Annals of Botany **128**: 407–418, 2021
doi: 10.1093/aob/mcab041, available online at www.academic.oup.com/aob

ANNALS OF BOTANY
Founded 1887

Lichens buffer tundra microclimate more than the expanding shrub *Betula nana*

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Received: 2 March 2021 Returned for revision: 22 February 2021 Editorial decision: 5 March 2021 Accepted: 11 March 2021
Electronically published: 14 March 2021

• **Background and Aims** In tundra systems, soil-borne lichens are often the dominant groundcover organisms, and act to buffer microclimate extremes within or at the surface of the soil. However, shrubs are currently expanding across tundra systems, potentially causing major shifts in the microclimate landscape.
• **Methods** Here, we compared soil temperature and moisture underneath the dwarf birch *Betula nana* and seven abundant lichen species in sub-alpine Norway. We also examined mixtures of lichens and dwarf birch – an intermediate phase of shrubification – and measured several functional traits relating to microclimate.
• **Key Results** We found that all lichen species strongly buffered the daily temperature range, on average reducing maximum temperatures by 6.9 °C (± 0.7 s.d.) and increasing minimum temperatures by 1.0 °C (± 0.2 s.d.) during summer. The dwarf birch had a much weaker effect (maximum reduced by 2.4 ± 5.0 °C and minimum raised by 0.2 ± 0.9 °C). In species mixtures, the lichen effect predominated, affecting temperature extremes by more than would be expected from their abundance. Lichens also tended to reduce soil moisture, which could be explained by their ability to intercept rainfall. Our trait measurements under laboratory conditions suggest that, on average, lichens can completely absorb a 4.09 mm (± 1.81 s.d.) rainfall event, which might be an underappreciated part of lichen–vascular plant competition in areas where summer rainfall events are small.
• **Conclusions** In the context of shrubification across tundra systems, our findings suggest that lichens will continue to have a large effect on microclimate until they are fully excluded, at which point microclimate extremes will increase greatly.

Key words: *Betula nana*, *Cladonia stellaris*, dwarf birch, functional traits, lichen, lichen mat, microclimate, non-additive, shrubification, shrub expansion, *Stereocaulon*.

INTRODUCTION

Climate change is occurring rapidly at regional scales, yet species-generated microclimates might serve to buffer its immediate impacts on the biosphere (De Frenne *et al.*, 2013). As macroclimates begin to exceed species niche limits, there may still be suitable microclimate patches within species ranges. These patches can arise from geographical variation, such as topography and aspect (Dobrowski, 2011; Maclean *et al.*, 2015; Graae *et al.*, 2018), or the effects of biota, such as temperature buffering in tree hollows and under forest canopies (von Arx *et al.*, 2012; O'Connell and Keppel, 2016). Where microclimate buffering is very strong, patches might be habitable for thousands of years (microrefugia) while others, often termed holdouts, can only delay the immediate effects of macroclimate change, leading to 'climatic lags' in species responses (De Frenne *et al.*, 2013; Hannah *et al.*, 2014).

Shrubs are currently expanding across arctic and alpine tundra systems (Martin *et al.*, 2017; Shevtsova *et al.*, 2020), largely due to elevated nitrogen and phosphorus mineralization rates with warmer temperatures (Hartley *et al.*, 1999; Hill and Henry, 2011; Fraser *et al.*, 2014). However, the expansion of shrubs has generally been matched by a decline in the abundance of lichen mats that grow on the soil surface (Van Wijk *et al.*, 2004; Hudson and Henry, 2010; Elmendorf *et al.*, 2012; Fraser *et al.*, 2014), although this pattern is weaker in the high arctic (Cornelissen *et al.*, 2001). This community shift towards darker, taller, less compact organisms represents a major change to microclimate dynamics in tundra systems (Chapin *et al.*, 2005).

Lichen mats cover substantial areas of tundra and play an important role in modifying the microclimate at ground level (Kershaw, 1978; Crittenden, 2000; Fig. 1). Early studies in Canadian conifer woodlands established that lichen mats reduce the temperature range of the underlying soil surface and delay evaporative water loss from the soil (Kershaw and Rouse, 1971; Kershaw and Field, 1975; Bell and Bliss, 1980; Coxson and Lancaster, 1989). It was not until more recently that similar effects were reported for soil-borne lichens in Antarctic (Molina-Montenegro *et al.*, 2013) and Fennoscandian tundra systems (Broll, 2000; Nystuen *et al.*, 2019; van Zuijlen *et al.*, 2020). It might be assumed that microclimate amelioration by lichens would enhance vascular plant recruitment in a similar manner to nurse plants or an insulating layer of leaf litter (Suding and Goldberg, 1999; Cavieres *et al.*, 2007), but this advantage trades off against light competition and other inhibitive effects (reviewed by Favero-Longo and Piervittori, 2010). Mixed results from

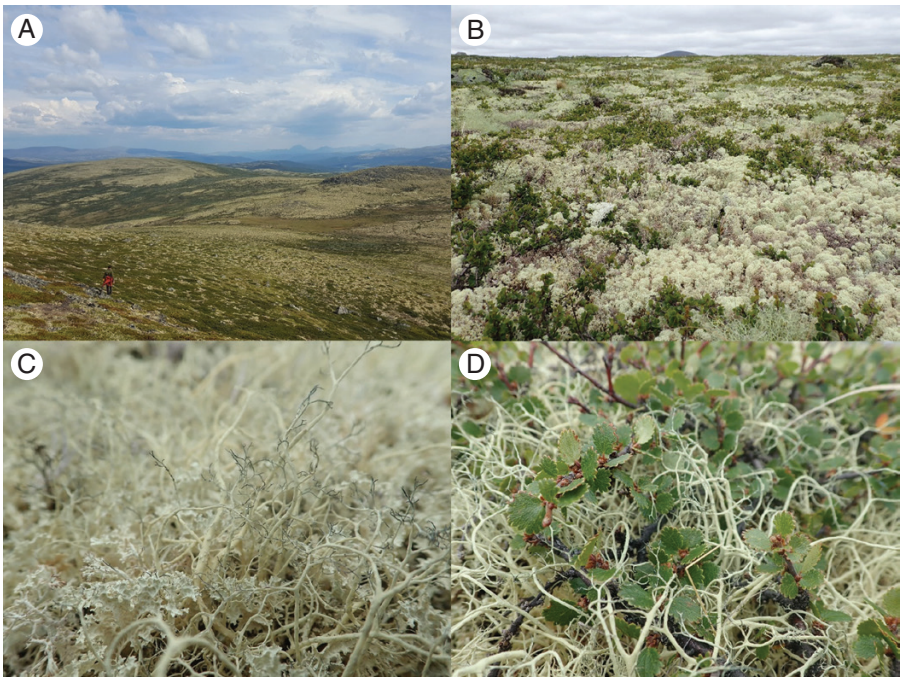

Fig. 1. Photographs of lichen mats in the Hjerkinn Protected Landscape, illustrating (A) lichen mats (yellow) covering the exposed areas of the landscape, (B) a typical mid-slope community of *Cladonia* spp. and the dwarf birch *Betula nana*, (C) intertwining thalli of *Alectoria ochroleuca* and *Flavocetraria nivalis*, and (D) lichens filling gaps in the canopy of *Betula nana* (photograph credit: M. Mallen-Cooper).

germination trials affirm that the relationship is complex, and the effect is more facilitative in more extreme climates (i.e. follows the stress gradient hypothesis *sensu* Bertness and Callaway, 1994) in some instances (Hawkes and Menges, 2003; Sedia and Ehrenfeld, 2003; Nystuen *et al.*, 2019).

Microclimate is mediated by water and energy balances (Weller and Holmgren, 1974; Davis *et al.*, 2019). At small scales, these balances are affected by the arrangement and structure of the organisms themselves (Larson and Kershaw, 1976). In lichens, there is a high degree of variation in physiological and morphological traits, particularly among species (Cornelissen *et al.*, 2007; Gauslaa and Coxson, 2011; Asplund and Wardle, 2014; Roos *et al.*, 2019). However, past microclimate research has generally treated lichen mats as one entity rather than a mixture of species with different microclimate effects and sets of traits. In this study, we adopt the latter approach, and thus test the generalizability of microclimate findings at the mat level and explore the possibility of fine-scale microclimate heterogeneity within lichen mats, which could play an important role in creating 'stepping stones' for expanding vascular plants (Lembrechts *et al.*, 2018).

In a mixture of species, the default approach is to assume that species have equal, or abundance-scaled, effects on an ecosystem property (Garnier *et al.*, 2004). Yet this approach does not account for synergistic and antagonistic interactions between species that result in 'non-additive' effects on functioning (Hättenschwiler *et al.*, 2005). For example, the fine leaf litter of one tree species can fill the spaces between the coarser litter of another, reducing ventilation in the litterbed and decreasing flammability more than can be expected from the average of species effects (Zhao *et al.*, 2016). This type of morphological interaction, which could be described as a three-dimensional packing effect, is also likely to be present in lichen mats, where species often intertwine their thalli (Fig. 1C), possibly producing a denser mat than any species could produce alone. In a similar way, lichens tend to fill the spaces in the canopy of dwarf shrubs (Fig. 1D), which might also increase the density of biomass in a given area and thus lead to non-additive effects on microclimate and traits associated with microclimate.

Here we examine microclimate heterogeneity in a lichen- and dwarf shrub-dominated tundra system in central Norway. Building on recent species-explicit approaches to measuring microclimates in lichen mats (Nystuen *et al.*, 2019; van Zuijlen *et al.*, 2020), which involve measuring single lichen species, we additionally measure a dwarf shrub species, *Betula nana*, and several species mixtures. It should be noted that our field measurements were restricted to 3 d periods (soil temperature) and point measurements (soil moisture) during summer, and thus the purpose of our study is not to capture the complete temporal extent of microclimate variation but rather to compare a snapshot of microclimate amelioration among species. The dwarf birch, *B. nana*, is known to be expanding in many tundra systems (Van Wijk *et al.*, 2004; Vanneste *et al.*, 2017), and could reduce microclimate buffering due to its more open structure relative to lichens and its ability to reduce water loss via stomatal closure. In contrast, lichens lack mechanisms to regulate water loss and thus passively re-release any absorbed rainfall (Kershaw and Field, 1975). We then perform a correlative investigation of functional traits, such as light interception and water-holding capacity, that might be driving microclimate effects. Tall species that were densely growing (high light interception), absorbent, reflective and slow to desiccate were expected to provide the greatest microclimate amelioration. We also test for non-additivity in traits and microclimate effects using mixtures of lichen species, as well as some mixtures of lichen

and dwarf birch. Finally, we conduct a vegetation survey to determine if species, or mixtures, with a high capacity to moderate microclimate support a higher abundance and richness of plants. In summary, we aim to address the following questions. (1) Are there *in situ* differences in the soil microclimate among the dwarf birch and species of lichen? (2) Are microclimate differences correlated with functional traits? (3) Are there non-additive effects in the traits and buffering capacities of species mixtures due to three-dimensional packing? (4) Does a more buffered microclimate coincide with a richer and more abundant plant community?

MATERIALS AND METHODS

Study site

The study was conducted in the alpine tundra of the Hjerkinn Protected Landscape (Hjerkinn landskapsvernområde; Fig. 1A) in Dovre, central Norway (62.24°N, 9.59°E). According to the Fokstugu weather station (930 m a.s.l.), located approx. 22 km south-west of the study site, mean annual precipitation in this area was 435 mm from 1961 to 1990. In 2019, the mean daily rainfall was 1.4 mm and daily rainfall rarely exceeded 10 mm (see Supplementary data Fig. S1). The mean annual air temperature for the 1961–1990 period was –0.1 °C, with mean temperatures in July and January of 9.8 °C and –8.8 °C, respectively (data available at http://www.yr.no/). The sampled regions of the study site range from 1140 to 1282 m a.s.l., and are likely to be 1.7 °C cooler, on average, than temperatures reported by the Fokstugu weather station, given a tropospheric lapse rate of 6 °C km^{-1} (Mokhov and Akperov, 2006). Our data suggest that the mean soil temperature underneath lichens and shrubs during the study period was 10.7 °C.

As is typical for alpine tundra systems, the distribution of plant communities in this area is strongly controlled by wind exposure and moisture availability (Holt *et al.*, 2007; Graae *et al.*, 2011). The well-drained, exposed ridgetops are characterized by patchy gravel and a community dominated by soil-borne lichens, such as *Alectoria* spp. and *Flavocetraria nivalis*, and sparse dwarf shrubs, including *Betula nana* and *Kalmia procumbens* (see Vanneste *et al.*, 2017 for a survey of the region). Only 10–30 m downslope, the community typically transitions to a near-complete cover of *Cladonia* lichen species and *B. nana*, intermixed with graminoids such as *Festuca ovina* and other dwarf shrubs such as *Vaccinium vitis-idaea* and *Empetrum nigrum* (Fig. 1B). It is worth noting that the dwarf birch *B. nana* can be found growing among most lichen species but most commonly occurs within patches of *Alectoria ochroleuca* (e.g. Fig. 1D) and *Cladonia stellaris*. With increasing soil moisture and shelter from wind, communities are characterized by a prominence of taller shrubs such as *Salix glauca* and *Juniperus communis*, fewer lichens and greater abundances of graminoids and herbaceous plants.

Experiment and survey design

Our study is comprised of three components, corresponding to research questions (1), (2) and (4). The first was a microclimate monitoring experiment with paired control removal plots (Supplementary data Fig. S2), comparing soil temperature and moisture among lichens and the dwarf birch. We then conducted field- and laboratory-based measurements of functional traits relating to microclimate and, finally, a survey of bryophytes and vascular plants growing within lichen mats. The microclimate monitoring and vegetation survey were conducted on five ridges, spaced at least 0.5 km apart, within the Hjerkinn Protected Landscape (Fig. 2). The local elevation maxima on selected ridges ranged between 1157 and 1282 m a.s.l.

For all components of this study, we measured the same 13 species or mixtures. This set included seven species of lichen which were abundant on exposed ridges: *Alectoria ochroleuca* (aloc), *Bryocaulon divergens* (brdi), *Cladonia arbuscula* (clar), *Cladonia rangiferina* (clra), *Cladonia stellaris* (clst), *Flavocetraria nivalis* (flni) and *Stereocaulon paschale* (stpa). We also included the dwarf birch, *B. nana* (bena), as a target species, i.e. a species in which we examined microclimate, trait and plant community relationships. To address the third research question relating to non-additive effects, we measured mixtures of species that commonly co-occur, namely *A. ochroleuca* + *F. nivalis* (Fig. 1C), *S. paschale* + *C. stellaris*, *B. nana* + *C. stellaris* and *B. nana* + *A. ochroleuca* (Fig. 1D), and a random trio of target lichen species. In summary, we measured seven lichen species, one shrub species, three lichen-only mixtures and two lichen–shrub mixtures.

Microclimate amelioration

We used an *in situ* paired control design to assess microclimate amelioration in target species and mixtures. On each ridge, we established four north–south transects that were 50 m in length and spaced approx. 50 m apart. Target species or mixtures were located by selecting a random point along the transect and searching radially outwards until a suitable patch was found. The criteria for a suitable patch was an area of at least

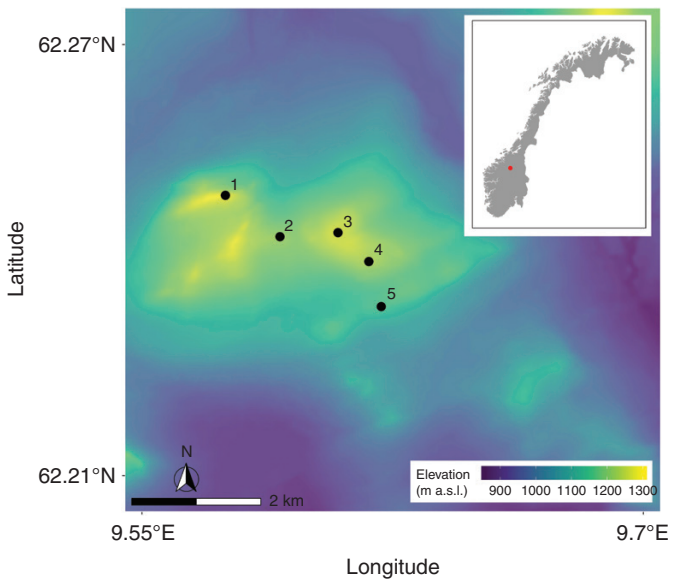

FIG. 2. Map of selected ridges in the Hjerkinn Protected Landscape overlaid on a digital elevation model of the region (inlaid map of Norway with the study site indicated by a red circle).

150 cm^2 and on a substrate of soil. When a patch of *B. nana* could not be found in isolation, underlying lichens or plants had to be removed to create a pure patch. For every patch ($n = 260$), a paired removal control plot ($n = 260$) was created 0.5 m away in the direction that best matched the elevation, slope and aspect of the patch (Supplementary data Fig. S2). Control plots were created by removing all plants and lichens in a 40 × 40 cm square and then left for 24 h before microclimate data were collected, allowing time for microclimate conditions to stabilize (the remaining disconnected root mass would not have influenced soil moisture since there were no leaves to drive a water potential gradient). In this way, the cleared control plots were similar to target patches in all variables (e.g. aspect, slope, elevation and soil properties) except lichen, or shrub, cover, and it was thus possible to evaluate the effects of that cover on microclimate conditions.

In July 2018, we measured soil temperature and moisture under all patches and in all control plots. Triplicate measurements of soil moisture at 5 cm depth were recorded on one dry day (no rainfall in the preceding 72 h and lichens in their brittle desiccated state) and one wet day (rainfall within the preceding 12 h and lichens in their soft hydrated state) using a hand-held Trime-Pico soil moisture probe (IMKO GmBh, Ettlingen, Germany). The triplicate measurements, spaced apart by 5–10 cm, were averaged for each patch or control plot, and were conducted after the 24 h stabilization period. Soil temperature was recorded hourly across a 72 h period in July 2018 using HOBO® Pendant UA-002-64 temperature loggers. The loggers were buried under 2 cm of soil to avoid direct sunlight heating the temperature sensor. Moisture measurements were conducted separately from temperature measurements in order to specifically capture the comparison of dry and wet days.

Functional traits

In all species and mixtures, including *Betula*, we measured the following functional traits: albedo, maximum height, ground-level light interception (proportion of the soil surface shaded by thallus or vegetative matter), mid-level light interception (proportional shading at 3 cm below the thallus or vegetative boundary), specific thallus (or vegetative) mass (Gauslaa and Coxson, 2011), time to 50 % evaporative water loss (T_{50}; Michel *et al.*, 2012) and water-holding capacity (Gauslaa and Coxson, 2011). All traits except albedo and height were measured in controlled laboratory conditions and all were averaged at the species level to examine their associations with microclimate effects ($n = 5$ per species for all traits except albedo, $n = 10$ per species, and height, $n = 55$ per species). A replicate represented one dwarf birch plant, or a collection of lichen thalli constituting a target species or mixture.

To measure the rate of water loss, we conducted a protocol similar to that of Zotz *et al.* (2000). We collected five samples of each species or mixture from Ridge 2, resulting in a total sample size of $n = 65$. Ridge 2 was selected for detailed trait measurements because it was representative of other ridgetop communities in the region and simple to access on foot. *Betula* samples were cut at soil level because our study only concerns the effects of above-ground biomass on soil microclimate. Each sample was submerged in water for 30 min in order to reach maximum water-holding capacity. Samples were then held aloft for 30 s, allowing large drips to fall off, and weighed to the nearest milligram. We chose not to blot the saturated samples because surface water is a valid component of total water-holding capacity (Gauslaa and Coxson, 2011). Samples were placed on flat trays in a room that had a stable mean temperature of 20.6 °C (± 0.6 s.d.), and reweighed every 30 min for 12 h, and every 12 h thereafter until a minimum mass was attained. Any pooled water under the samples was dried during each weighing. Since *Betula* is not poikilohydric, samples containing *Betula* steadily lost mass over the measuring period as the wood slowly dried (Simpson, 1983). We therefore stopped measuring *Betula* samples at 8 d and used this value as a minimum mass, by which time we assumed all external water had evaporated. We derived the maximum water-holding capacity of each sample by dividing the difference between wet and dry masses by the area of the sample (Gauslaa and Coxson, 2011). We also calculated the potential rainfall interception of a lichen as its water-holding capacity (g cm^{-2}) multiplied by 10, given that 1 mm of rainfall corresponds to 0.1 g of water per cm^2. Specific thallus mass (or vegetative mass for *Betula*) was simply the dry mass divided by the area of the sample, as per Gauslaa and Coxson (2011). The area of the lichen thallus or vegetative biomass was calculated in ImageJ (Abràmoff *et al.*, 2004) using a photo taken directly above the intact sample.

Previously, light interception by lichen mats was determined by setting a specimen in resin and placing it between a light source and a photometric sensor (Kershaw and Harris, 1971). However, this method is impractical in a field setting and is complicated by the absorption of light by the resin block. We therefore developed a novel method to rapidly estimate light interception in the field, by measuring the proportion of the soil surface that was shaded by thallus or vegetative matter [often termed 'ground cover' (Chakwizira *et al.*, 2015) but, to avoid confusion with other cover variables, we will refer to this trait as light interception]. We did not include photosynthetically active radiation (PAR) in our measurements because our aim was to examine the effects of light interception on the soil microclimate rather than on carbon cycling. First, lichen samples were separated from the soil, and shrub samples were cut at ground level. Most soil-borne tundra lichens die off at their base and so are easily separated (Crittenden, 2000), while others, such as *C. stellaris*, have a long necromass that gradually transitions into soil, in which case we removed the lower layer of necromass containing soil particles. Lichen or shrub samples were then placed on a single sheet of white paper suspended at half the height of an enclosed box (Supplementary data Fig. S3). A torch from 10 cm above the sample was then shone directly downwards onto the sample, casting a shadow onto the paper, which was then photographed from below. We observed that when a patch of fruticose lichen is removed from the continuous mat, there are often edge branches that would have been intertwined in adjacent mat organisms, and therefore do not truly represent the vertical shading of that species. To avoid this source of error, we took a circular sub-sample of 4 cm diameter from the centre of each shadow, and calculated light interception as the proportion of this area that was shaded from torchlight. In practical terms, the calculation of

light interception involved setting a brightness threshold (120) in ImageJ, which was constant for all species and mixtures, and deriving the shaded area from a binary mask. Different thresholds were used for different species because species with fine wispy thalli (e.g. *A. ochroleuca*) produced a more diffuse shading than those with thicker or wider thalli (e.g. *F. nivalis*). Using the same method but cutting the specimens at a different height, we also measured light interception at 3 cm below the upper thallus or vegetative boundary (hereafter, mid-level light interception). The 3 cm value was chosen because this was the average height of those plant species that grew underneath a higher thallus or vegetative boundary, according to our survey, and therefore represents the height at which PAR is typically absorbed by underlying plants.

We measured a simple proxy of albedo using a smartphone camera and the Albedo app (available at https://play.google.com/store/apps/details?id=com.h2optics.albedo). The app normalizes the light intensity values in the red, green and blue colour channels using a grey balance and then calculates broad-band albedo as the mean of the three channels (similar to Leeuw and Boss, 2018). Averaging reflectance across the visible spectrum in this manner has been used in the long-term monitoring of snow albedo with reasonable success (Garvelmann *et al.*, 2012).

Maximum height was simply the perpendicular distance from the mineral soil surface to the uppermost living tissue of the lichen or plant.

Vegetation survey

The aim of the survey was to record the plant communities that co-occur within areas dominated by the 13 target species and mixtures, and thus investigate correlations between microclimate amelioration and plant community properties. On each ridge in July 2019, we established 50 m long north–south transects (not those used in the microclimate experiment) with a 10 m spacing. A 20 × 20 cm quadrat was placed every metre and if it was dominated by a target species or mixture (i.e. contained >75 % of a single species, >40 % of each species in a two-species mixture or >30% of each species in a three-species mixture), we recorded the identity, abundance and maximum height of all plant species. We also recorded the maximum height of the target lichen or shrub. Quadrat sampling continued until there were five replicates of all species or mixtures on each ridge (except for Ridge 2, where there were ten replicates per species, thus total $n = 390$).

Statistical analysis

All microclimate results are presented as arithmetic means. For the water retention trait T_{50}, we first fitted three different models (negative exponential, Weibull and discrete parallel) for each replicate using the 'litterfitter' R package (Cornwell and Weedon, 2014). From the model with the lowest Akaike information criterion (AIC), in most cases the discrete parallel model, we extracted T_{50} as the time (h) at 50 % mass loss (Supplementary data Fig. S4).

If an effect is additive, a mixture of species will exhibit the average effect of the component species in monoculture. The average can be weighted by the abundance of the component species (Michel *et al.*, 2012), but abundance is difficult to measure in complex interwoven lichen mats and thus we calculated the unweighted average as the expected additive value. For example, in a mixture of three lichen species, we used the average of the three trait, or microclimate, values as the expected value, which assumes the component species were equally abundant within the mixture. When the observed effect, or trait, of a mixture of species is different from the expected value, it is considered non-additive. Paired *t*-tests were used to compare observed and expected trait values in species mixtures, and the traits were considered significantly non-additive if the confidence interval (CI) did not include 0.

RESULTS

Microclimate amelioration

All species and mixtures, except the dwarf birch alone, significantly buffered temperature extremes in the uppermost soil layer (Fig. 3; Supplementary data Fig. S5). The dwarf birch significantly reduced maximum temperature, by a mean of 3.0 °C, but did not affect minimum temperature (mean 0.2 °C, 95% CI: –0.2 to 0.5). The lichen *C. stellaris*, even when intermixed with birch, had an outstanding ability to reduce maximum temperature. Temperature buffering in mixtures of dwarf birch and *A. ochroleuca* was also dominated by the lichen component, which represents a non-additive effect (Supplementary data Fig. S6). In lichen-only mixtures, temperature buffering tended to align with the average value of the component species, i.e. the effect was additive (Supplementary data Fig. S6). However, other than the dwarf birch, which had a particularly weak buffering effect, species and mixtures were largely indistinguishable in their buffering capacities (Fig. 3).

We found no evidence of moisture amelioration by any species or mixture (Fig. 3C). On the contrary, many lichen species and *Betula* significantly reduced soil moisture. Given that the average soil moisture under lichens and shrubs was 11.6 %, soil moisture was reduced, at most, by a factor of 0.21 relative to the control (Supplementary data Fig. S7). There was a strong correlation between maximum temperature buffering and light interception (Pearson's $r = –0.74$; Supplementary data Fig. S8), but no strong correlations between other traits and temperature variables ($r < 0.51$), suggesting that shading was the main driver of temperature buffering.

Functional traits and non-additivity

There were strong linear relationships between water-holding capacity and specific thallus mass (Pearson's $r = 0.95$; Fig. 4) and between T_{50} and specific thallus mass (Pearson's $r = 0.84$). It is worth noting that the mass per area trait – specific thallus mass – should be considered as vegetative mass for *B. nana*. Water-holding capacity, T_{50} and specific thallus mass were typically highest in *S. paschale* and species of *Cladonia*. Given their water-holding capacities at saturation,

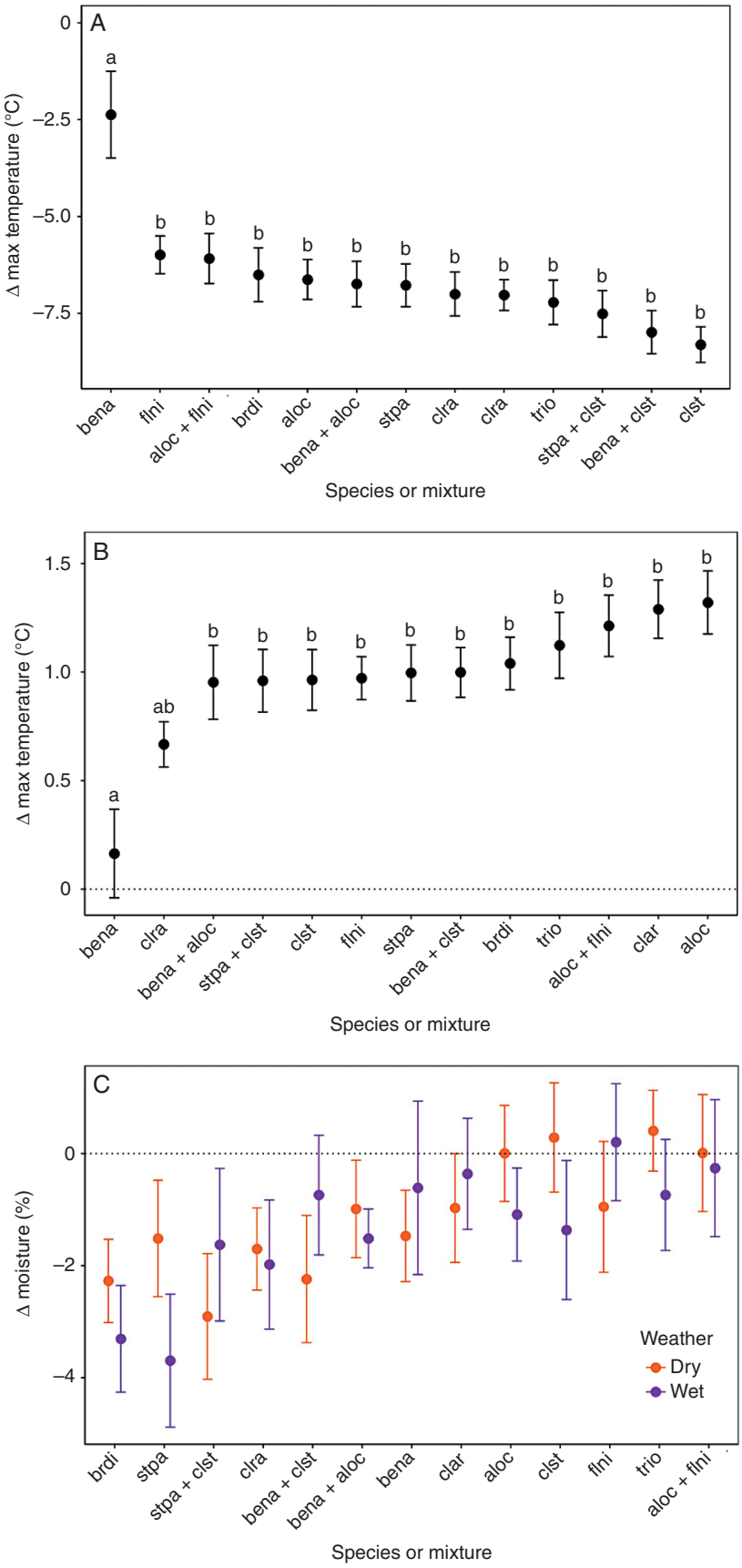

FIG. 3. Means and standard errors for (A) minimum temperature, (B) maximum temperature and (C) soil moisture effects among species and mixtures (Δ = target patch – control; $n = 20$ per species or mixture). Species or mixtures that do not share a lowercase letter were significantly different (there were no significant differences in soil moisture effects). For species abbreviations, see the Materials and Methods.

the average lichen (i.e. not including the dwarf birch and its mixtures) could theoretically fully absorb a 4.09 mm (± 1.81 s.d.) rainfall event, based on laboratory conditions and starting completely dry, which corresponds to the 82nd percentile of rain events measured in 2019 at the Fokstugu weather station (Supplementary data Fig. S1). The least absorbent lichen that we measured, *A. ochroleuca*, was capable of completely absorbing a 1.51 mm (± 0.08 s.d.) rainfall event, while the most absorbent lichen, *S. paschale*, was able to fully absorb a 5.88 mm (± 0.50 s.d.) event, which correspond to the 63rd and 90th percentile of 2019 rainfall events, respectively. Although it would vary with fluctuating temperature and humidity in the field, possibly taking a shorter time in sun-exposed microsites with high evaporation, the average time for lichens in laboratory conditions to completely dry after saturation was 75.6 h (± 35.7 s.d.), while 50 % drying was attained in 7.2 h (± 3.5 s.d.; Table 1).

Lichens provided near-complete interception of light at the soil surface, with the exception of *A. ochroleuca*, which has a more open, wispy structure (Table 1). In the mid-level region, mean interception for lichens (not including the dwarf birch and its mixtures) was 72.6 ± 22.5 % SD. There was a moderate association between mid-level light interception and specific thallus mass (Pearson's $r = 0.70$). The dwarf birch was characterized by low values of albedo, light interception and water-holding capacity.

Species mixtures exhibited significant non-additivity in all traits except T_{50} (Fig. 5; Supplementary data Table S1), i.e. community functioning tended to deviate from the average trait value of the component species. For example, albedo was

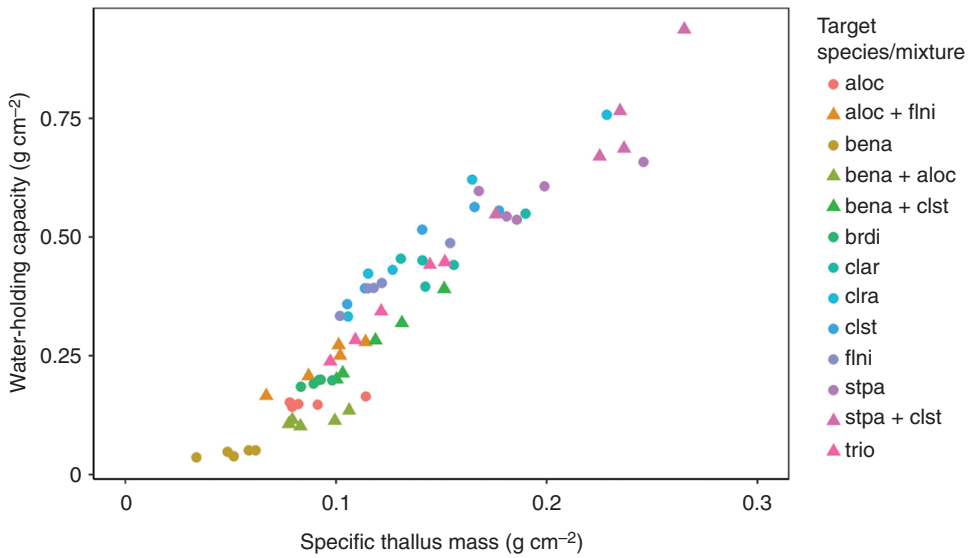

FIG. 4. Specific thallus mass (g dry matter cm^{-2}) and water-holding capacity (g water cm^{-2}) in all species (circles) and mixtures (triangles), with Pearson's $r = 0.95$. For species abbreviations, see the Materials and Methods.

TABLE 1. *Trait means (± s.d.) by species*

	Trait	T_{50}	WHC	Specific thallus mass	Light interception (ground level)	Light interception (mid level)	Height	Albedo
	Units	h	g cm^{-2}	g cm^{-2}	Unitless	Unitless	cm	Unitless
	Total *n*	65	65	65	65	65	715	130
Species or mixture	aloc	2.4 ± 0.6	0.15 ± 0.01	0.09 ± 0.02	0.73 ± 0.18	0.23 ± 0.12	9.5 ± 2.6	0.17 ± 0.01
	aloc + flni	3.8 ± 1.2	0.24 ± 0.05	0.09 ± 0.02	0.97 ± 0.03	0.67 ± 0.11	7.9 ± 1.6	0.17 ± 0.02
	bena	2.6 ± 0.8	0.04 ± 0.01	0.05 ± 0.01	0.75 ± 0.12	0.35 ± 0.14	17.6 ± 7.6	0.03 ± 0.01
	bena + aloc	1.9 ± 0.2	0.11 ± 0.01	0.09 ± 0.01	0.87 ± 0.05	0.66 ± 0.13	11.3 ± 3.2	0.08 ± 0.02
	bena + clst	5.7 ± 0.8	0.28 ± 0.08	0.12 ± 0.02	0.96 ± 0.06	0.92 ± 0.04	16.4 ± 5.1	0.13 ± 0.03
	brdi	5.9 ± 1.0	0.19 ± 0.01	0.09 ± 0.01	0.99 ± 0.01	0.73 ± 0.16	7.1 ± 2.3	0.01 ± 0.00
	clar	10.3 ± 2.2	0.46 ± 0.06	0.15 ± 0.02	0.97 ± 0.02	0.90 ± 0.08	8.2 ± 2.0	0.24 ± 0.03
	clra	7.1 ± 1.1	0.51 ± 0.17	0.15 ± 0.05	1.00 ± 0.00	0.81 ± 0.06	9.2 ± 3.4	0.09 ± 0.01
	clst	6.8 ± 2.5	0.48 ± 0.10	0.14 ± 0.03	1.00 ± 0.01	0.60 ± 0.17	9.5 ± 2.4	0.28 ± 0.05
	flni	5.1 ± 1.0	0.40 ± 0.05	0.12 ± 0.02	0.98 ± 0.02	0.94 ± 0.05	5.7 ± 1.4	0.26 ± 0.04
	stpa	11.9 ± 2.2	0.59 ± 0.05	0.20 ± 0.03	0.96 ± 0.04	0.94 ± 0.02	5.9 ± 1.1	0.16 ± 0.03
	stpa + clst	12.2 ± 2.5	0.72 ± 0.14	0.23 ± 0.03	0.95 ± 0.06	0.88 ± 0.04	7.7 ± 1.9	0.19 ± 0.03
	trio	6.4 ± 2.1	0.35 ± 0.09	0.12 ± 0.02	0.98 ± 0.05	0.81 ± 0.04	7.9 ± 2.4	0.14 ± 0.04

Evaporation T_{50}, water-holding capacity (WHC), specific thallus (or vegetative) mass, ground- and mid-level light interception, height above ground and albedo (for each of the 13 species and mixtures, $n = 5$ except height, where $n = 55$, and albedo, where $n = 10$).

For species abbreviations, see the Materials and Methods.

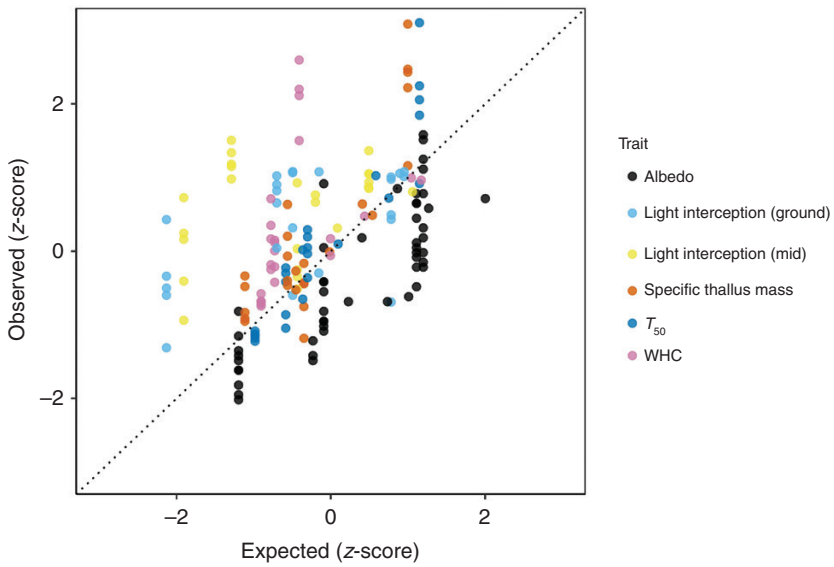

FIG. 5. Observed trait values (WHC = water-holding capacity) in species mixtures plotted against expected values based on the average trait value of the component species, with a dotted line to represent a perfectly additive effect (all values were *z*-standardized for graphical reasons).

generally lower than expected from average trait values, while light interception and water retention traits were typically higher. Height was not assessed for non-additivity because it always represented the tallest species in the mixture and so was intrinsically non-additive.

Co-occurring plant communities in lichen-dominated mats

We recorded 22 species of vascular plant, other than dwarf birch, living within ridgetop lichen mat communities (Supplementary data Fig. S9). The mean cover of vascular plants, excluding dwarf birch, within lichen mats was 8.8 % (± 10.7 s.d.), with the highest mean cover recorded within quadrats dominated by dwarf birch (17.2 ± 19.0 % s.d.) and *A. ochroleuca* (14.7 ± 12.2 % s.d.; Supplementary data Table S2). The lowest vascular plant cover (3.6 ± 3.2 % s.d.) and richness (0.64 ± 0.64 s.d.) were recorded within mats where *C. stellaris* was intermixed with *B. nana*, although this mixture had the highest mean bryophyte cover (10.8 ± 18.7 % s.d.). The mean richness of vascular plants within lichen mats was 1.42 (± 0.49 s.d.), with the highest recorded within patches of *S. paschale* (2.17 ± 1.36 s.d.). The overall mean cover of bryophytes was 6.8 % (± 8.1 s.d.). Most plants tended to grow close to the thallus or vegetative canopy boundary, with only 5 % protruding >5 cm, most of which were graminoids (Supplementary data Fig. S9).

There was a moderately strong negative relationship between trait values of mid-level light interception and mean vascular plant cover (Pearson's $r = –0.85$; Fig. 6A). However, there was no strong relationship between mid-level interception and mean vascular plant richness (Pearson's $r = –0.13$). Species with poorer abilities to reduce maximum temperature were associated with higher vascular plant cover (Pearson's $r = 0.86$; Fig. 6B).

DISCUSSION

We found strong evidence that lichens play a major role in buffering the soil temperature during summer temperature extremes, while the influence of the dwarf birch *Betula nana* on soil temperature was far weaker. In mixtures of lichens and dwarf birch, soil temperature was predominantly controlled by the lichens (Supplementary data Fig. S6). Contrary to expectations, most species reduced soil moisture (Fig. 3C), which could relate to both the strong water-holding capacity of many of the lichen species and the distribution of rain event sizes that would allow lichens to absorb rainfall before it reaches the soil. Mixed communities tended to intercept more light, absorb more water and have a lower albedo than the trait values of their component species would predict. Finally, we found that species with high light interception tended to have the greatest capacity to buffer temperature yet supported the lowest vascular plant cover.

Role of lichens in regulating local water and energy balance

Temperature buffering underneath the dwarf birch was small in comparison with lichens, which probably relates to the relatively poor shading capacity of the birch. Two previous studies also reported high insulating effects in lichens, particularly in *Cladonia* species (Nystuen *et al.*, 2019; van Zuijlen *et al.*, 2020). Unlike van Zuijlen *et al.* (2020), we found no clear correlation between temperature effects and water-holding capacity, although this may be a consequence of the limited temporal extent of our study. In the Siberian Arctic tundra, it has been shown that removing *B. nana*, while leaving the lichen mat intact, significantly enhances permafrost thaw, indicating that the shrub buffers maximum temperatures during summer (Blok *et al.*, 2010). Our results comparing dwarf birch and

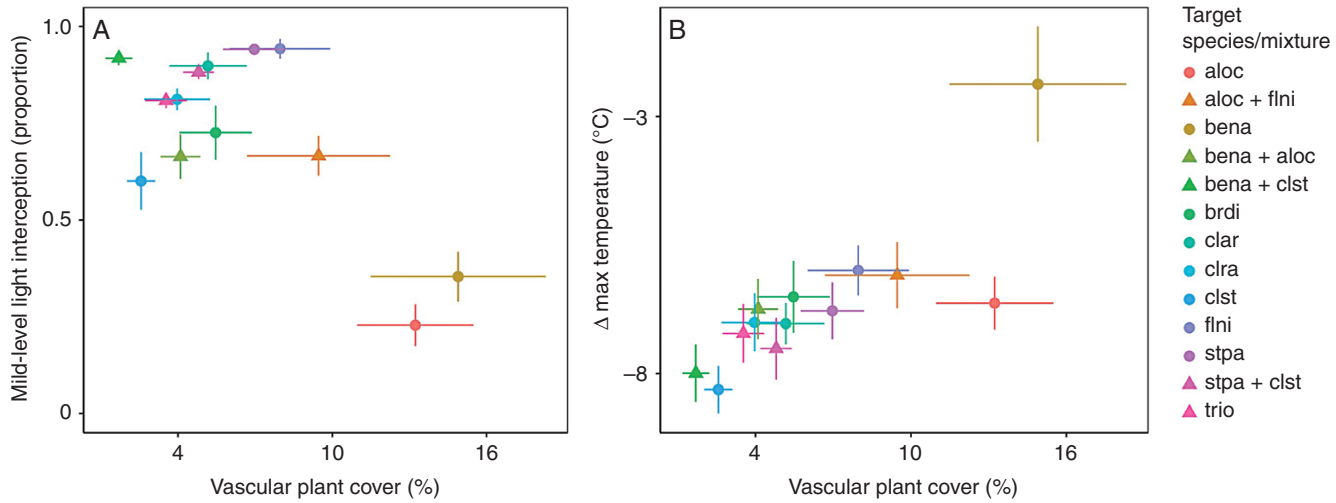

FIG. 6. Correlation plots, for all species (circles) and mixtures (triangles), showing the relationships between co-occurring vascular plant cover (± s.e.) and (A) mid-level light interception (± s.e.) and (B) maximum temperature buffering (target patch – control, ± s.e.). For species abbreviations, see the Materials and Methods.

lichens indicate that lichens may play an even greater role than the dwarf birch in reducing summer permafrost thaw in Arctic tundra and thus offsetting permafrost degradation with climate change (Yang *et al.*, 2010). It is interesting to note that all lichen species reduced maximum temperature considerably more than they raised minimum temperature, suggesting that, at least in summer, lichens play a greater role in ameliorating afternoon heat stress than in avoiding summer frost events (Tolvanen, 1997; Marchand *et al.*, 2005). While the study is contained within one season, summer represents an important time for soil microbial activity and plant growth and establishment (Billings and Mooney, 1968; Sistla and Schimel, 2013). In addition, maximum temperatures are highest in summer and most likely to damage or kill new seedlings and regenerating growth, and thus maximum temperature buffering is most critical in this season.

A surprising result was that some lichen species significantly reduced soil moisture relative to paired controls (Fig. 3C). Our trait measurements suggest that the average lichen, under laboratory conditions and starting completely dry, can fully absorb 4.09 mm (± 1.81 s.d.) of rainfall, which was only exceeded by 18 % of rainfall events in 2019 in the study region (Supplementary data Fig. S1). It is therefore possible that rainfall is largely absorbed by some species and then evaporates from their thalli during hot parts of the day without having reached the soil (i.e. no throughfall). Although soil moisture effects were not clearly greater on rainy days across all species, the rainfall interception signal is likely to be complicated by soil hydrological lags and horizontal water movement within the topsoil profile. It has been shown in a previous study that lichen mats can completely intercept a small rainfall event (Crittenden, 1989), which could provide a competitive advantage over vascular plants in climates where most summer rainfall events are small. In tundra systems, this advantage is unlikely to be important at snowmelt and in poorly drained areas where soil water is never limiting, but pre-emptive uptake of water by lichens during small- to-medium sized rainfall events could be an underappreciated part of lichen–vascular plant competition in sites with frequent, small rainfall events during summer. However, there is also a possibility that lichens reducing soil moisture by at most a factor of 0.21 does not represent a biologically significant effect, particularly given low evaporation rates in tundra systems (Miralles *et al.*, 2011). Further studies would be required to determine the threshold of biological significance.

Based on studies of epiphytic lichens, traits are thought to affect water and energy balances primarily through changes to water-holding capacity, which is in turn driven by thallus mass per area (Gauslaa and Solhaug, 1998; Gauslaa and Coxson, 2011; Phinney *et al.*, 2018). Our trait results suggest that the relationship between water-holding capacity and thallus mass also applies for soil-borne lichens in a tundra system (Fig. 4). In addition, our results demonstrated that lichens with a higher specific thallus mass are able to retain water for longer (higher T_{50}) and tend to intercept more light than less compact lichens. Water retention has two potential effects on the soil microclimate: first, greater water mass per ground area increases the thermal inertia of the microsite and thus its capacity to buffer daily temperature extremes; and second, greater total water capture allows for more evaporative cooling over a longer time frame post-rainfall event, especially during the hottest parts of the day. However, our data suggest that temperature buffering was most closely associated with shading, not water-holding capacity, which implies that the influence of evaporative cooling and enhanced thermal inertia on the soil microclimate is weak. There remains a possibility that water retention plays a role in buffering the near-surface air microclimate.

Non-additive effects of lichens in multispecies mixtures

Non-additivity in the traits of species mixtures supports our hypothesis that the intertwining of species produces a denser, and thus more water-absorbent, mat. A study on bryophytes showed that mixed-species patches often had a greater than expected capacity to retain water because the

component species produced a more compact cushion than when they were growing alone (Michel *et al.*, 2012). Michel *et al.* (2012) argued that because bryophytes, like lichens, lack mechanisms to regulate their water loss, it is beneficial for them to facilitate community water retention rather than compete for soil water as vascular plants do. In a similar manner, lichens can increase their water uptake and water-holding capacity by clumping into a compact multispecies mat, enabling a longer period of photosynthesis that probably outweighs the negative effects of internal shading. Interestingly, it is likely to have been internal shading that produced the lower than expected values of albedo in species mixtures (Holmgren and Thuresson, 1998). The finding that temperature buffering in mixtures of lichen species was additive may be useful for fine-scale predictive models of the soil surface, since temperature buffering in lichen communities can be predicted solely using species means, rather than having to account for non-additivity.

Trade-off between temperature buffering and light competition

We found that co-occurring (non-*Betula*) vascular plants growing within lichen- and *Betula*-dominated patches were less abundant when the dominant species was more densely growing and strongly insulating (Fig. 6). This finding provides correlative evidence that, for plants growing within lichen mats, competition for light and water might outweigh the benefits of temperature buffering. A similar result has been observed for young juniper (*Juniperus communis* subsp. *nana*) bushes, whereby the benefits of microclimate buffering to underlying plants are outweighed by competition until the junipers age and develop a thinner canopy (Allegrezza *et al.*, 2016). On one hand, our results imply that densely growing lichens may be resistant to expanding woody plants. Yet, on the other hand, it may be that already established dwarf shrubs with relatively open canopies, such as *B. nana*, will facilitate the expansion of other shrub species (i.e. a local-scale 'invasional meltdown', *sensu* Simberloff and Von Holle, 1999).

Implications for shrub expansion in tundra

The lichen–shrub patches in this study may represent an intermediate stage in the global trend towards increased woody plant dominance in tundra systems (Myers-Smith *et al.*, 2011). It may be that many expanding plant species are already present in lichen mats and are poised to overgrow lichens when conditions become more favourable (e.g. Bret-Harte *et al.*, 2001). While there may be some climatic changes that impair shrubs, such as early snowmelt (Wipf *et al.*, 2009), most factors, including soil mineralization rates and disturbance by grazing and wildfire, are aligned in favour of shrub expansion and lichen exclusion (Sturm *et al.*, 2005; Joly *et al.*, 2009). Our results suggest that lichens will continue to have a large effect on microclimate until they are fully excluded by woody plant shading. That point – full lichen exclusion – may represent a tipping point in the system when microclimate extremes increase greatly.

SUPPLEMENTARY DATA

Supplementary data are available online at https://academic.oup.com/aob and consist of the following. Figure S1: daily precipitation values in 2019 at Fokstugu weather station for days with >0 mm precipitation. Figure S2: a target patch of lichen and its accompanying paired removal control plot. Figure S3: diagram of the lightbox set-up for measuring light interception traits, and an example photograph of the shadow cast by a specimen of *Bryocaulon divergens*. Figure S4: average fitted evaporation curves for all species and mixtures. Figure S5: buffering effect of each target species and mixture. Figure S6: means and standard errors for maximum and minimum temperature buffering in each two-species mixture and their component species growing alone. Figure S7: moisture difference as a proportion of the cleared control plot. Figure S8: correlation plot showing the relationship between maximum temperature buffering and light interception at ground level for mixtures and single species. Figure S9: height of co-occurring plants relative to the height of the dominant lichen. Table S1: results of paired *t*-tests in species mixtures. Table S2: mean vascular plant and bryophyte cover among species and mixtures.

ACKNOWLEDGEMENTS

We thank Matteo Tolosano, Jessie Foest and Floor Marsman for fieldwork assistance, and the Norsk Villreinsenter for their hospitality. M.M. conceived the project and led the data collection in consultation with B.J.G. M.M. and W.K.C. contributed to data analysis. All authors contributed to interpretation of results. M.M. wrote the first draft of the manuscript and all authors contributed critically to edits therein. All data and the analysis code will be publicly archived on the Open Science Framework.

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