Research article

Bryophytes dominate plant regulation of soil microclimate in alpine grasslands

Francesca Jaroszynska[1], Inge Althuizen[1,2], Aud Helen Halbritter[1], Kari Klanderud[3], Hanna Lee[2,4], Richard J. Telford[1] and Vigdis Vandvik[1]

[1]Department of Biological Sciences and Bjerknes Centre for Climate Research, University of Bergen, Bergen, Norway
[2]NORCE Norwegian Research Centre AS and Bjerknes Centre for Climate Research, Bergen, Norway
[3]Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway
[4]Department of Biology, Norwegian University of Science and Technology, Trondheim, Norway

Correspondence: Francesca Jaroszynska (fjaroszynska@gmail.com)

Soil temperature and moisture are important regulators of a broad range of biotic and abiotic processes in terrestrial ecosystems. Vegetation can, in turn, play a role in regulating soil microclimate, which creates potential for powerful and interactive feedbacks from soil and vegetation on the atmosphere. Although the regulatory effect of vegetation on soil microclimatic conditions has been quite extensively and empirically assessed, most studies have determined the net effect of intact woody vegetation versus bare ground. However, for other plant functional groups we lack a clear understanding of their role and any climate-context dependency in controlling microclimatic conditions.

We investigated the role of three major plant functional groups – graminoids, forbs and bryophytes – in regulating soil microclimate in semi-natural alpine grasslands. Using a fully factorial above-ground biomass removal experiment, we assessed the role of these plant functional groups in regulating soil temperature amplitude, soil moisture, and number of freezing days. The experiment was replicated across orthogonal temperature and precipitation gradients in Norway to assess whether the effects of functional group abundance varied with climate.

The effect of plant biomass on soil microclimate varied among functional groups across the climatic gradients. Bryophytes reduced growing season soil temperature, whereas graminoids and forbs did not (0.5°C compared to 0°C), and with a stronger effect in colder climates at higher elevations and on days with high solar radiation. Bryophyte biomass further reduced the number of soil freezing days at boreal and sub-alpine sites. Finally, graminoid biomass partly explained variation in soil moisture: soils dried more under graminoids at drier sites.

Our findings highlight that functional group identity plays a key role in regulating soil microclimate in alpine grasslands across seasons. The strong effect of bryophytes on soil temperature points to their importance in the plant community for a variety of ecosystem functions, some of which may be indirectly vulnerable to future warming via biomass reductions of bryophytes.

Keywords: alpine, climate change, forb, graminoid, plant functional group, soil microclimate, bryophyte

Introduction

Soil microclimate regulates a range of ecological processes, many of which exert strong impacts on ecosystem functioning. For example, soil microclimate directly impacts plant growth and performance through the regulation of metabolic rates (Criddle et al. 1997, Xu and Huang 2000) and indirectly through water and nutrient availability (Schimel et al. 1996). In alpine and arctic systems in particular, variation in soil microclimate is important for decomposition rates (Risch et al. 2007, van Zuijlen et al. 2020), seed germination (Soudzilovskaia et al. 2011), and carbon fluxes (Chen et al. 2017, Happonen et al. 2022), because the low stature of the alpine plant canopy strengthens the interaction of atmosphere, vegetation and soil. Enhancing our understanding of factors influencing soil microclimate will improve our predictions of how ecosystem processes will respond to climate change in alpine regions.

Climate is a primary regulator of soil microclimatic conditions in alpine areas, as soil and ambient air temperatures are coupled, at least during the growing season (Graae et al. 2012). The magnitude of the effect of regional climate is also in part determined by precipitation, whereby increased soil moisture via precipitation increases soil heat capacity and latent heating effects (Bonan 2015). Soil microclimate is also affected by cloud cover, both through regulating incoming solar radiation and thus direct heating of vegetation and soil, and through dampening fluctuations in diurnal air temperatures (Dai et al. 1999). This biosphere–atmosphere coupling collapses when the ground is covered by snow (Rixen et al. 2022), suggesting differing dynamics during winter depending on snow cover, which is affected by temperature and precipitation, but also on local wind and topographic conditions (Bonan 2015).

While much variation in soil microclimate is attributable to regional climate, topographical heterogeneity and soil substrate (Wundram et al. 2010, Ashcroft and Gollan 2013), a growing number of studies suggest that vegetation itself can also strongly influence local soil microclimates (Scherrer and Körner 2010, Graham et al. 2012, Aalto et al. 2013, De Frenne et al. 2021, Kemppinen et al. 2021). Plants vary in their capacity to regulate microclimate, according to their physical and functional characteristics such as sward openness, structure and height (von Oppen et al. 2022), although this variation often seems consistent within functional groups. For example, there has been extensive research on the mechanisms determining microclimate regulating capacity for woody plants and in a range of ecosystems (D'Odorico et al. 2013), from semi-arid woodlands (Breshears et al. 1998), to coastal mangrove communities (Devaney et al. 2017, Guo et al. 2017), and arctic-alpine heath (Kemppinen et al. 2021). However, very few studies have assessed how low-stature grassland plants and functional groups regulate soil microclimate in alpine regions (but see von Oppen et al. 2022), which are considered one of the most vulnerable to global climate change (IPBES 2019).

Climate change is driving shifts in the abundance of functional groups (Wookey et al. 2009, Peng et al. 2017).

Graminoid abundance in particular has been found to increase with warming (Brooker and van der Wal 2003, Elmendorf et al. 2012, Winkler et al. 2016), resulting in reduced forb abundance (Jaroszynska 2019) and declines in bryophyte cover (Van Der Wal and Brooker 2004, Klanderud and Totland 2005, Elmendorf et al. 2012, Lang et al. 2012). Alpine plant communities are becoming taller with warming (Bjorkman et al. 2018, Henry et al. 2022). Since alpine regions are greening faster than ever (Rumpf 2022), it is increasingly important to understand how low-stature alpine vegetation regulates microclimate in alpine regions. Despite the importance of soil microclimate in regulating many ecological processes, and our knowledge of the directional changes in functional group abundance and structure with climate change, we still lack a clear understanding of how changing vegetation will affect soil microclimate and thus ecosystem functioning.

Most studies of the relationship between vegetation and soil microclimate in alpine and arctic systems are observational and conducted on whole communities (Zellweger et al. 2019). This makes it difficult to disentangle whether, how, and to what extent plant functional groups differentially affect soil microclimate. While some evidence exists that bryophytes buffer extremes in soil temperature despite the principal influence of topography, climate, and soil properties (Olofsson et al. 2004, Van Der Wal and Brooker 2004, Aalto et al. 2013, Lett et al. 2021, von Oppen et al. 2022), we know very little about the specific regulatory and interactive effects of the major plant functional groups on soil microclimate, and to what extent these effects vary along climate gradients. Because climate change affects plant functional groups differentially, this potentially has consequences for future climate feedbacks. A powerful approach to disentangle the contributions of different plant functional groups is through in situ targeted plant removals. Removal experiments have been used to identify the contributors within plant communities to a variety of ecological processes (Díaz et al. 2003), from biotic interactions (Olsen et al. 2016) to carbon flux (McLaren and Turkington 2010).

We use removal experiments to disentangle the contributions of three functionally unique and important plant functional groups in arctic alpine systems – graminoids, forbs and bryophytes – to regulating soil microclimate. Specifically, we investigate the role of plant functional group identity in regulating soil temperature and soil moisture in summer, and soil freezing in winter, by experimentally removing the aboveground biomass of the three functional groups following a fully factorial design. These removals were replicated along natural temperature and precipitation gradients in Norway, thereby scaling our experiment to the landscape and in so doing explicitly addressing the context-dependency of our findings (Post et al. 2009). We hypothesised that functional groups will differentially moderate the direct effect of temperature and precipitation on local soil microclimate. Specifically, we hypothesised that 1) bryophytes will play the largest role of the three functional groups in regulating local soil temperature relative to

vascular plants because of their mat-like growth form which creates an insulating blanket on the soil (Gornall et al. 2007, Aalto et al. 2013, Lett et al. 2021). We further hypothesised this effect to be strongest at cold alpine sites and sites with high rainfall because of their high water-holding capacity and ability to regulate their transpiration rate (Brodribb et al. 2020) strengthening their heat capacity. We further hypothesised 2) these differences in soil temperature to be largest on sunny days, where evaporative forces are strongest and incoming solar radiation highest. Similarly, we hypothesised that 3) all functional groups would retain soil moisture, and more so at higher biomass levels, since shading generally decreases evaporative moisture loss (Asbjornsen et al. 2011), with the strongest effect by bryophytes because of their high water-holding capacity. Finally, we hypothesised that 4) increased functional group biomass would reduce soil freezing. Specifically, we expected bryophytes would be most effective in reducing the number of freezing events by insulating the soil from frost because of their perennial persistence. We expected differences among functional groups only where there is little snow cover (i.e. low precipitation).

Material and methods

Study locations and removal experiment

The study area encompassed twelve grassland sites in south-western Norway (Klanderud et al. 2015, Olsen et al. 2016, Althuizen et al. 2018, Vandvik et al. 2020, Fig. 1). To quantify both the independent and interactive effects of temperature and precipitation, sites were selected to form a climate grid combining three levels of summer temperature, i.e. the mean of the four warmest months June–September, representing different biogeographic zones (alpine ≈ 6.5°C, sub-alpine ≈ 8.5°C, boreal ≈ 10.5°C) with four levels of mean annual precipitation (1 ≈ 600 mm, 2 ≈ 1200 mm, 3 ≈ 2000 mm, 4 ≈ 2700 mm). Sites were selected to be similar in aspect, slope, soil and bedrock type (see the Supporting information and Klanderud et al. 2015 for further details). At each site, we continuously measured air temperature at 2 m aboveground with UTL-3 ver. 3.0 temperature loggers (GEOTEST AG) and solar radiation with a UVB SKU 430 sensor at 1 m aboveground at 10 min intervals.

At each site we set up four blocks containing eight 25 × 25 cm plots in 2015 (Fig. 1). We removed the aboveground biomass of graminoids, forbs and bryophytes with hand scissors and tweezers in a fully factorial removal experiment. For this study, we used all plots with removal of two functional groups at a time, leaving a single functional group present in each plot (Fig. 1b). The removals were done at the start and peak of the growing season in 2015 and 2016, the timing of which varied across the climate grid. In 2015, biomass removal only occurred once at all alpine and two intermediate sites due to unusually late snowmelt. Further methodological details are described in Vandvik et al. (2022).
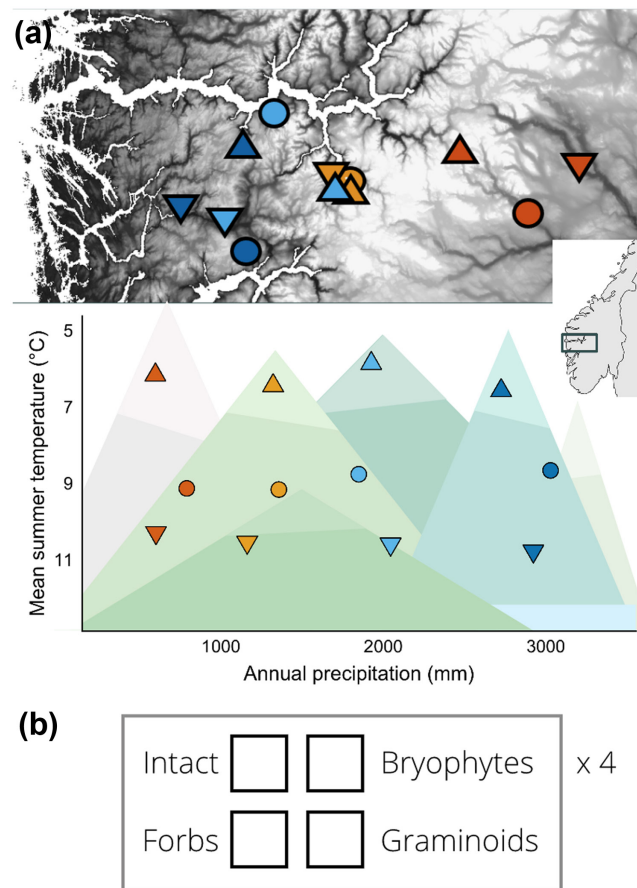

Figure 1. Study area, site selection, and experimental set-up, where (a) depicts the geographical and climatic location of the study area and the 12 study sites. The sites are distributed along independent climate gradients of summer temperature (mean of four warmest months, °C), and annual precipitation (mean annual precipitation, mm). (b) The removal treatments, which are replicated four times at each of the twelve sites, are described in all figures by the functional groups remaining. Note that 'Intact' refers to no removal.

Measurements of functional group cover, structure and biomass

Each year, plant functional group cover was estimated visually at peak growing season as the total percent cover of each separate functional group within the boundaries of the plot. Observations were made from a vertical position above the plot, using a 5 × 5 cm grid placed above the vegetation as a guide (one 5 × 5 cm box corresponds to 4% of the plot's surface). Due to layering of the vegetation, the summed functional group cover may exceed 100%, although no single functional group can exceed 100%. The dominant species found for graminoids were *Nardus stricta*, *Anthoxanthum odoratum* and *Agrostis capillaris*; dominant forb species found were *Potentilla erecta*, *Veronica officinalis* and *Alchemilla* sp. Vascular plant height (mm) was measured as the mean of four point measurements of the vegetative height per plot. Similarly, bryophyte height (mm) was the mean of four measurements from the soil surface. Vascular plant height and

bryophyte height and cover have asymmetrical distributions along the climate gradients, being predominantly taller and covering a greater surface area under warmer growing conditions (Supporting information). To estimate plant functional group biomass, four extra plots were established at each site in 2016, in which vegetation height and cover was recorded as described above before all above-ground biomass was harvested, sorted to functional groups, and dried at 65ºC for 72 h before being weighed.

Measurements of soil microclimate

We measured soil temperature 3–5 cm below the soil surface for each plot using iButton temperature sensors with a resolution of 0.0625°C at 2.4 h intervals from June 2015 to July 2016. These data can be summarised to reveal seasonal patterns in temperature (Fig 2a; note that soil temperature is stable and above freezing under snow in winter), number of soil frost days (Fig. 2b), and diurnal patterns in temperature (Fig 2c). In 2015 and 2016, we measured volumetric soil moisture 3–5 times during each growing season by taking the average of measurements at four places in each plot.

Data cleaning and preparation

Soil temperature was split into daytime and night-time temperatures. We limited daytime temperatures to those recorded between 10:00 and 18:00, when all our sites have the potential for direct sun exposure during the peak growing season (15 June–15 September). Temperatures at other times of the day (from 06:00 to 10:00) were discarded because topographical variation prevents direct sun exposure at some of the sites. Soil temperature data were cleaned by removing loggers that logged infrequently or inconsistently. We visually inspected the data and where loggers began malfunctioning during the year, data were removed from the point at which they deviated from the block norm (i.e. if the variation among loggers in the same block became substantial, such as large temperature spikes, or unrealistically high values (> 30ºC)). Loggers that recorded temperature less frequently than their programmed 2.4 h intervals were also excluded.

To estimate sunniness we ran quantile regressions for UVB with a back spline for date (df = 10, tau = 0.95) for the uppermost 95% of the data for each hour of the day at each site. For each day and each site we calculated a sunniness proportion, which was then weighted by the fitted line to give an estimate of cloudiness where 0 is complete cloud cover and 1 is clear sky. We assigned 'sunny' status to the top third (0.66–1.0, n = 3453) and 'cloud' status to the lowest third (0–0.33, n = 1283). Days with intermediary values (0.34–0.65) were discarded. Missing site-level UVB data were filled with data from a neighbouring site (Supporting information).

To calculate functional group biomass estimates for the remaining functional group in each plot, we ran zero-intercept linear models for each functional group for the extra control plots, whereby functional group biomass varied as a function of its cover. Since bryophyte height was not

measured in 2015, we used bryophyte height data from 2017, averaged across blocks for each treatment and site. We extracted the coefficients for each model, and multiplied the cover of each functional group in the studied treatment plots by the biomass coefficient. See the Supporting information for further details on the regression models.

Data analyses

Only plots with a single functional group present (i.e. where the two other groups were removed) were used in the analyses. We used linear mixed effects models (Gaussian error distribution family) to analyse the effect of functional group biomass on soil microclimate during peak growing season (15 July 2015–15 September 2015). First, to gauge the importance of large-scale variation in climate across sites and local weather fluctuations on soil temperature (Fig. 2b), we ran linear models for the effect of temperature, precipitation, and sunniness on maximum daily soil temperature T_{max},

$$T_{max} \sim S + P_{site} \times T_{site} \qquad (1)$$

where S is the degree of sunniness, and P_{site} is the scaled and centred 1970–2010 interpolated mean annual precipitation (100 ml year^{-1}, hereafter precipitation) per site and T_{site} is the scaled and centred 1970–2010 interpolated mean summer temperature (ºC, four warmest months, hereafter summer temperature) per site. We found sunniness and regional temperature to be the strongest drivers of soil temperature (Supporting information), which led us to split the following models into two – one for soil temperature on sunny days and one on cloudy days (Fig. 2c). Furthermore, due to a lack of significance of the interaction term $P_{site} \times T_{site}$ and model overfitting we split each climate axis in the above sunniness scenarios, resulting in a total four separate models. Thus, the model for the response of maximum daily soil temperature T_{max} to functional group biomass quantity biomass and summer temperature on sunny days is as follows:

$$T_{max} \sim \text{Biomass} \times T_{site} \qquad (2)$$

where T_{site} is mean site summer temperature. We used a nested random effect structure to account for variation among plots and among sites and to avoid pseudoreplication; thus plots nested within sites. A further model was run for T_{max}, replacing T_{site} with P_{site}. Identical models were set up for cloudy days (Supporting information). Next, we set up linear mixed effects models to test the effect of functional group biomass and climate on soil moisture (SM) on all days (sunny and overcast), following the same model specifications as in Eq. 2 but with SM as the response variable.

Finally, we ran zero-inflated mixed effects models (Poisson error distribution family) for the effect of functional group biomass quantity biomass and climate on the sum of frost days (FD) (Fig. 2b). The model employed the following structure:
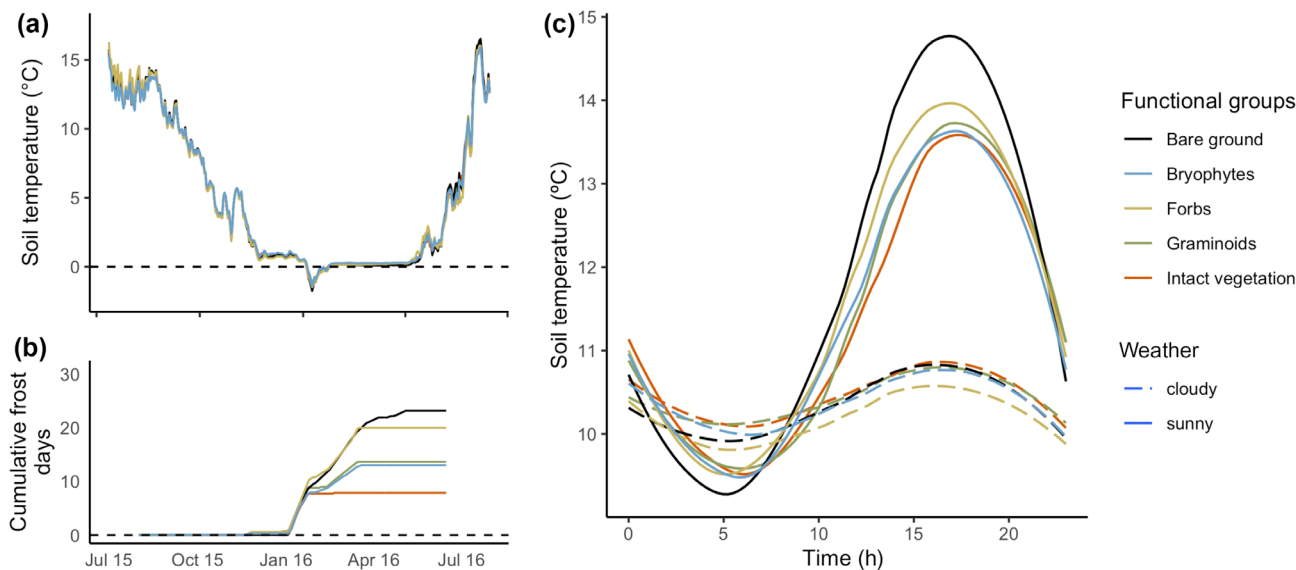
Figure 2. Illustration of the effect of different plant functional groups on soil temperature at the sub-alpine sites (n = 4). (a) Seasonal trends in daily maximum soil temperature from July 2015 to July 2016, and (b) the cumulative frost day sum. (c) Average diurnal temperature fluctuation for August and September 2015 on sunny (solid lines) and cloudy (dashed lines) days. Colours indicate presence of plant functional groups.

$$FD \sim Biomass \times T_{site}$$

$$z_i = \sim Biomass \times T_{site} \tag{3}$$

where T_{site} is summer temperature per site, and with a nested random effects structure (plots nested within sites). The zero-inflated model structure z_i contained an interaction between summer temperature and precipitation, to account for the insulation of snow that appeared towards wetter and colder sites. We ran a further model for FD, replacing T_{site} with P_{site}, precipitation. Model diagnostics were checked by examining the normality of the residuals, and via a residuals plot. All statistical analyses were performed in R ver. 4.2.0 (www.r-project.org) and models fitted with the 'lme4' package for soil temperature and moisture (Bates et al. 2015) and the 'glmmTMB' package for soil freezing (Brooks et al. 2017), and illustrated with the 'sjPlot' package (Lüdecke 2023).

Results

Variation in maximum daily growing season soil temperature across sites is predominantly explained by regional climate, increasing by a mean of 0.97°C on sunny days and 0.90°C on overcast days with each 1°C increase of mean summer temperature along the temperature gradient (Fig. 3, Supporting information). Nevertheless, plant biomass explained further variation in soil temperature, but this effect is only apparent on sunny days, and varied among functional groups and along bioclimatic gradients. Indeed, solar radiation proved to be the primary regulator of soil temperature, with large daily temperature amplitudes on sunny days but not on overcast days (Supporting information).

Soil temperatures are affected by functional group biomass

Bryophytes had the strongest effect on soil microclimate of the three functional groups, significantly reducing daily maximum soil temperatures on sunny days by 0.38°C g⁻¹ biomass (significant biomass term, Fig. 3a, Supporting information), and this effect varied significantly along the regional temperature gradient, with bryophyte biomass reducing soil temperature more strongly in alpine sites than at boreal and sub-alpine sites (significant biomass × temperature term, Fig. 3a, Supporting information), and at drier compared to wetter sites (significant biomass × precipitation term Fig. 4a, Supporting information). In contrast, graminoids and forbs had much weaker effects on soil maximum temperature than bryophytes overall, and these effects only became evident in relation to precipitation in the precipitation models (Supporting information). Graminoid biomass reduced daily soil temperature maxima increasingly towards drier sites (Fig. 4c, Supporting information); in contrast, forb biomass marginally increased soil temperatures at drier sites but reduced soil temperatures at wetter sites (Fig. 4b, Supporting information). Soil temperature did not vary with biomass of any functional group on overcast days (Fig. 3).

Biomass reduces soil freezing and soil moisture

We found that while the number of soil frost days was strongly affected by regional temperature and precipitation, with significant increases towards both colder conditions and drier conditions, plant functional group biomass also plays a significant role (Fig. 5, Supporting information). In general, there were fewer soil freezing days in plots with greater bryophyte biomass at higher site temperatures (Fig. 5a). In contrast,
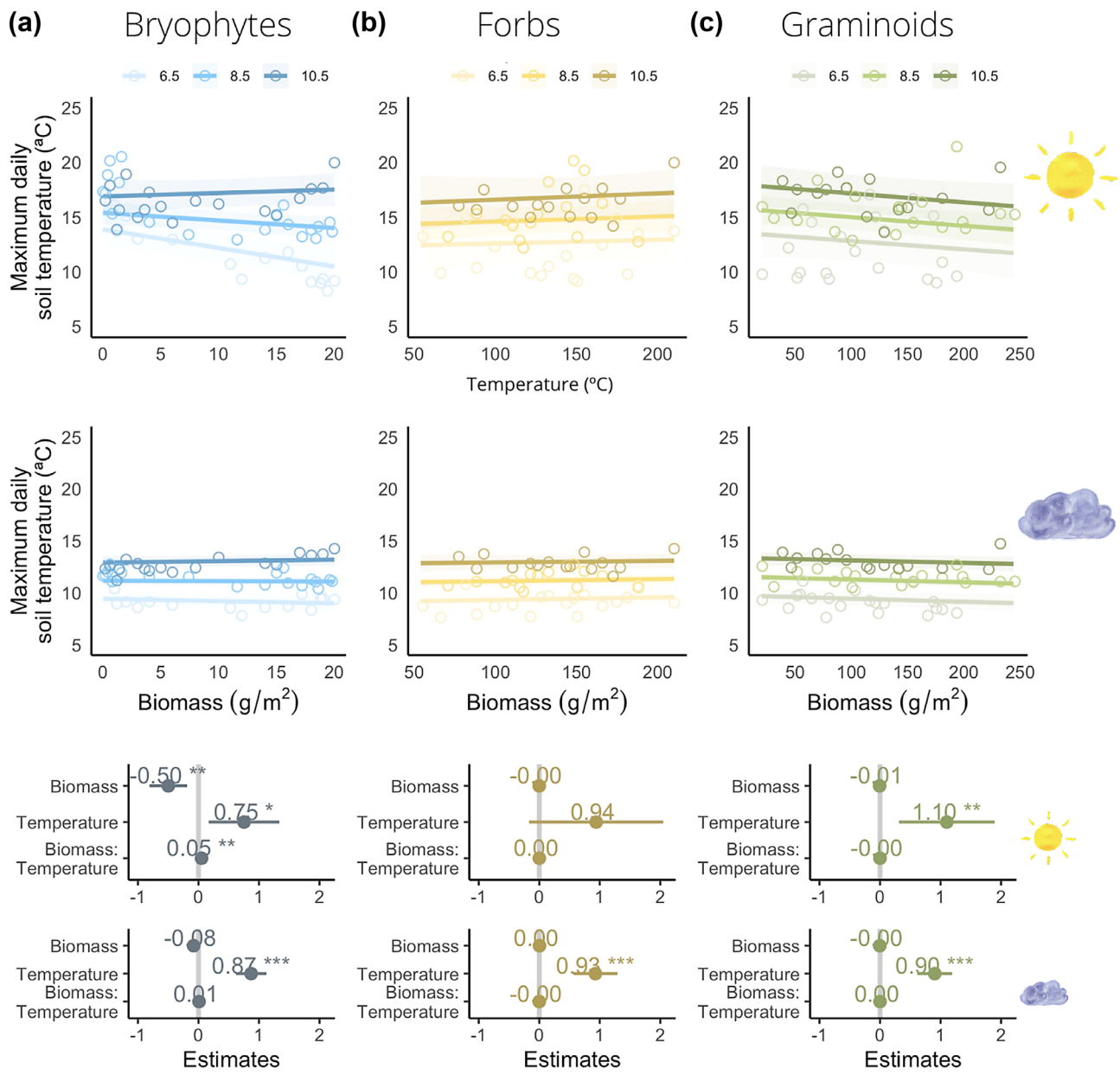
Figure 3. Effect of plant functional group biomass and site temperature on daily maximum growing season soil temperature in alpine (6.5ºC), sub-alpine (8.5ºC), and boreal (10.5ºC) grasslands on sunny (upper panels) and cloudy days (lower panels) for (a) bryophytes (blue), (b) forbs (yellow) and (c) graminoids (green). Ribbons on the upper panels show the 95% confidence interval around the predicted lines, and points represent the mean maximum temperature for each plot. Colour intensity of the prediction lines represents alpine (lighter), sub-alpine, and boreal (darker) climates. Note the range of biomass differs for each functional group, from 0–20 g m^{-2} for bryophytes, to 0–250 g m^{-2} for graminoids. Standardised forest plots of effect sizes or estimates (doubled SD) are illustrated below the prediction figures, where variables that deviate left of the solid grey line demonstrate a reduction in soil temperature with the corresponding variable, and variables that deviate right of the line demonstrate an increase in soil temperature. Significant variables are shown as *** = p < 0.001, ** = p < 0.01, and * = p < 0.05.

forb biomass significantly increased the number of frost days at warmer temperatures, although the effect size is negligible (Fig. 5b). Graminoid biomass did not affect soil freezing along the temperature gradient. Along the precipitation gradient, soil freezing was unaffected by plant biomass except for forbs (whose effect was negligible, see Supporting information).

Soil moisture varied significantly as an effect of graminoid biomass along the precipitation gradient (significant biomass × precipitation, Fig. 6c). Increased graminoid biomass significantly increased soil moisture at high precipitation sites, but reduced soil moisture in drier sites (Fig. 6). Neither bryophyte nor forb biomass affected soil moisture (Fig. 6a–b).
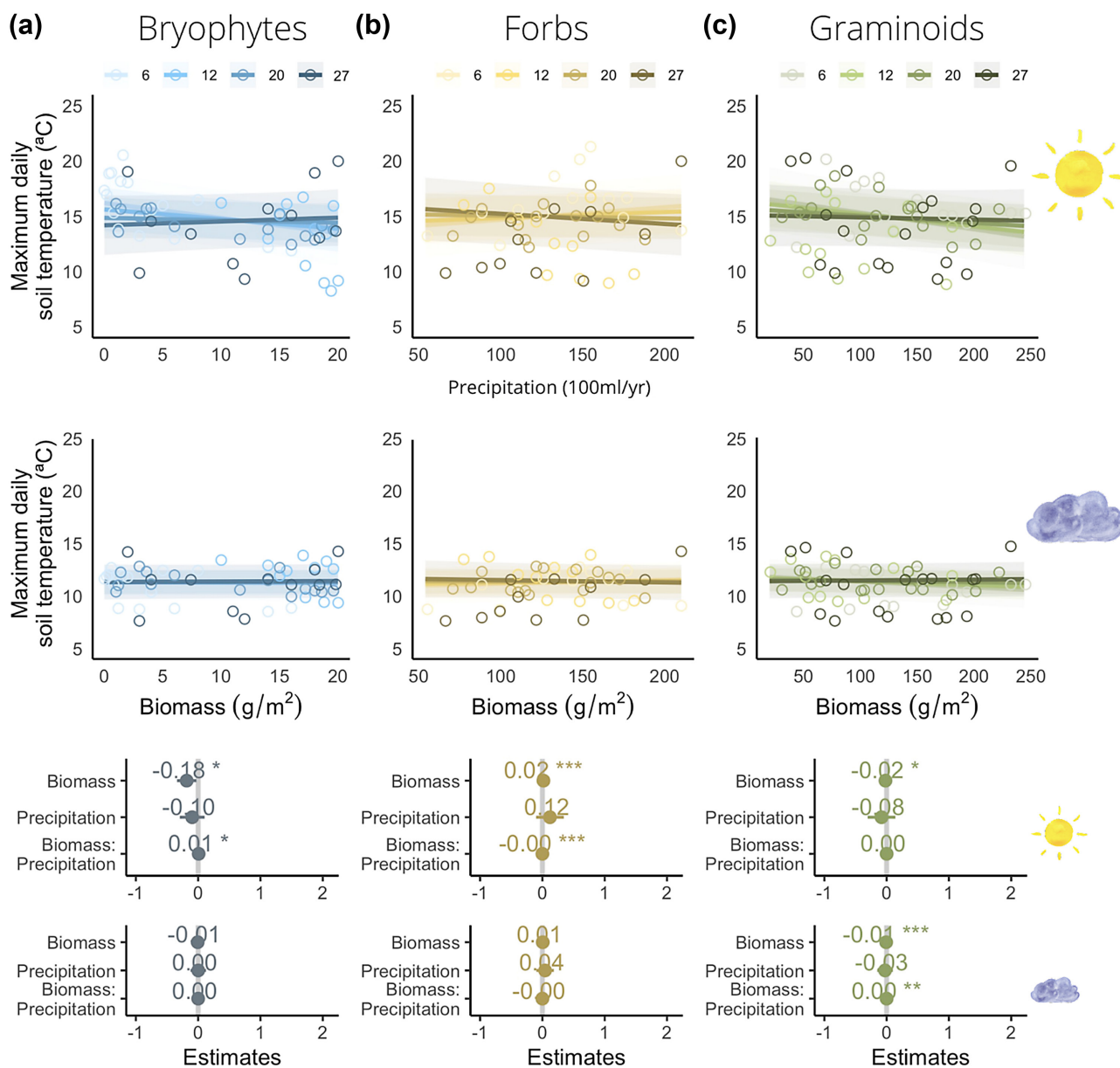
Figure 4. Effect of plant functional group biomass and annual site precipitation on daily maximum growing season soil temperature in dry (600 ml year⁻¹), semi-dry (1200 ml year⁻¹), semi-wet (2000 ml year⁻¹), and wet (2700 ml year⁻¹) grasslands on sunny (upper panels) and cloudy days (lower panels) for (a) bryophytes (blue), (b) forbs (yellow), and (c) graminoids (green). Ribbons on the upper panels show the 95% confidence interval around the predicted lines, and points represent the mean maximum temperature for each plot. Colour intensity of the prediction lines represents dry (lighter), semi-dry, semi-wet, and wet (darker) climates. Note the range of biomass differs for each functional group, from 0–20 g m⁻² for bryophytes, to 0–250 g m⁻² for graminoids. Standardised forest plots of effect sizes or estimates (doubled SD) are illustrated below the prediction figures, where variables that deviate left of the solid grey line demonstrate a reduction in soil temperature with the corresponding variable, and variables that deviate right of the line demonstrate an increase in soil temperature. Significant variables are shown as ***=p < 0.001, **=p < 0.01 and *=p < 0.05.

Discussion

Our study demonstrates the importance of vegetation, in particular bryophytes, in moderating the strong effect of solar radiation and ambient summer air temperature on soil microclimate (in line with Isard 1986, Wundram et al. 2010, Scherrer and Körner 2011). During the growing season, high bryophyte biomass was linked to significantly cooler soils, especially at alpine sites and in drier regions, while increased forb or graminoid biomass had similar but much weaker effects, which largely materialised as variable responses along the precipitation gradient. Increased bryophyte biomass is further associated with a reduced occurrence of soil freezing events during the winter season
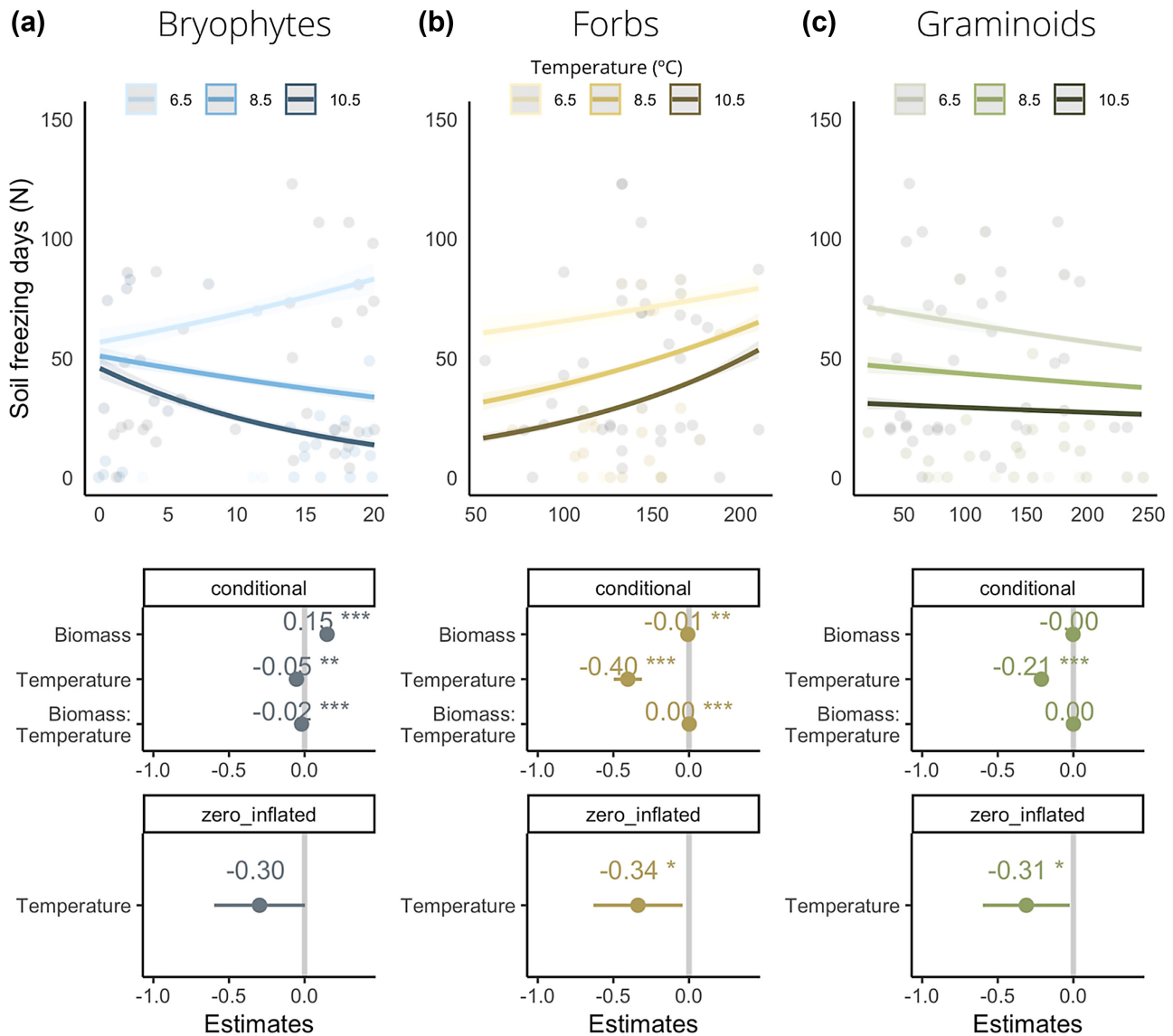
Figure 5. Effect of plant functional group biomass and site temperature on accumulated soil freezing days in alpine (6.5°C), sub-alpine (8.5°C), and boreal (10.5°C) grasslands for (a) bryophytes (blue), (b) forbs (yellow), and (c) graminoids (green). Ribbons on the upper panels show the 95% confidence interval around the predicted lines, and points represent the mean maximum temperature for each plot. Colour intensity of the prediction lines represents alpine (lighter), sub-alpine, and boreal (darker) climates. Note the range of biomass differs for each functional group, from 0–20 g m⁻² for bryophytes, to 0–250 g m⁻² for graminoids. Standardised forest plots of effect sizes or estimates (doubled SD) of the conditional and zero-inflated components are illustrated below the prediction figures, where variables that deviate left of the solid grey line demonstrate a reduction in soil freezing days with the corresponding variable, and variables that deviate right of the line demonstrate an increase in soil freezing days. Significant variables are shown as ***=$p < 0.001$, **=$p < 0.01$ and *=$p < 0.05$.

in warmer regions, unlike forb and graminoid biomass. In contrast to our expectations, soil moisture variation was affected only by graminoid biomass, with soils drying more under graminoids at drier sites. Our results highlight that the effect of plant functional groups on the direction and magnitude of soil temperature and moisture mediation along the climate gradients varies among groups. Consequently, climate change-induced shifts in functional group abundances could have significant consequences for soil microclimate, and subsequently ecosystem functioning, in alpine grasslands.

Bryophytes regulate soil temperature

Bryophyte biomass was an important predictor of summer soil temperatures, reducing soil temperatures more than forbs and graminoids (Fig. 3). We found that increased bryophyte biomass is progressively more effective at dampening soil temperature fluctuations towards alpine conditions, which supports previous findings that bryophyte mats have an insulating effect for alpine soils (Gornall et al. 2007, 2011, Soudzilovskaia et al. 2013). Such a disproportionate effect of bryophytes compared to forbs and graminoids, both overall
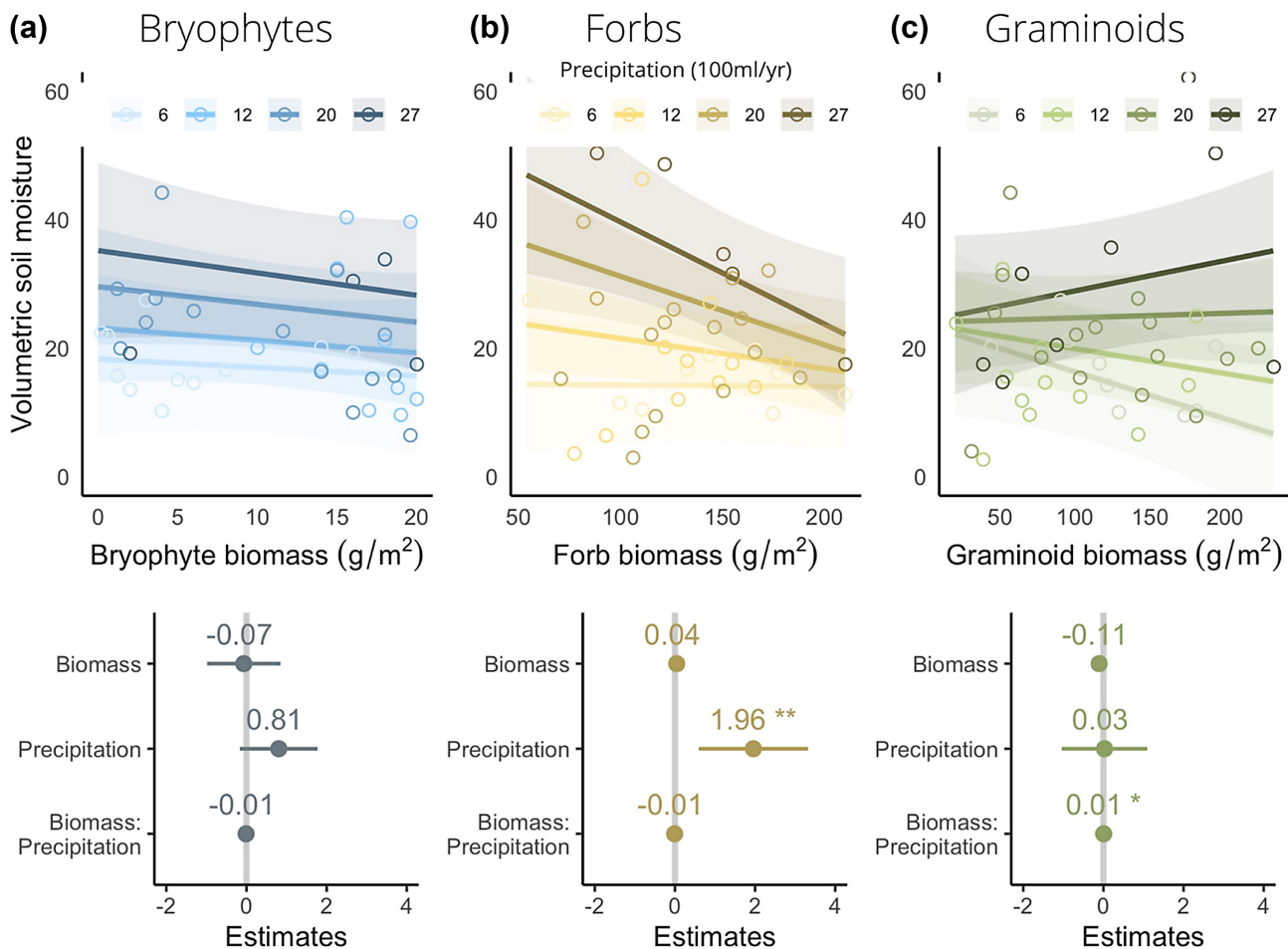
Figure 6. Effect of plant functional group biomass and annual site precipitation on growing season soil moisture in dry (600 ml year⁻¹), semi-dry (1200 ml year⁻¹), semi-wet (2000 ml year⁻¹), and wet (2700 ml year⁻¹) grasslands for (a) bryophytes (blue), (b) forbs (yellow), and (c) graminoids (green). Ribbons on the upper panels show the 95% confidence interval around the predicted lines, and points represent the mean maximum temperature for each plot. Colour intensity of the prediction lines represents dry (lighter), semi-dry, semi-wet, and wet (darker) climates. Note the range of biomass differs for each functional group, from 0–20 g m⁻² for bryophytes, to 0–250 g m⁻² for graminoids. Standardised forest plots of effect sizes or estimates (doubled SD) are illustrated below the prediction figures, where variables that deviate left of the solid grey line demonstrate a reduction in soil moisture with the corresponding variable, and variables that deviate right of the line demonstrate an increase in soil moisture. Significant variables are shown as *** = p < 0.001, ** = p < 0.01 and * = p < 0.05.

and along the temperature gradient, may be explained by their high water-holding capacity and thus large heat capacity.

Forb and graminoid biomass had much weaker effects on soil temperature. Indeed, along both the temperature and precipitation gradients, the effect of forb and graminoid abundance is much smaller than that of bryophytes. This could be explained by the difference in canopy structure between the three functional groups, since canopy structure has been found to be important for regulating both canopy and soil temperature, whereby soils under canopies that are characterised by erecto-linear leaves are generally warmer (Fliervoet and Werger 1984, although note that in their study, intact communities were studied). Bryophytes are characterised by a low and dense canopy, whereas the graminoid sward is relatively erect-linear and also more open. Nevertheless, the variation in canopy openness of bryophytes along the temperature gradient, with denser-canopy forming species found

in alpine terrain may explain the increased cooling effect of bryophytes in alpine sites (see the Supporting information for the most dominant species). This suggests that different functional characteristics of the vegetation are important for determining physical soil microclimate, at least in alpine regions. The differences in canopy structure could therefore be an explanation for the observed differences among functional groups in soil temperature regulation. The cooling effect of bryophytes on alpine soils may have indirect consequences for ecosystem functioning, such as summer permafrost thaw. A meta-analysis of vegetation change in the tundra biome suggested that increased vegetation height (including bryophytes and graminoids) resulted in reduced summer permafrost thaw (Heijmans et al. 2022). Such effects could be extended to other ecosystem processes such as soil decomposition rates, which are generally slower in cold conditions (Heijmans et al. 2022).

Bryophyte biomass protects soils from freezing events

We found that bryophyte abundance limits the number of soil-freezing days in winter at boreal and sub-alpine regions, while graminoids and forbs are less capable of doing so (Fig. 5). This is in line with previous findings that bryophytes reduce the number of freeze–thaw events in subarctic ecosystems (Soudzilovskaia et al. 2013). Freeze–thaw frequency affects the composition of microbial communities in soil, which can alter carbon and nitrogen release (Yergeau and Kowalchuk 2008, Vestgarden and Austnes 2009, Haei et al. 2011). In this way, the presence of bryophytes can significantly influence carbon and nutrient turnover (Soudzilovskaia et al. 2013). Our finding that bryophytes reduce soil freezing suggests that their dampening effect on soil temperature may be negated by their extension of decomposition processes into colder seasons, with potentially substantial consequences for carbon sequestration in alpine grasslands (Bjerke et al. 2015). Microbial effects may also be at play under bryophyte mats, thus regulating microclimate and decomposition rates through their associated microbial communities, with knock-on consequences for carbon sequestration and release (Ward et al. 2015).

Carbon release from alpine soils under warming might therefore be exacerbated under climate warming, since the effect of bryophytes on soil temperature regulation is strongest under colder conditions. Nevertheless, the effect that plant functional group biomass has on soil freezing is small in comparison to the large-scale climate gradient effects. This may be due to variation in interannual winter conditions and snow cover and thickness extent. Non-woody functional groups may have a smaller effect than other plant functional groups such as shrubs or dwarf shrubs, since these freezing days occur during the shoulder periods of winter, where the non-woody biomass is least. This may be the case for forbs and most graminoids, which die back towards the onset of winter, but biomass persistence of bryophytes could explain why the number of frost days is lower where bryophyte biomass is higher. Some graminoids (e.g. *Poa alpina*) also retain some biomass across years, but the abundance of these species, and the amount of biomass that this amounts to, may only have extremely local effects.

At cold sites and at dry sites, the number of frost days was elevated despite the presence of plant biomass, and higher under bryophytes than other functional groups (Fig. 5, Supporting information). Such sites are prone to snow-free periods during the winter, and our results suggest that low-stature functional groups are unable to moderate soil freezing events under these conditions, with greater potential for freeze–thaw events (Bokhorst et al. 2010). This could be an indication, however, of the role that bryophytes have on maintaining soil freezing, and thus on the persistence of permafrost.

Evapotranspiration effects by graminoids

We found that little to no variation in soil moisture was explained by forb and bryophyte biomass. This is contrary to previous findings of a mediative effect by bryophyte presence on soil moisture in alpine and tundra soils, whereby a decrease in bryophyte cover resulted not only in greater soil heating but also increased evaporative rates (Blok et al. 2011, Bueno et al. 2016, von Oppen et al. 2022). Such disparities might be explained by differences in the precipitation space covered in these studies, where the mean annual precipitation falls as low as 205 mm year^{-1}. In our high-precipitation study region, where annual precipitation ranges from 600 to over 3000 mm year^{-1}, any effect of vegetation on soil moisture via transpiration or evaporation might be negligible compared to the effect of mean annual precipitation (Fig. 6, Supporting information). One would expect that effects of vegetation on soil moisture depend on the ratios of supply to demand, and evaporation versus transpiration, which vary widely among ecosystems (Ehrenfeld et al. 2005).

However, our findings suggest that at the drier sites, graminoid biomass is associated with soil drying. Another removal experiment has also demonstrated that soil moisture was higher in plots with forbs and graminoids removed compared to intact controls (McLaren and Turkington 2010). This could be indicative of an increased evapotranspirative effect of graminoids. Graminoids are characterised by their fast, opportunistic functional traits and high evapotranspiration rates (Díaz et al. 2016), which would explain why graminoids and not forbs exhibit this drying effect. In places where soil moisture reaches saturation, any drying effect of biomass is lost (Fig. 6).

Nevertheless, our soil moisture findings should be interpreted with caution, since our data are limited (point measurements only) and the functional group effects small and variable. Continuous soil moisture data may have revealed a more accurate picture of the underlying mechanisms determining soil moisture. The discrepancy among the studies mentioned above, and our own findings, indicates that soil moisture might act at a different scale to that which is measured at our plot scale, being either even more localised and heterogeneous, or acting at the much larger catchment scale. In both scenarios, more measurements and a better estimation of catchment size might give better estimations of the true role that vegetation plays in mediating soil moisture, although this would be complicated experimentally. A third alternative is that water stress may act by thresholds rather than as a continuum, which implies that further investigation across larger precipitation and soil moisture gradients should be conducted. As suggested by Wundram et al. (2010) and Legates et al. (2011), the interaction of soil temperature with soil moisture may not be linear, soil temperatures being reduced where soils are wet as a result of their heat capacity.

Implications under climate change and ecosystem functioning

The functional properties of vegetation appear to be key in determining multiple aspects of soil microclimate. For example, canopy structure (density and height) could explain the

strong effects of bryophytes on soil temperature; vegetation persistence and deciduousness may be important in reducing soil freezing events before snow cover; and, finally, leaf area and sward openness may determine soil moisture. Thus, functional traits may be important indirectly for ecosystem processes such as decomposition (Scherer-Lorenzen 2008). The complementary effect of different functional groups on varying aspects of soil microclimate may interplay to result in an overall cooling effect of vegetation, as suggested by von Oppen et al. (2022).

Alpine areas in Europe are rapidly increasing in vascular plant diversity, height and cover (Bjorkman et al. 2018, Steinbauer et al. 2018, Rumpf et al. 2022), mirrored by similar declines in bryophyte cover and richness (Alatalo et al. 2020). Bryophyte cover and abundance vary in response to climate warming (Elmendorf et al. 2012, Alatalo et al. 2016, Vanneste et al. 2017) and they have been shown to have locally varying insulating properties both in permafrost regions (Blok et al. 2011, Porada et al. 2016) and in tundra and alpine vegetation (Soudzilovskaia et al. 2013, Lett et al. 2017). Our findings demonstrate that bryophytes, and not low-stature forbs and graminoids, are most important for regulating soil microclimate in alpine grasslands. We advocate that direct and indirect effects of climate change on bryophyte abundance, especially in alpine areas, could have substantial effects on soil microclimate, and therefore ecosystem functioning and feedbacks such as lowland species' colonisation of alpine communities (Vandvik et al. 2020). This supports previous findings of functional group-regulated and soil temperature-dependent ecosystem respiration (Cahoon et al. 2012).

Our findings also suggest that the predictions of increased precipitation in southern Norway (Hanssen-Bauer et al. 2017), and thus increased cloud cover and reduced direct solar radiation, may lead to more homogeneous soil microclimates.

Conclusions

We show that functional group abundance can have important impacts on soil microclimate, and this could have important implications for ecosystem processes under climate change. We argue that bryophytes have a disproportionate effect on soil microclimate, reducing soil temperature on sunny days and causing an overall homogenisation of soil microclimate throughout the growing season in alpine environments. Because of these strong effects, a shift in bryophyte abundance and functional composition with climate change will have significant local effects on soil microclimate and biogeochemical processes. Our study implies that vegetation–soil–atmosphere feedbacks may strengthen under climate change, emphasising the importance of taking effects of the functional composition of vegetation on microclimate into consideration when assessing climate change effects on ecosystem functioning. This demonstrates that more detailed information of plant functioning will improve predictions of ecosystem functioning.

Author contributions

Francesca Jaroszynska: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Methodology (equal); Resources (supporting); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Inge Althuizen**: Conceptualization (lead); Formal analysis (supporting); Methodology (equal); Visualization (supporting); Writing – review and editing (supporting). **Aud Helen Halbritter**: Data curation (supporting); Writing – review and editing (supporting). **Kari Klanderud**: Conceptualization (supporting); Funding acquisition (supporting); Project administration (supporting); Supervision (equal); Writing – review and editing (supporting). **Hanna Lee**: Conceptualization (supporting); Methodology (supporting); Writing – review and editing (supporting). **Richard J. Telford**: Formal analysis (supporting); Methodology (supporting); Writing – review and editing (supporting). **Vigdis Vandvik**: Conceptualization (lead); Funding acquisition (lead); Methodology (equal); Project administration (lead); Resources (lead); Supervision (equal); Writing – review and editing (equal).

Data availability statement

Data are available at : https://doi.org/10.1038/s41597-022-01559-0 (Vandvik et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Aalto, J., le Roux, P. C. and Luoto, M. 2013. Vegetation mediates soil temperature and moisture in arctic-alpine environments. – Arct. Antarct. Alp. Res. 45: 429–439.

Alatalo, J. M., Jägerbrand, A. K. and Molau, U. 2016. Impacts of different climate change regimes and extreme climatic events on an alpine meadow community. – Sci. Rep. 6: 21720.

Alatalo, J. M., Jägerbrand, A. K., Erfanian, M. B., Chen, S., Sun, S.Q. and Molau, U. 2020. Bryophyte cover and richness decline after 18 years of experimental warming in alpine Sweden. – AoB Plants 12: plaa061.

Althuizen, I. H. J., Lee, H., Sarneel, J. M. and Vandvik, V. 2018. Long-term climate regime modulates the impact of short-term climate variability on decomposition in alpine grassland soils. – Ecosystems 21: 1580–1592.

Asbjornsen, H., Goldsmith, G. R., Alvarado-Barrientos, M. S., Rebel, K., Van Osch, F. P., Rietkerk, M., Chen, J., Gotsch, S., Tobon,

C., Geissert, D. R., Gomez-Tagle, A., Vache, K. and Dawson, T. E. 2011. Ecohydrological advances and applications in plant–water relations research: a review. – J. Plant Ecol. 4: 3–22.

Ashcroft, M. B. and Gollan, J. R. 2013. Moisture, thermal inertia, and the spatial distributions of near-surface soil and air temperatures: understanding factors that promote microrefugia. – Agric. For. Meteorol. 176: 77–89.

Bates, D., Mächler, M., Bolker, B. and Walker, S. 2015. Fitting linear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48.

Bjerke, J. W., Tømmervik, H., Zielke, M. and Jørgensen, M. J. E. R. L. 2015. Impacts of snow season on ground-ice accumulation, soil frost and primary productivity in a grassland of sub-Arctic Norway. – Environ. Res. Lett. 10: 095007.

Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Rüger, N., Beck, P. S., Blach-Overgaard, A., Blok, D., Cornelissen, J. H. C. and Forbes, B. C. 2018. Plant functional trait change across a warming tundra biome. – Nature 562: 57–62.

Blok, D., Heijmans, M. M. P. D., Schaepman-Strub, G., van Ruijven, J., Parmentier, F. J. W., Maximov, T. C. and Berendse, F. 2011. The cooling capacity of mosses: controls on water and energy fluxes in a Siberian tundra site. – Ecosystems 14: 1055–1065.

Bokhorst, S., Bjerke, J. W., Melillo, J., Callaghan, T. V. and Phoenix, G. K. 2010. Impacts of extreme winter warming events on litter decomposition in a sub-Arctic heathland. – Soil Biol. Biochem. 42: 611–617.

Bonan, G. 2015. Ecological climatology: concepts and applications, 3rd edn. – Cambridge Univ. Press.

Breshears, D. D., Nyhan, J. W., Heil, C. E. and Wilcox, B. P. 1998. Effects of woody plants on microclimate in a semiarid woodland: soil temperature and evaporation in canopy and intercanopy patches. – Int. J. Plant Sci. 159: 1010–1017.

Brodribb, T. J., Carriquí, M., Delzon, S., McAdam, S. A. M. and Holbrook, N. M. 2020. Advanced vascular function discovered in a widespread moss. – Nat. Plants 6: 273–279.

Brooker, R. and van der Wal, R. 2003. Can soil temperature direct the composition of high arctic plant communities? – J. Veg. Sci. 14: 535–542.

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M. and Bolker, B. M. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. – R J. 9: 378–400.

Bueno, C. G., Williamson, S. N., Barrio, I. C., Helgadóttir, Á. and HiK, D. S. 2016. Moss mediates the influence of shrub species on soil properties and processes in alpine tundra. – PLoS One 11: e0164143.

Cahoon, S. M., Sullivan, P. F., Shaver, G. R., Welker, J. M., Post, E. and Holyoak, M. 2012. Interactions among shrub cover and the soil microclimate may determine future Arctic carbon budgets. – Ecol. Lett. 15: 1415–1422.

Chen, J., Luo, Y., Xia, J., Wilcox, K. R., Cao, J., Zhou, X., Jiang, L., Niu, S., Estera, K. Y., Huang, R., Wu, F., Hu, T., Liang, J., Shi, Z., Guo, J. and Wang, R. 2017. Warming effects on ecosystem carbon fluxes are modulated by plant functional types. – Ecosystems 20: 515–526.

Criddle, R. S., Smith, B. N. and Hansen, L. D. 1997. A respiration based description of plant growth rate responses to temperature. – Planta 201: 441–445.

Dai, A., Trenberth, K. E. and Karl, T. R. 1999. Effects of clouds, soil moisture, precipitation, and water vapor on diurnal temperature range. – J. Clim. 12: 2451–2473.

Devaney, J. L., Lehmann, M., Feller, I. C. and Parker, J. D. 2017. Mangrove microclimates alter seedling dynamics at the range edge. – Ecology 98: 2513–2520.

De Frenne, P. et al. 2021. Forest microclimates and climate change: importance, drivers and future research agenda. – Global Change Biol. 27: 2279–2297.

Díaz, S., Symstad, A. J., Stuart Chapin, F., Wardle, D. A. and Huenneke, L. F. 2003. Functional diversity revealed by removal experiments. – Trends Ecol. Evol. 18: 140–146.

Díaz, S. et al. 2016. The global spectrum of plant form and function. – Nature 529: 167–171.

D'Odorico, P., He, Y., Collins, S., De Wekker, S. F. J., Engel, V. and Fuentes, J. D. 2013. Vegetation–microclimate feedbacks in woodland-grassland ecotones. – Global Ecol. Biogeogr. 22: 364–379.

Ehrenfeld, J. G., Ravit, B. and Elgersma, K. 2005. Feedback in the plant–soil system. – Annu. Rev. Environ. Resour. 30: 75–115.

Elmendorf, S. C. et al. 2012. Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. – Ecol. Lett. 15: 164–175.

Fliervoet, L. M. and Werger, M. J. A. 1984. Canopy structure and microclimate of two wet grassland communities. – New Phytol. 96: 115–130.

Gornall, J. L., Jónsdóttir, I. S., Woodin, S. J. and Van der Wal, R. 2007. Arctic mosses govern below-ground environment and ecosystem processes. – Oecologia 153: 931–941.

Gornall, J. L., Woodin, S. J., Jónsdóttir, I. S. and van der Wal, R. 2011. Balancing positive and negative plant interactions: how mosses structure vascular plant communities. – Oecologia 166: 769–782.

Graae, B. J., De Frenne, P., Kolb, A., Brunet, J., Chabrerie, O., Verheyen, K., Pepin, N., Heinken, T., Zobel, M., Shevtsova, A., Nijs, I. andMilbau, A. 2012. On the use of weather data in ecological studies along altitudinal and latitudinal gradients. – Oikos 121: 3–19.

Graham, E. A., Rundel, P. W., Kaiser, W., Lam, Y., Stealey, M. and Yuen, E. M. 2012. Fine-scale patterns of soil and plant surface temperatures in an alpine fellfield habitat, White Mountains, California. – Arct. Antarct. Alp. Res. 44: 288–295.

Guo, H., Weaver, C., Charles, S. P., Whitt, A., Dastidar, S., D'Odorico, P., Fuentes, J. D., Kominoski, J. S., Armitage, A. R. and Pennings, S. C. 2017. Coastal regime shifts: rapid responses of coastal wetlands to changes in mangrove cover. – Ecology 98: 762–772.

Haei, M., Rousk, J., Ilstedt, U., Öquist, M., Bååth, E. and Laudon, H. 2011. Effects of soil frost on growth, composition and respiration of the soil microbial decomposer community. – Soil Biol. Biochem. 43: 2069–2077.

Hanssen-Bauer, I., E. Førland, I. Haddeland, H. Hisdal, D. Lawrence, S. Mayer, A. Nesje, J. Nilsen, S. Sandven, and A. Sandø. 2017. Climate in Norway 2100–A knowledge base for climate adaptation. – Norwegian Centre for Climate Services

Happonen, K., Virkkala, A.-F., Kemppinen, J., Niittynen, P. and Luoto, M. 2022. Relationships between above-ground plant traits and carbon cycling in tundra plant communities. – J. Ecol. 110: 700–716.

Heijmans, M. M. P. D., Magnússon, R. Í., Lara, M. J., Frost, G. V., Myers-Smith, I. H., van Huissteden, J., Jorgenson, M. T., Fedorov, A. N., Epstein, H. E., Lawrence, D. M. and Limpens, J. 2022. Tundra vegetation change and impacts on permafrost. – Nat. Rev. Earth Environ. 3: 68–84.

Henry, G. H. R., Hollister, R. D., Klanderud, K., Björk, R. G., Bjorkman, A. D., Elphinstone, C., Jónsdóttir, I. S., Molau, U., Petraglia, A., Oberbauer, S. F., Rixen, C. and Wookey, P. A. 2022. The International Tundra Experiment (ITEX): 30 years of research on tundra ecosystems. – Arct. Sci. 8: 550–571.

IPBES 2019. Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on biodiversity and Ecosystem Services. – (Brondizio, E. S., Settele, J., Díaz, S. and Ngo, H. T. (eds)). IPBES Secretariat.

Isard, S. A. 1986. Factors influencing soil moisture and plant community distribution on Niwot Ridge, Front Range, Colorado, USA. – Arct. Alp. Res. 18: 83–96.

Jaroszynska, F. 2019. Climate and biotic interactions–drivers of plant community structure and ecosystem functioning in alpine grasslands. – PhD thesis, Univ. of Bergen.

Kemppinen, J., Niittynen, P., Virkkala, A. M., Happonen, K., Riihimäki, H., Aalto, J. and Luoto, M. 2021. Dwarf shrubs impact tundra soils: drier, colder, and less organic carbon. – Ecosystems 24: 1378–1392.

Klanderud, K. and Totland, Ø. 2005. Simulated climate change altered dominance hierarchies and diversity of an alpine biodiversity hotspot. – Ecology 86: 2047–2054.

Klanderud, K., Vandvik, V. and Goldberg, D. 2015. The importance of biotic vs abiotic drivers of local plant community composition along regional bioclimatic gradients. – PLoS One 10: e0130205.

Lang, S. I., Cornelissen, J. H. C., Shaver, G. R., Ahrens, M., Callaghan, T. V., Molau, U., Ter Braak, C. J. F., Hölzer, A. and Aerts, R. 2012. Arctic warming on two continents has consistent negative effects on lichen diversity and mixed effects on bryophyte diversity. – Global Change Biol. 18: 1096–1107.

Legates, D. R., Mahmood, R., Levia, D. F., DeLiberty, T. L., Quiring, S. M., Houser, C. and Nelson, F. E. 2011. Soil moisture: a central and unifying theme in physical geography. – Prog. Phys. Geogr. 35: 65–86.

Lett, S., Nilsson, M.-C., Wardle, D. A. and Dorrepaal, E. 2017. Bryophyte traits explain climate-warming effects on tree seedling establishment. – J. Ecol. 105: 496–506.

Lett, S. et al. 2021. Can bryophyte groups increase functional resolution in tundra ecosystems? – Arct. Sci. 8: 609–637.

Lüdecke D. 2023. sjPlot: data visualization for statistics in social science. – R package ver. 2.8.14, https://CRAN.R-project.org/package=sjPlot.

McLaren, J. R. and Turkington, R. 2010. Ecosystem properties determined by plant functional group identity. – J. Ecol. 98: 459–469.

Olofsson, J., Stark, S. and Oksanen, L. 2004. Reindeer influence on ecosystem processes in the tundra. – Oikos 105: 386–396.

Olsen, S. L., Töpper, J. P., Skarpaas, O., Vandvik, V. and Klanderud, K. 2016. From facilitation to competition: temperature-driven shift in dominant plant interactions affects population dynamics in seminatural grasslands. – Global Change Biol. 22: 1915–1926.

Peng, F., Xue, X., Xu, M., You, Q., Jian, G. and Ma, S. 2017. Warming-induced shift towards forbs and grasses and its relation to the carbon sequestration in an alpine meadow. – Environ. Res. Lett. 12: 044010.

Porada, P., Ekici, A. and Beer, C. 2016. Effects of bryophyte and lichen cover on permafrost soil temperature at large scale. – Cryosphere 10: 2291–2315.

Post, E. et al. 2009. Ecological dynamics across the Arctic associated with recent climate change. – Science 325: 1355–1358.

Risch, A. C., Jurgensen, M. F. and Frank, D. A. 2007. Effects of grazing and soil micro-climate on decomposition rates in a spatio-temporally heterogeneous grassland. – Plant Soil 298: 191–201.

Rixen, C. et al. 2022. Winters are changing: snow effects on Arctic and alpine tundra ecosystems. – Arct. Sci. 18 8: 572–608.

Rumpf, S. B., Gravey, M., Brönnimann, O., Luoto, M., Cianfrani, C., Mariethoz, G. and Guisan, A. 2022. From white to green: snow cover loss and increased vegetation productivity in the European Alps. – Science 376: 1119–1122.

Scherer-Lorenzen, M. 2008. Functional diversity affects decomposition processes in experimental grasslands. – Funct. Ecol. 22: 547–555.

Scherrer, D. and Körner, C. 2010. Infra-red thermometry of alpine landscapes challenges climatic warming projections. – Global Change Biol. 16: 2602–2613.

Scherrer, D. and Körner, C. 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. – J. Biogeogr. 38: 406–416.

Schimel, J. P., Kielland, K. and Chapin, F. S. 1996. Nutrient availability and uptake by tundra plants. – In: Reynolds, J. F. and Tenhunen, J. D. (eds), Landscape function and disturbance in arctic tundra. Springer, pp. 203–221.

Soudzilovskaia, N. A., Graae, B. J., Douma, J. C., Grau, O., Milbau, A., Shevtsova, A., Wolters, L. and Cornelissen, J. H. C. 2011. How do bryophytes govern generative recruitment of vascular plants? – New Phytol. 190: 1019–1031.

Soudzilovskaia, N. A., van Bodegom, P. M. and 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. – Funct. Ecol. 27: 1442–1454.

Steinbauer, M. J. et al. 2018. Accelerated increase in plant species richness on mountain summits is linked to warming. – Nature 556: 231–234.

Van Der Wal, R. and Brooker, R. W. 2004. Mosses mediate grazer impacts on grass abundance in arctic ecosystems. – Funct. Ecol. 18: 77–86.

van Zuijlen, K., Roos, R. E., Klanderud, K., Lang, S. I. and Asplund, J. 2020. Mat-forming lichens affect microclimate and litter decomposition by different mechanisms. – Fungal Ecol. 44: 100905.

Vandvik, V., Skarpaas, O., Klanderud, K., Telford, R. J., Halbritter, A. H. and Goldberg, D. E. 2020. Biotic rescaling reveals importance of species interactions for variation in biodiversity responses to climate change. – Proc. Natl Acad. Sci. USA 117: 22858–22865.

Vandvik, V., Althuizen, I. H. J., Jaroszynska, F., Krüger, L. C., Lee, H., Goldberg, D. E., Klanderud, K., Olsen, S. L., Telford, R. J., Östman, S. A. H., Busca, S., Dahle, I. J., Egelkraut, D. D., Geange, S. R., Gya, R., Lynn, J. S., Meineri, E., Young, S. and Halbritter, A. H. 2022. The role of plant functional groups mediating climate impacts on carbon and biodiversity of alpine grasslands. – Sci. Data 9: 451.

Vanneste, T., Michelsen, O., Graae, B. J., Kyrkjeeide, M. O., Holien, H., Hassel, K., Lindmo, S., Kapás, R. E. and De Frenne, P. 2017. Impact of climate change on alpine vegetation of mountain summits in Norway. – Ecol. Res. 32: 579–593.

Vestgarden, L. S. and Austnes, K. 2009. Effects of freeze–thaw on C and N release from soils below different vegetation in a montane system: a laboratory experiment. – Global Change Biol. 15: 876–887.

von Oppen, J., Assmann, J. J., Bjorkman, A. D., Treier, U. A., Elberling, B., Nabe-Nielsen, J. and Normand, S. 2022. Cross-scale regulation of seasonal microclimate by vegetation and snow in the Arctic tundra. – Global Change Biol. 28: 7296–7312.

Ward, S. E., Orwin, K. H., Ostle, N. J., Briones, J. I., Thomson, B. C., Griffiths, R. I., Oakley, S., Quirk, H. and Bardget, R. D. 2015. Vegetation exerts a greater control on litter decomposition than climate warming in peatlands. – Ecology 96: 113–123.

Winkler, D. E., Chapin, K. J. and Kueppers, L. M. 2016. Soil moisture mediates alpine life form and community productivity responses to warming. – Ecology 97: 1553–1563.

Wookey, P. A., Aerts, R., Bardgett, R. D., Baptist, F., Bråthen, K. A., Cornelissen, J. H. C., Gough, L., Hartley, I. P., Hopkins, D. W., Lavorel, S. and Shaver, G. R. 2009. Ecosystem feedbacks and cascade processes: understanding their role in the responses of Arctic and alpine ecosystems to environmental change. – Global Change Biol. 15: 1153–1172.

Wundram, D., Pape, R. and Löffler, J. 2010. Alpine soil temperature variability at multiple scales. – Arct. Antarct. Alp. Res. 42: 117–128.

Xu, Q. and Huang, B. 2000. Effects of differential air and soil temperature on carbohydrate metabolism in creeping bentgrass. – Crop Sci. 40: 1368–1374.

Yergeau, E. and Kowalchuk, G. A. 2008. Responses of Antarctic soil microbial communities and associated functions to temperature and freeze–thaw cycle frequency. – Environ. Microbiol. 10: 2223–2235.

Zellweger, F., De Frenne, P., Lenoir, J., Rocchini, D. and Coomes, D. 2019. Advances in microclimate ecology arising from remote sensing. – Trends Ecol. Evol. 34: 327–341.