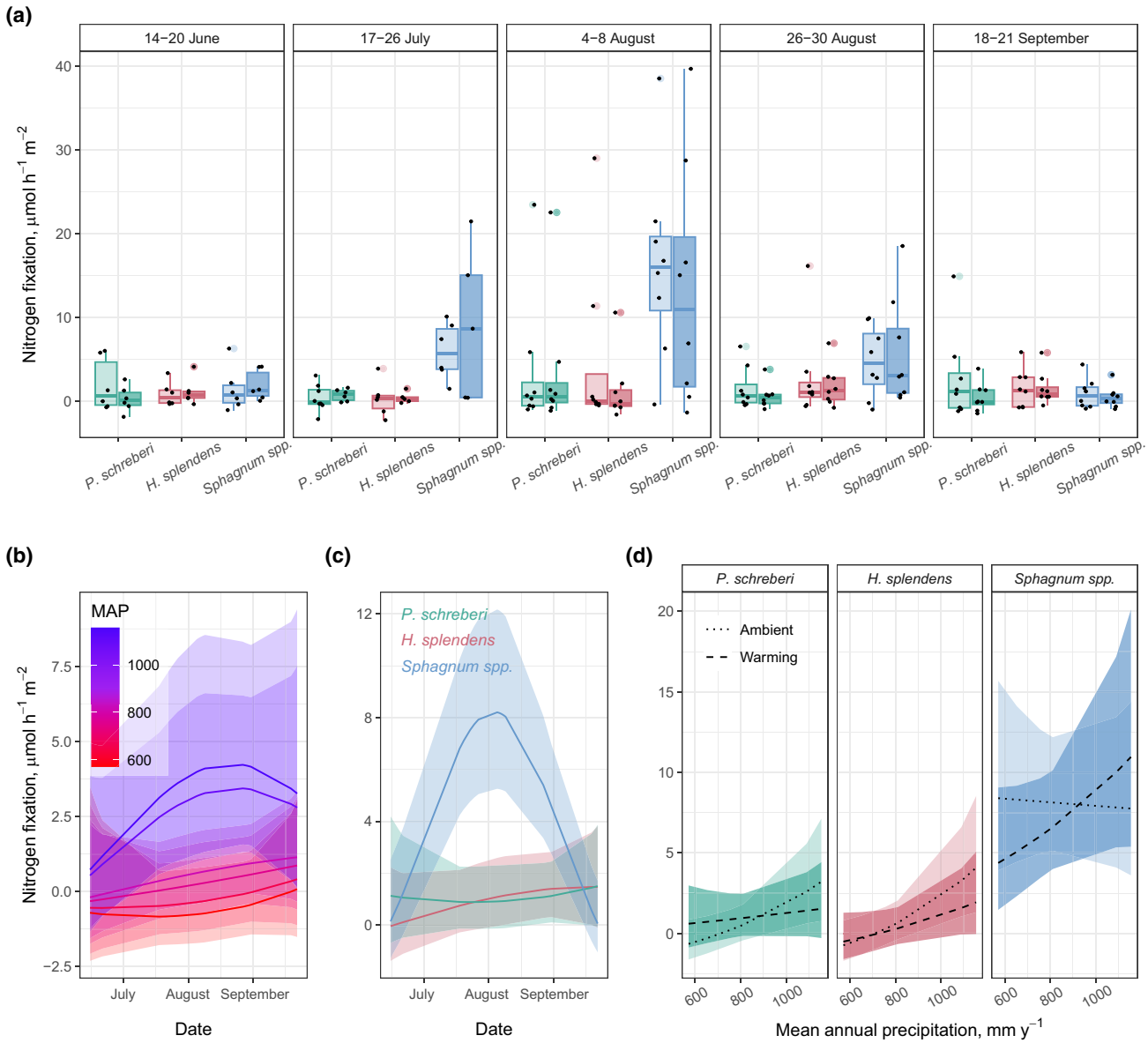

FIGURE 3 Nitrogen fixation rates in mono-specific colonies of three moss species *Pleurozium schreberi*, *Hylocomium splendens* and *Sphagnum* spp. during five measurement periods in the summer of 2018 at eight sites situated along a mean annual precipitation (MAP) gradient in plots that were artificially warmed using open-top chambers (dashed, darker shade) or left unmanipulated (dotted, lighter shade). On 14–20 June, one of the eight sites was not measured due to bad weather. (a) observed N_2 fixation activity and datapoints within a box represent individual precipitation sites; (b, c) model predictions and 95% CI, highlighting significant interactions (Table 4). Note differences between panels in *y*-axis scale. N_2 fixation was estimated from in situ acetylene reduction assays and measured species-specific conversion factors between ethylene production and ^{15}N incorporation.

all five field measurements and this relationship did not depend on moss species (Figure S8).

3.8 | N input into tundra ecosystems

The moss-specific generalised additive models varied in their overall goodness of fit. The *Sphagnum* GAM had the best fit with 44.9% deviance explained, while *H. splendens* and *P. schreberi* models had 22.2% and 14.3% deviance explained, respectively. In contrast to soil temperature and day of year, soil moisture remained the only smoothing variable with a significant effect on N_2 fixation in all three GAMs ($p < .05$; Table S5). At the moss colony scale and integrated across the season, *Sphagnum* spp. fixed around 50% more than the feather mosses. OTC decreased the total input of N through fixation especially in the early season and especially at high precipitation sites where plots were dryer in the warm plots (Figure S9a). *P. schreberi* was associated with the lowest N input at the colony scale. At high compared with sites with low mean annual precipitation, *P. schreberi* was associated with less than half the associated N input (Figure S9a). At the landscape level (based on cover estimates from Rzepczynska et al. (2022)) and our modelled seasonal N input via

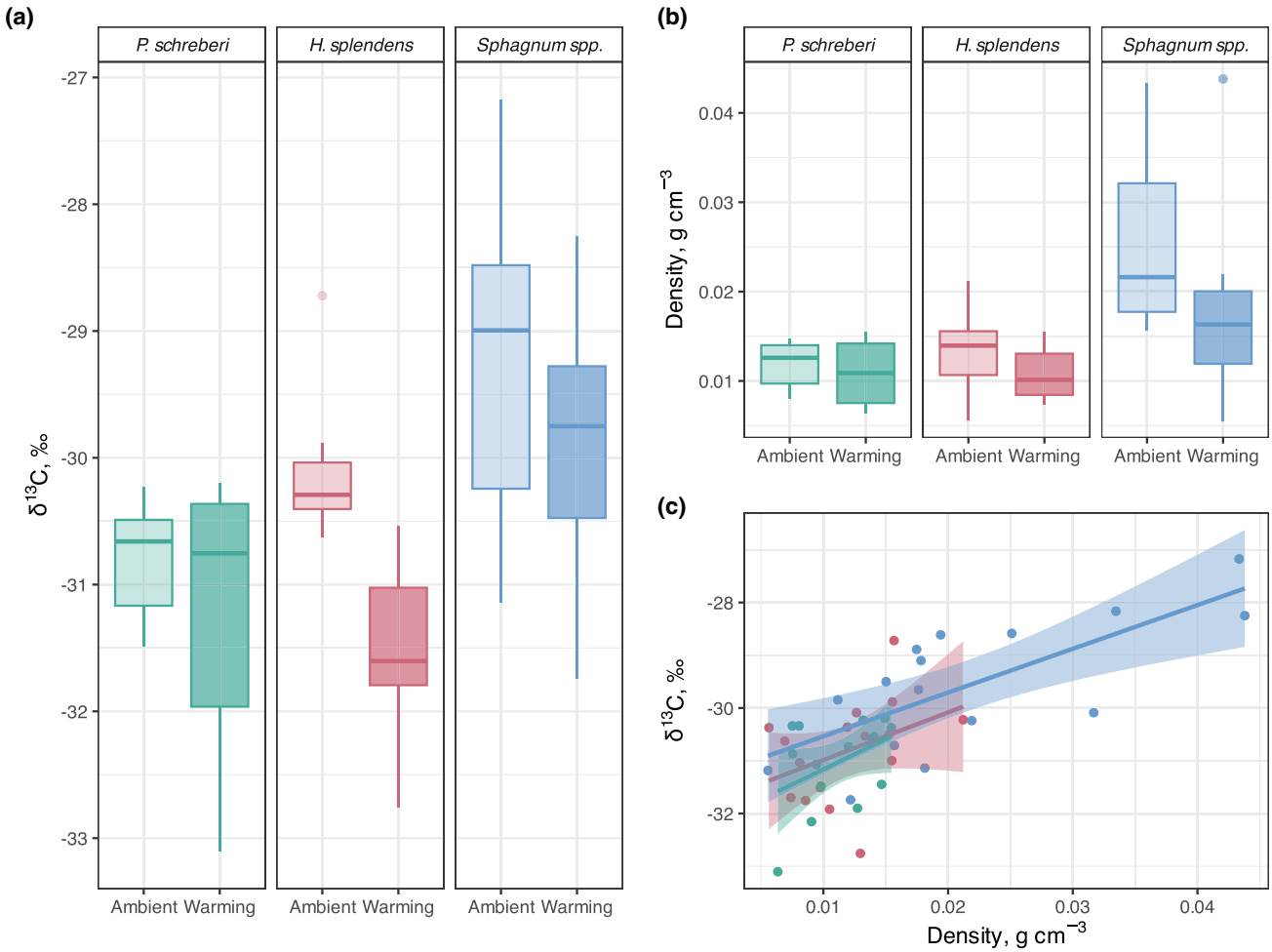

FIGURE 4 Moss shoot (a) $\delta^{13}C$ and (b) top layer density and (c) their linear relationship ($r^2 = .51$, $p < .001$), in three moss species *Pleurozium schreberi* (green), *Hylocomium splendens* (red) and *Sphagnum* spp. (blue) measured across eight sites situated along a natural precipitation gradient in plots that were artificially warmed using open-top chambers (darker shade) or left unmanipulated (lighter shade). The top layer includes the upper 1 and 2 cm for *Sphagnum* and feather mosses, respectively. Plots include all data points, but plots a and b highlight significant effects, warming and moss species $p < .001$. See full statistics for plot a and b in Table S3.

N_2 fixation at the wet and of our mean annual precipitation gradient, the pleurocarpous mosses were each responsible for around twice the input of *Sphagnum* spp. (Figure S9b). The total ecosystem contribution of N by the three species at the landscape scale was $0.16 \pm 0.28\,kg\,N\,ha^{-1}$ (±95% CI of model fit to observations).

4 | DISCUSSION

Our results show that warming affects moss-associated N_2 fixation rates differently depending on moss species and mean annual precipitation level. Surprisingly, the warming treatment decreased N_2 fixation at higher mean annual precipitation in dry feather mosses, whereas in *Sphagnum* spp. the warming treatment and higher mean annual precipitation had a small but expected synergistic effect. Higher mean annual precipitation increased N_2 fixation rates in the middle of the growing season when temperatures were highest, and risk of drying was similarly high. *Sphagnum* spp., which has a higher water holding capacity and thus generally a constant high moisture content compared with feather mosses, had the highest overall N_2 fixation activity throughout the growing season. Below, we discuss these findings in relation to our hypotheses and discuss the consequences for moss performance and ecosystem N dynamics.

4.1 | Experimental warming effects on N_2 fixation depend on mean annual precipitation and moss species

The experimental warming treatment generally did not promote N_2 fixation across sites with high mean annual precipitation, counter to our hypothesis. Only in *Sphagnum* spp. did higher mean annual precipitation have the hypothesised effect of inducing an, albeit modest, positive effect of warming. In the feather mosses, increasing mean annual precipitation caused experimental warming to decrease N_2 fixation rates, which conflicts with our first hypothesis.

That moss species affected this precipitation-induced warming effect was in line with our second hypothesis. However, we expected feather mosses, rather than *Sphagnum* spp. to be stimulated by the warming treatment at higher mean annual precipitation.

Lacking or negative experimental warming effects on moss-associated N_2 fixation is not uncommon and may be caused by a drying effect (Lagerström et al., 2007; Permin et al., 2022; Sorensen et al., 2012). Higher incubation temperature was indeed associated with lower moisture content across the whole core. Also, moss shoots in cores from OTC plots had lower shoot $\delta^{13}C$ values, which indicate low moisture availability integrated across time (Deane-Coe et al., 2015; Rzepczynska et al., 2022). Indeed, higher $\delta^{13}C$ values were associated with higher N_2 fixation in a similar way across moss species. However, higher mean precipitation did not prevent negative effects associated with drying by warming. This could partly be because in July, which had the highest temperatures, rainfall was not higher at the high than at the low end of the gradient. In addition, the ^{15}N labelling at the end of the study showed that the majority of N_2 fixation took place in the moss shoots. Warming decreased the density of the moss shoots, which is also observed in other studies and is a consequence of faster growth (Dorrepaal et al., 2004; van Zuijlen et al., 2022). A lower shoot density likely resulted in reduced shoot water holding capacity in the warmed mosses (Elumeeva et al., 2011; Grau-Andrés et al., 2022; van Zuijlen et al., 2022). In feather mosses, a further decrease in their already low shoot moisture holding capacity may have prevented N_2-fixing bacteria from benefiting from more precipitation or may have changed the bacterial community (Renaudin et al., 2022). Indeed, $\delta^{13}C$ supported that feather moss shoots were markedly more water limited than *Sphagnum* spp. shoots. So, although warming reduced density in shoots across all moss species, only in feather mosses did this lead to a negative warming effect on N_2 fixation.

It is worth noting that the incubation temperature was not increased by the OTCs. This is not surprising as mosses were moved from the plots into incubation jars. However, it tells us that the effects we observed of OTC on N_2 fixation were likely due to effects on bacterial community or activity, rather than direct temperature effects on enzymatic activity. Mosses show great host specificity to diazotroph community composition (Ininbergs Karolina et al., 2011). The specificity may be due to the variation in moss traits relating to water economy which control cyanobacterial colonisation and N_2 fixation rates in non-*Sphagnum* mosses (Liu & Rousk, 2022). Our results suggest that these traits can be modified by the environment with consequences for N_2 fixation rates. Unlike other moss genera, *Sphagnum* has N_2 fixers living inside specialised water holding cells (hyaline cells), which might explain why a decrease in water holding capacity in *Sphagnum* spp. did not affect N_2 fixation rates (Granhall & Hofsten, 1976). It is possible that warming-induced shoot density changes caused N_2 fixation in feather mosses to not benefit from higher mean annual precipitation in warmed plots, while this was not the case for *Sphagnum* Spp. Ultimately, negative drying effects on N_2 fixation by warming of a few degrees, as seen in this and other experiments, may not be alleviated in all moss species by increase in mean annual precipitation.

4.2 | Large seasonal differences in N_2 fixation across moss species

Higher mean annual precipitation generally increased moss-associated N_2 fixation, and this effect was more pronounced during peak growing season when temperatures were higher than in the early and late seasons and therefore likely to induce drying. This agrees with our second hypothesis stating that the precipitation effect on N_2 fixation would depend on period. Despite the important role of moisture for N_2 fixation, responses of moss-associated N_2 fixation to natural variation in mean annual precipitation level have not been studied across moss species and climate treatments in the field in the Boreal–Arctic zone. Responses to higher precipitation can be confounded with responses to N deposition. Even low N amendments of 0.8–4.4 $kg\,ha^{-1}\,year^{-1}$ can depress N_2 fixation (Salemaa et al., 2019). However, our results are unlikely to be impacted by N addition as in this area N deposition is very low, <2 $kg\,h^{-1}\,year^{-1}$ and does not differ between the high and the low end of the mean annual precipitation gradient. Also, our results are in line with results from short-term water addition studies showing clear positive effects of amount and frequency of added water alone or in combination with experimentally increased temperatures (Gundale et al., 2012; Jackson et al., 2011; Rousk et al., 2018). We cannot separate the effect of precipitation amount and frequency of events in our results. Our results show that mean annual precipitation is an important factor for determining the input of N during the warmest period. Also, our finding highlights that the timing of precipitation changes likely would influence the impact on ecosystem processes, here N_2 fixation. If summer precipitation continues to increase in this region and as predicted for the Arctic region in general (Figure S1, SMHI, (Bintanja & Andry, 2017)), this could promote N_2 fixation rates considerably.

Moss species generally, greatly influenced N_2 fixation rates. At peak fixation in early August, *Sphagnum* spp. had more than twice the N_2 fixation of each of the two feather mosses. Furthermore, high mean annual precipitation promoted N_2 fixation more *in H. splendens* than it did in *P. schreberi* and *Sphagnum* spp. This partly also agrees with our *second hypothesis*, stating that positive precipitation effects would be more pronounced in dry-adapted moss species. *Hylocomium splendens* and *P. schreberi* were generally drier than *Sphagnum* spp. throughout the measurement period. Moss core moisture content was positively correlated with N_2 fixation. *Sphagnum* has the highest water holding capacity of the three species (Elumeeva et al., 2011; Lett et al., 2022), and consequently, *Sphagnum* showed the largest response in N_2 fixation rates to peak growing season temperatures. This pattern was also observed in a boreal peatland where *Sphagnum*-associated N_2 fixation was higher in wetter parts of the mire and the wetter part also had more extreme peak during the warm period of the growing season (Živković et al., 2022).

The highest rates of N_2 fixation in all three species were around 20°C but it seemed that high N_2 fixation rates in *Sphagnum* spp. depended more on a higher moisture content than the two other

species, which likely reflects that *Sphagnum* spp. and its microbiome are adapted to wetter habitats. N_2 fixation optima at around 20°C is similar to or slightly lower than the 22–25°C, which is considered optimum for N_2 fixation at the bacterial cell level in terrestrial ecosystems (Darnajoux et al., 2022; Houlton et al., 2008). However, the temperature optimum for N_2 fixation could also depend on the form of nitrogenases (molybdenum vs. alternative nitrogenase) (Darnajoux et al., 2022). However, we measured N_2 fixation in the field under natural conditions, that is not watered, and it is therefore more straightforward to interpret the optimum as a consequence of moisture and temperature playing together. These species-specific microclimate responses may indicate that N_2 fixation in more dry-adapted mosses will respond more positively to a higher mean annual precipitation, whereas N_2 fixation in *Sphagnum* could be promoted more by higher temperatures.

4.3 | Moss species-specific N input across scales

Sphagnum spp. was associated with the highest rates of N_2 fixation of the three moss species when considered at the moss colony scale. These differences in rates are equivalent to other studies finding higher N_2 fixation in *Sphagnum* spp. compared with feather mosses (Jean et al., 2021; Rzepczynska et al., 2022) although N_2 fixation rates of feather mosses may be as high as those of *Sphagnum* in other ecosystems (Stuart, Holland-Moritz, et al., 2020). Our measured average N_2 fixation rate by *Sphagnum* spp. was $7.7 \pm 1.3\,\mu mol\,m^{-2}\,h^{-1}$, which is 50% of the average N_2 fixation rate at a climatically similar North American site for June–August (Stewart et al., 2011). Acetylene reduction rates were comparable to *Sphagnum* and *H. splendens* rates measured at a lowland site at the dry end of our mean annual precipitation gradient (Rousk et al., 2015). When integrated across the season, the modelled seasonal colony scale N input by pleurocarpous moss was less than half of that of *Sphagnum*.

When species N contribution to the ecosystem and the landscape scale was estimated for the wet end of our annual precipitation gradient by taking cover of the species into account, the pleurocarpous mosses were responsible for twice as high a seasonal input of N through associated N_2 fixation, compared with *Sphagnum*. Together, the estimated contribution of the three moss species was equivalent to 7% of the total ecosystem N input via N_2 fixation as estimated in a tundra site in the dry part of our gradient which had 50% moss cover (Rousk & Michelsen, 2017). Our estimates are associated with uncertainty related to the conversion of acetylene reduction to N_2 fixation. Our conversion rate of 1.6 is low compared with other studies of moss-associated N_2 fixation in sub-low arctic ecosystems and moss species ranging from 1.8–4.2 (Leppänen et al., 2013; Rousk, Degboe, et al., 2017; Rousk & Michelsen, 2017; Sorensen et al., 2006), although lower rates are also found, for example 0.85 (Stewart et al., 2011). Low conversion rates could indicate the presence of the more cold-adapted vanadium and iron nitrogenase forms (Bellenger et al., 2020). Also, conversion rates may change across the season due to potential shift between nitrogenase forms (Soper et al., 2021), and our calibration was done at the end of the experiment. However, the estimated contribution of N input serves to exemplify the importance of moss cover when estimating ecosystem N input at the landscape scale. Importantly, the differences between moss species were primarily driven by the differences in cover of the three moss species, which vary tremendously from ecosystem to ecosystem. For example, *Sphagnum* may at a more local scale in *Sphagnum* mires contribute to ecosystem N input, which by far exceed that of surrounding tundra and which may have important impacts on the mire ecosystem (Živković et al., 2022). Also, the *Sphagnum* species included in this study are those associated with tundra and drier part of mires, while *Sphagnum* species in wetter habitats are associated with higher N_2 fixation rates.

Importantly, species-specific estimates of moss cover at the landscape scale are missing at large (but see Rzepczynska et al., 2022; Stewart et al., 2011; Stuart, Pederson, et al., 2020). Furthermore, changes in cover of mosses due to climate change may modify landscape N input through moss-associated N_2 fixation. Bryophytes are generally observed to decline across tundra ecosystem in response to warming (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe, et al., 2012), which would result in a lower overall N input via moss-associated N_2 fixation. Change in precipitation patterns and amounts may impact bryophyte abundance. For instance, *Sphagnum magellanicum* growth (length increment) is positively linked to precipitation across 99 Holarctic peatland sites (Bengtsson et al., 2021) but *Sphagnum* may be negatively affected by drying. However, *P. schreberi* and *H. splendens* are pan-boreal species and thus associated also with warmer climates. Hence, these species may expand across tundra in a warmer climate (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Lang et al., 2012), which would increase their contribution to ecosystem N input. While the possibility for scaling species-specific N_2 rates is still limited, we provide here an example of how species-specific climate responses of N_2 fixation at the moss scale may not reflect the species contribution to the ecosystem N input.

The fate of fixed N is still not fully understood (Rousk, 2022). Mosses can take up fixed by their associated diazotrophs and use it for growth (Berg et al., 2013; Stuart, Pederson, et al., 2020), but N may also be lost N to the environment (Arróniz-Crespo et al., 2022; Eckstein, 2000). Our results suggest that mosses with higher moisture content or growing at higher mean annual precipitation have higher N_2 fixation at the time of peak vascular plant growth and N demand (Michelsen et al., 1999). If mosses access the fixed N_2, this will likely benefit mosses in their competition with vascular plants under future climate scenarios. Although the spatiotemporal scale is unknown, depending on moss species, N might also leave the bryosphere through leaching, decay and herbivory and in this way fertilise the environment (DeLuca et al., 2022; Eckstein, 2000; Rousk et al., 2016; Rousk, Sorensen, & Michelsen, 2017).

4.4 | Conclusion

Both temperature and precipitation are observed and predicted to increase in the Arctic and here we show that they affect N_2 fixation associated with dominant tundra moss species differently. Our results suggest that feather mosses may not experience much higher N_2 fixation in warmer conditions due to drying. Higher mean annual precipitation does not seem to compensate for this drying effect likely because of changed morphology in faster-growing mosses and warm and wet conditions. Due to a high cover of feather mosses in tundra ecosystems, their N_2 fixation rates can substantially increase N input under wet but not necessarily in warmer conditions. For *Sphagnum*, on the contrary, warming could promote N_2 fixation, and the increase is less dependent on mean annual precipitation level. In *Sphagnum*-dominated ecosystems such as mires, warming could lead to a substantial increase in N input via increased N_2 fixation, while in heath tundra ecosystems higher rates associated with *Sphagnum* may have relatively modest impact.

AUTHOR CONTRIBUTIONS

Signe Lett: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; visualization; writing – original draft. **Casper T. Christiansen:** Formal analysis; visualization; writing – review and editing. **Ellen Dorrepaal:** Conceptualization; funding acquisition; investigation; methodology; project administration; resources; writing – review and editing. **Anders Michelsen:** Conceptualization; funding acquisition; investigation; methodology; project administration; resources; supervision; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

There is no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad respository at https://doi.org/10.5061/dryad.6wwpzgn6m.

ORCID

Signe Lett https://orcid.org/0000-0003-2515-8413
Ellen Dorrepaal https://orcid.org/0000-0002-0523-2471
Anders Michelsen https://orcid.org/0000-0002-9541-8658

REFERENCES

Arróniz-Crespo, M., Bougoure, J., Murphy, D. V., Cutler, N. A., Souza-Egipsy, V., Chaput, D. L., Jones, D. L., Ostle, N., Wade, S. C., Clode, P. L., & DeLuca, T. H. (2022). Revealing the transfer pathways of cyanobacterial-fixed N into the boreal forest through the feather-moss microbiome. *Frontiers in Plant Science*, *13*, 1036258.

Bellenger, J. P., Darnajoux, R., Zhang, X., & Kraepiel, A. M. L. (2020). Biological nitrogen fixation by alternative nitrogenases in terrestrial ecosystems: A review. *Biogeochemistry*, *149*(1), 53–73. https://doi.org/10.1007/s10533-020-00666-7

Bengtsson, F., Rydin, H., Baltzer, J. L., Bragazza, L., Bu, Z.-J., Caporn, S. J. M., Dorrepaal, E., Flatberg, K. I., Galanina, O., Gałka, M., Ganeva, A., Goia, I., Goncharova, N., Hájek, M., Haraguchi, A., Harris, L. I., Humphreys, E., Jiroušek, M., Kajukało, K., … Granath, G. (2021). Environmental drivers of sphagnum growth in peatlands across the Holarctic region. *Journal of Ecology*, *109*(1), 417–431. https://doi.org/10.1111/1365-2745.13499

Berg, A., Danielsson, Å., & Svensson, B. H. (2013). Transfer of fixed-N from N_2-fixing cyanobacteria associated with the moss *Sphagnum riparium* results in enhanced growth of the moss. *Plant and Soil*, *362*(1), 271–278. https://doi.org/10.1007/s11104-012-1278-4

Bintanja, R., & Andry, O. (2017). Towards a rain-dominated Arctic. *Nature Climate Change*, *7*(4), 263–267. https://doi.org/10.1038/nclimate3240

Cobos, D. R. (2010). Calibrating ECH$_2$O soil moisture sensors. Decagon Devises, Application Note 800-755-2751, 8.

Darnajoux, R., Bradley, R., & Bellenger, J.-P. (2022). In vivo temperature dependency of molybdenum and vanadium nitrogenase activity in the heterocystous cyanobacteria *Anabaena variabilis*. *Environmental Science & Technology*, *56*(4), 2760–2769. https://doi.org/10.1021/acs.est.1c05279

Deane-Coe, K. K., Mauritz, M., Celis, G., Salmon, V., Crummer, K. G., Natali, S. M., & Schuur, E. A. G. (2015). Experimental warming alters productivity and isotopic signatures of tundra mosses. *Ecosystems*, *18*(6), 1070–1082. https://doi.org/10.1007/s10021-015-9884-7

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

DeLuca, T. H., Zackrisson, O., Nilsson, M.-C., Sun, S., & Arróniz-Crespo, M. (2022). Long-term fate of nitrogen fixation in *Pleurozium schreberi* Brid (Mit.) moss carpets in boreal forests. *Applied Soil Ecology*, *169*, 104215. https://doi.org/10.1016/j.apsoil.2021.104215

Deslippe, J. R., Egger, K. N., & Henry, G. H. R. (2005). Impacts of warming and fertilization on nitrogen-fixing microbial communities in the Canadian high Arctic. *FEMS Microbiology Ecology*, *53*(1), 41–50. https://doi.org/10.1016/j.femsec.2004.12.002

Dormann, C. F., & Woodin, S. J. (2002). Climate change in the Arctic: Using plant functional types in a meta-analysis of field experiments. *Functional Ecology*, *16*(1), 4–17. https://doi.org/10.1046/j.0269-8463.2001.00596.x

Dorrepaal, E., Aerts, R., Cornelissen, J. H. C., Callaghan, T. V., & Logtestijn, R. S. P. V. (2004). Summer warming and increased winter snow cover affect *Sphagnum fuscum* growth, structure and production in a sub-arctic bog. *Global Change Biology*, *10*(1), 93–104. https://doi.org/10.1111/j.1365-2486.2003.00718.x

Du, E., Terrer, C., Pellegrini, A. F. A., Ahlström, A., van Lissa, C. J., Zhao, X., Xia, N., Wu, X., & Jackson, R. B. (2020). Global patterns of terrestrial nitrogen and phosphorus limitation. *Nature Geoscience*, *13*, 221–226. https://doi.org/10.1038/s41561-019-0530-4

Eckstein, R. L. (2000). Nitrogen retention by *Hylocomium splendens* in a subarctic birch woodland. *Journal of Ecology*, *88*(3), 506–515. https://doi.org/10.1046/j.1365-2745.2000.00480.x

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. *Ecology Letters*, *15*(2), 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. C. (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

Ferm, M., Granat, L., Engardt, M., Pihl Karlsson, G., Danielsson, H., Karlsson, P. E., & Hansen, K. (2019). Wet deposition of ammonium, nitrate and non-sea-salt sulphate in Sweden 1955 through 2017. *Atmospheric Environment: X*, *2*, 100015. https://doi.org/10.1016/j.aeaoa.2019.100015

Furness, S. B., & Grime, J. P. (1982). Growth rate and temperature responses in bryophytes: II. A comparative study of species of contrasted ecology. *Journal of Ecology*, *70*(2), 525–536. https://doi.org/10.2307/2259920

Granhall, U., & Hofsten, A. V. (1976). Nitrogenase activity in relation to intracellular organisms in sphagnum mosses. *Physiologia Plantarum*, *36*(1), 88–94. https://doi.org/10.1111/j.1399-3054.1976.tb05033.x

Grau-Andrés, R., Kardol, P., & Gundale, M. J. (2022). Trait coordination in boreal mosses reveals a bryophyte economics spectrum. *Journal of Ecology*, *110*(10), 2493–2506. https://doi.org/10.1111/1365-2745.13965

Gundale, M. J., Gustafsson, H., & Nilsson, M. C. (2009). The sensitivity of nitrogen fixation by a feathermoss-cyanobacteria association to litter and moisture variability in young and old boreal forests. *Canadian Journal of Forest Research*, *39*(12), 2542–2549. https://doi.org/10.1139/X09-160

Gundale, M. J., Wardle, D. A., & Nilsson, M.-C. (2012). The effect of altered macroclimate on N-fixation by boreal feather mosses. *Biology Letters*, *8*, 805–808.

Hollister, R. D., Elphinstone, C., Henry, G. H. R., Bjorkman, A. D., Klanderud, K., Björk, R. G., Björkman, M. P., Bokhorst, S., Carbognani, M., Cooper, E. J., Dorrepaal, E., Elmendorf, S. C., Fetcher, N., Gallois, E. C., Gudmundsson, J., Healey, N. C., Jónsdóttir, I. S., Klarenberg, I. J., Oberbauer, S. F., … Wookey, P. (2022). A review of open top chamber (OTC) performance across the ITEX network. *Arctic Science*, *9*, 331–344. https://doi.org/10.1139/AS-2022-0030

Houlton, B. Z., Wang, Y.-P., Vitousek, P. M., & Field, C. B. (2008). A unifying framework for dinitrogen fixation in the terrestrial biosphere. *Nature*, *454*(7202), 327–330. https://doi.org/10.1038/nature07028

IPCC. (2021). In V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, & B. Zhou (Eds.), *Climate change 2021: The physical science basis. Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change*. Cambridge University Press.

Jackson, B. G., Martin, P., Nilsson, M.-C., & Wardle, D. A. (2011). Response of feather moss associated N_2 fixation and litter decomposition to variations in simulated rainfall intensity and frequency. *Oikos*, *120*(4), 570–581. https://doi.org/10.1111/j.1600-0706.2010.18641.x

Jean, M., Fenton, N. J., Bergeron, Y., & Nilsson, M.-C. (2021). Sphagnum and feather moss-associated N_2 fixation along a 724-year chronosequence in eastern boreal Canada. *Plant Ecology*, *222*(9), 1007–1022. https://doi.org/10.1007/s11258-021-01157-x

Karolina, I., Guillaume, B., Ulla, R., Wardle, D. A., & Marie-Charlotte, N. (2011). Composition and diversity of nifH genes of nitrogen-fixing cyanobacteria associated with boreal forest feather mosses. *New Phytologist*, *192*(2), 507–517. https://doi.org/10.1111/j.1469-8137.2011.03809.x

Lagerström, A., Nilsson, M. C., Zackrisson, O., & Wardle, D. A. (2007). Ecosystem input of nitrogen through biological fixation in feather mosses during ecosystem retrogression. *Functional Ecology*, *21*(6), 1027–1033. https://doi.org/10.1111/j.1365-2435.2007.01331.x

Lang, S. I., Cornelissen, J. H. C., Shaver, G. R., Ahrens, M., Callaghan, T. V., Molau, U., Ter Braak, C. J. F., Hölzer, A., & Aerts, R. (2012). Arctic warming on two continents has consistent negative effects on lichen diversity and mixed effects on bryophyte diversity. *Global Change Biology*, *18*(3), 1096–1107. https://doi.org/10.1111/j.1365-2486.2011.02570.x

Leppänen, S. M., Salemaa, M., Smolander, A., Mäkipää, R., & Tiirola, M. (2013). Nitrogen fixation and methanotrophy in forest mosses along a N deposition gradient. *Environmental and Experimental Botany*, *90*, 62–69. https://doi.org/10.1016/j.envexpbot.2012.12.006

Lett, S., Jónsdóttir, I. S., Becker-Scarpitta, A., Christiansen, C. T., During, H., Ekelund, F., Henry, G. H. R., Lang, S. I., Michelsen, A., Rousk, K., Alatalo, J. M., Betway, K. R., Rui, S. B., Callaghan, T., Carbognani, M., Cooper, E. J., Cornelissen, J. H. C., Dorrepaal, E., Egelkraut, D., … van Zuijlen, K. (2022). Can bryophyte groups increase functional resolution in tundra ecosystems? *Arctic Science*, *8*(3), 609–637. https://doi.org/10.1139/as-2020-0057

Lett, S., & Michelsen, A. (2014). Seasonal variation in nitrogen fixation and effects of climate change in a subarctic heath. *Plant and Soil*, *379*(1–2), 193–204. https://doi.org/10.1007/s11104-014-2031-y

Lett, S., Teuber, L. M., Krab, E. J., Michelsen, A., Olofsson, J., Nilsson, M.-C., Wardle, D. A., & Dorrepaal, E. (2020). Mosses modify effects of warmer and wetter conditions on tree seedlings at the alpine treeline. *Global Change Biology*, *26*(10), 5754–5766. https://doi.org/10.1111/gcb.15256

Li, Z., Zeng, Z., Tian, D., Wang, J., Wang, B., Chen, H. Y. H., Quan, Q., Chen, W., Yang, J., Meng, C., Wang, Y., & Niu, S. (2020). Global variations and controlling factors of soil nitrogen turnover rate. *Earth-Science Reviews*, *207*, 103250. https://doi.org/10.1016/j.earscirev.2020.103250

Liu, X., & Rousk, K. (2022). The moss traits that rule cyanobacterial colonization. *Annals of Botany*, *129*(2), 147–160. https://doi.org/10.1093/aob/mcab127

Lüdecke, D. (2018). Ggeffects: Tidy data frames of marginal effects from regression models. *Journal of Open Source Software*, *3*(26), 772. https://doi.org/10.21105/joss.00772

Marion, G. M., Henry, G. H. R., Freckman, D. W., Johnstone, J., Jones, G., Jones, M. H., Lévesque, E., Molau, U., Mølgaard, P., Parsons, A. N.,

Svoboda, J., & Virginia, R. A. (1997). Open-top designs for manipulating field temperature in high-latitude ecosystems. *Global Change Biology*, *3*(S1), 20–32. https://doi.org/10.1111/j.1365-2486.1997.gcb136.x

Michelsen, A., Graglia, E., Schmidt, I. K., Jonasson, S., Sleep, D., & Quarmby, C. (1999). Differential responses of grass and a dwarf shrub to long-term changes in soil microbial biomass C, N and P following factorial addition of NPK fertilizer, fungicide and labile carbon to a heath. *The New Phytologist*, *143*(3), 523–538. https://doi.org/10.1046/j.1469-8137.1999.00479.x

Moisander, P., Lehtimäki, J., Sivonen, K., & Kononen, K. (1996). Comparison of $^{15}N_2$ and acetylene reduction methods for the measurement of nitrogen fixation by Baltic Sea cyanobacteria. *Phycologia*, *35*(Supp.6), 140–146. https://doi.org/10.2216/i0031-8884-35-6S-140.1

Mulholland, M. R., Bronk, D. A., & Capone, D. G. (2004). Dinitrogen fixation and release of ammonium and dissolved organic nitrogen by Trichodesmium IMS101. *Aquatic Microbial Ecology*, *37*(1), 85–94. https://doi.org/10.3354/ame037085

Nadelhoffer, K. J., Giblin, A. E., Shaver, G. R., & Linkins, A. E. (1992). Microbial processes and plant nutrient availability in arctic soils. In F. Stuart Chapin III, R. L. Jefferies, R. Reynolds, G. R. Shaver, & J. Svoboda (Eds.), *Arctic ecosystems in a changing climate: An ecophysiological perspective* (pp. 281–300). Academic Press.

Pedersen, A. R. (2020). *HMR*: *Flux estimation with static chamber data*. (R package version 1.0.1.) [Computer software].

Permin, A., Michelsen, A., & Rousk, K. (2022). Direct and indirect effects of warming on moss abundance and associated nitrogen fixation in subarctic ecosystems. *Plant and Soil*, *471*(1), 343–358. https://doi.org/10.1007/s11104-021-05245-9

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & the R Development Core Team. (2018). *nlme*: *Linear and nonlinear mixed effects models*. (R package version 3.1–144) [Computer software].

Porada, P., Bader, M. Y., Berdugo, M. B., Colesie, C., Ellis, C. J., Giordani, P., Herzschuh, U., Ma, Y., Launiainen, S., Nascimbene, J., Petersen, I., Raggio Quílez, J., Rodríguez-Caballero, E., Rousk, K., Sancho, L. G., Scheidegger, C., Seitz, S., Van Stan, J. T., II, Veste, M., … Weston, D. J. (2023). A research agenda for nonvascular photoautotrophs under climate change. *New Phytologist*, *237*, 1495–1504. https://doi.org/10.1111/nph.18631

R Core Team. (2022). *R*: *A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. (4.2.0) [Computer software]. https://www.R-project.org/

Reed, S., Cleveland, C., & Townsend, A. (2011). Functional ecology of free-living nitrogen fixation: A contemporary perspective. *Annual Review of Ecology, Evolution, and Systematics*, *42*, 489–512. https://doi.org/10.1146/annurev-ecolsys-102710-145034

Renaudin, M., Laforest-Lapointe, I., & Bellenger, J.-P. (2022). Unraveling global and diazotrophic bacteriomes of boreal forest floor feather mosses and their environmental drivers at the ecosystem and at the plant scale in North America. *Science of the Total Environment*, *837*, 155761. https://doi.org/10.1016/j.scitotenv.2022.155761

Rousk, K. (2022). Biotic and abiotic controls of nitrogen fixation in cyanobacteria–moss associations. *New Phytologist*, *235*(4), 1330–1335. https://doi.org/10.1111/nph.18264

Rousk, K., Degboe, J., Michelsen, A., Bradley, R., & Bellenger, J.-P. (2017). Molybdenum and phosphorus limitation of moss-associated nitrogen fixation in boreal ecosystems. *New Phytologist*, *214*(1), 97–107. https://doi.org/10.1111/nph.14331

Rousk, K., & Michelsen, A. (2017). Ecosystem nitrogen fixation throughout the snow-free period in subarctic tundra: Effects of willow and birch litter addition and warming. *Global Change Biology*, *23*(4), 1552–1563. https://doi.org/10.1111/gcb.13418

Rousk, K., Pedersen, P. A., Dyrnum, K., & Michelsen, A. (2017). The interactive effects of temperature and moisture on nitrogen fixation in two temperate-arctic mosses. *Theoretical and Experimental Plant Physiology*, *29*(1), 25–36. https://doi.org/10.1007/s40626-016-0079-1

Rousk, K., Sorensen, P. L., Lett, S., & Michelsen, A. (2015). Across-habitat comparison of diazotroph ctivity in the subarctic. *Microbial Ecology*, *69*(4), 778–787. https://doi.org/10.1007/s00248-014-0534-y

Rousk, K., Sorensen, P. L., & Michelsen, A. (2016). Nitrogen transfer from four nitrogen-fixer associations to plants and soils. *Ecosystems*, *19*(8), 1491–1504. https://doi.org/10.1007/s10021-016-0018-7

Rousk, K., Sorensen, P. L., & Michelsen, A. (2017). Nitrogen fixation in the high Arctic: A source of 'new' nitrogen? *Biogeochemistry*, *136*(2), 213–222. https://doi.org/10.1007/s10533-017-0393-y

Rousk, K., Sorensen, P. L., & Michelsen, A. (2018). What drives biological nitrogen fixation in high arctic tundra: Moisture or temperature? *Ecosphere*, *9*(2), e02117. https://doi.org/10.1002/ecs2.2117

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

Saiz, E., Sgouridis, F., Drijfhout, F. P., & Ullah, S. (2019). Biological nitrogen fixation in peatlands: Comparison between acetylene reduction assay and $^{15}N_2$ assimilation methods. *Soil Biology and Biochemistry*, *131*, 157–165. https://doi.org/10.1016/j.soilbio.2019.01.011

Salazar, A., Rousk, K., Jónsdóttir, I. S., Bellenger, J.-P., & Andrésson, Ó. S. (2020). Faster nitrogen cycling and more fungal and root biomass in cold ecosystems under experimental warming: A meta-analysis. *Ecology*, *101*(2), e02938. https://doi.org/10.1002/ecy.2938

Salemaa, M., Lindroos, A.-J., Merilä, P., Mäkipää, R., & Smolander, A. (2019). N_2 fixation associated with the bryophyte layer is suppressed by low levels of nitrogen deposition in boreal forests. *Science of the Total Environment*, *653*, 995–1004. https://doi.org/10.1016/j.scitotenv.2018.10.364

Soper, F. M., Simon, C., & Jauss, V. (2021). Measuring nitrogen fixation by the acetylene reduction assay (ARA): Is 3 the magic ratio? *Biogeochemistry*, *152*(2), 345–351. https://doi.org/10.1007/s10533-021-00761-3

Sorensen, P. L., Jonasson, S., & Michelsen, A. (2006). Nitrogen fixation, denitrification, and ecosystem nitrogen pools in relation to vegetation development in the Subarctic. *Arctic, Antarctic, and Alpine Research*, *38*(2), 263–272. https://doi.org/10.1657/1523-0430(2006)38[263:NFDAEN]2.0.CO;2

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.

St. Martin, P., & Mallik, A. U. (2017). The status of non-vascular plants in trait-based ecosystem function studies. *Perspectives in Plant Ecology, Evolution and Systematics*, *27*, 1–8. https://doi.org/10.1016/j.ppees.2017.04.002

Stal, L. J. (2017). The effect of oxygen concentration and temperature on nitrogenase activity in the heterocystous cyanobacterium *Fischerella* sp. *Scientific Reports*, *7*, 5402. https://doi.org/10.1038/s41598-017-05715-0

Stewart, K. J., Coxson, D., & Grogan, P. (2011). Nitrogen inputs by associative cyanobacteria across a low arctic tundra landscape. *Arctic, Antarctic, and Alpine Research*, *43*(2), 267–278. https://doi.org/10.1657/1938-4246-43.2.267

Stewart, W. D., Fitzgerald, G. P., & Burris, R. H. (1967). In situ studies on N2 fixation using the acetylene reduction technique. *Proceedings of the National Academy of Sciences of the United States of America*, *58*(5), 2071–2078.

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. (2020). Host identity as a driver of moss-associated N_2 fixation rates in Alaska. *Ecosystems*, *24*, 530–547. https://doi.org/10.1007/s10021-020-00534-3

Stuart, R. K., Pederson, E. R. A., Weyman, P. D., Weber, P. K., Rassmussen, U., & Dupont, C. L. (2020). Bidirectional C and N transfer and a

potential role for sulfur in an epiphytic diazotrophic mutualism. *The ISME Journal*, *14*(12), 3068–3078. https://doi.org/10.1038/s41396-020-00738-4

Stuiver, B. M., Wardle, D. A., Gundale, M. J., & Nilsson, M.-C. (2014). The impact of moss species and biomass on the growth of *Pinus sylvestris* tree seedlings at different precipitation frequencies. *Forests*, *5*(8), 1931–1951. https://doi.org/10.3390/f5081931

van Zuijlen, K., Klanderud, K., Knutsen, M. S., Dahle, O. S., Hasvik, Å., Sundsbø, S., Olsen, S. L., & Asplund, J. (2022). Community-level functional traits of alpine vascular plants, bryophytes and lichens after 19 years of experimental warming. *Arctic Science*, *8*(3), 843–857. https://doi.org/10.1139/as-2020-0007

Zielke, M., Ekker, A. S., Olsen, R. A., Spjelkavik, S., & Solheim, B. (2002). The influence of abiotic factors on biological nitrogen fixation in different types of vegetation in the High Arctic, Svalbard. *Arctic Antarctic and Alpine Research*, *43*(3), 293–299. https://doi.org/10.1080/15230430.2002.12003497

Živković, T., Helbig, M., & Moore, T. R. (2022). Seasonal and spatial variability of biological N_2 fixation in a cool temperate bog. *Journal of Geophysical Research: Biogeosciences*, *127*(2), e2021JG006481. https://doi.org/10.1029/2021JG006481

SUPPORTING INFORMATION

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