

Domenica Janeth Naranjo Orrico

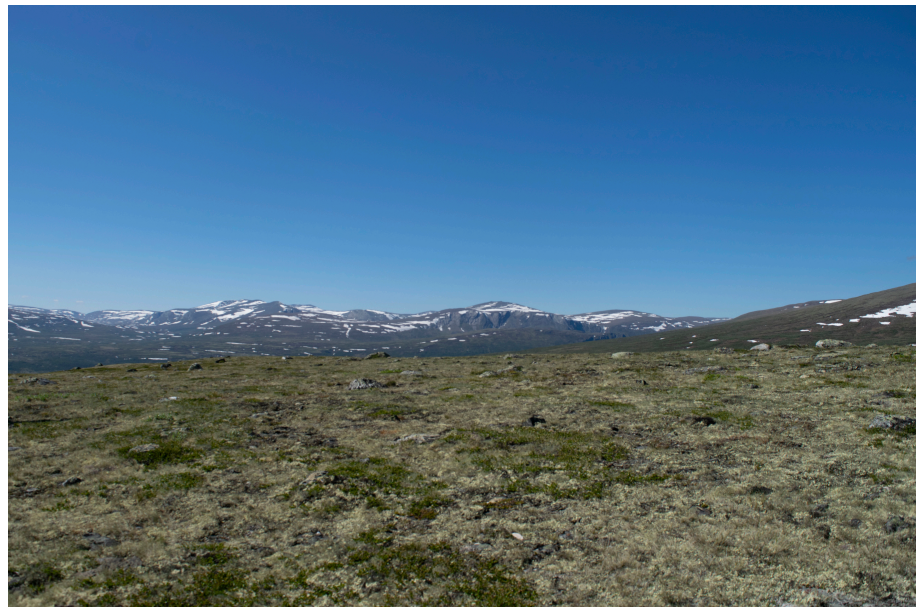
# How do lichens, willow shrubs, meadow and heath plant communities affect microclimate?

Master's thesis in Biology: Ecology, Behaviour, Evolution and  
Biosystematics

Supervisor: Richard Strimbeck

Co-supervisor: Bente Jessen Graae

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Kunnskap for en bedre verden



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## Abstract

Increases in earth surface temperature because of climate change in the last decades have already shown consequences in different ecosystems and in different taxonomic groups. Alpine environments are among the most threatened by the effects of climate change because the organisms that live there are conditioned to low temperatures. Several changes in alpine communities have already been observed, however, shrub encroachment is one of the most evident. This encroachment affects especially smaller organisms that are not good competitors, such as cryptogams. Leading to changes in the community that have shown to affect macro- and microclimate. The most common way of reporting temperature is the mean annual temperature that does not reflect what plants and lichens are experiencing. Microclimate is the actual temperature that the organism is experiencing. Studies have shown that microclimate can impact community structure and its dynamics over time. Moreover, community structure can affect the microclimate via organisms' interactions. Little is known about how functional groups of established plants affect the microclimate. In this project, we study and describe how different community types such as willow shrubs, meadow, heath, and lichen ridgetop, and environmental variables affect the microclimate through the use of thermal imaging. During June-July 2020 thermo-photographs were taken and environmental variables were measured in a heath, a lichen ridgetop, a meadow, and a willow dominated community in Dovrefjell. It was found that all the plots presented a higher temperature than that recorded for air temperature. The models showed that wind speed decreased decoupling and light intensity increase decoupling from air temperature. The willow, a community dominated by deciduous shrubs, and the meadow (dominated by grasses and forbs) were more coupled to air temperature while the heath (dominated by dwarf evergreen shrubs) and the lichen ridgetop (dominated by lichens) were more decoupled from air temperature. Deciduous shrubs presented the lowest and lichens presented the highest surface temperatures. No significant differences in surface temperature were found for lichen species, colouration nor growth form.

## Introduction

An increase in earth surface temperature, because of climate change, has been occurring and for the last two decades it has been even more dramatic especially over land and at high latitudes with an average increase of 0.3 °C per decade (Hock et al., 2019; IPCC, 2021). Some consequences of climate change can already be seen in different ecosystems and in different taxonomic groups (Aalto, Le Roux, & Luoto, 2014; Dangles et al., 2017; Nottingham et al., 2020; Pacifici et al., 2017). Alpine and tundra environments are particularly threatened by the effects of climate change because their species are conditioned to low temperatures (Pauli et al., 2012; Pauli et al., 2015; Vanneste et al., 2018). Several changes have already been reported in alpine plant communities, some examples being the increase in species richness and graminoid cover (Cannone & Pignatti, 2014; Grabherr, Gottfried, & Pauli, 2010; Matteodo et al., 2016). However, one of the more evident changes in these ecosystems in recent years has been the increase in shrub cover (Klanderud, 2008; Malfasi & Cannone, 2020; McLaren et al., 2017; Michelsen et al., 2011; Vanneste et al., 2018; Wilson & Nilsson, 2009), often referred to as “shrub encroachment”. Shrub encroachment is especially detrimental to smaller species and organisms that are not very good competitors such as lichens and mosses (Cornelissen et al., 2001; Michelsen et al., 2011; Robinson et al., 2010; Vanneste et al., 2018; Vittoz et al., 2010). Furthermore, experimental warming studies have shown decreases in the cryptogam layer (Cornelissen et al., 2001; Ferrenberg, Reed, & Belnap, 2015).

Temperature, precipitation and humidity are the most commonly used variables to describe how macroclimate shapes Earth’s communities (Jiang et al., 2017). Moreover, temperature is a very important determinant, but not the only one, of the fundamental niche of an organism (Graae et al., 2018). Thus, changes in temperature can drive changes in populations and communities. However, in many cases the most common temperature measures, mean annual temperature and even hourly measures, recorded by weather stations, fail to accurately show the actual temperature that the organisms are experiencing (Körner & Hiltbrunner, 2018). Microclimate is the term used to describe the actual climate experienced by an organism (Jones, 1985). This happens because plants and lichens are rather decoupled from the atmospheric changes. Usually, changes in microclimate are more important for sessile organisms such as lichens and plants because they cannot move if the conditions become unfavorable, thus, they must withstand them. For plants, the decoupling depends on their height —distance from the soil, arrangement of their leaves and the surface roughness of the canopy (Körner, 2021a; Körner et al., 2018), as explained by the aerodynamic decoupling from free atmospheric circulation (Körner et al., 2018; Larcher, 2012). In the case of lichens, the decoupling depends on the growth form, thallus thickness and color (Asplund & Wardle, 2017; Sundstøl & Odland, 2017; van Zuijlen et al., 2020). In both cases short and long wave radiation, cloud cover and wind velocity play an important role as well (Körner, 2021a; Nobel, 2009).

Likewise, lichens and plants can modify their microclimate. For example, cushion plants in arctic-alpine environments trap heat, maintaining a higher temperature than their environment, increasing soil moisture and reducing wind velocity (Cavieres et al., 2007; Molenda, Reid, & Lortie, 2012). However, microclimate modification is not exclusive to cushion plants and there are several studies with examples of how different plant lifeforms modify their microclimate (Breshears et al., 1998; Rae et al., 2006; Sklenář et al., 2016). A review reported that the presence of woody plants raises the temperature beneath the canopy during the night in various environments like deserts, coastal landscapes, and arctic and alpine ecosystems specially in clear-



sky and low wind speed nights (D'Odorico et al., 2013). In coastal landscapes and arctic and alpine ecosystems this happens because canopies absorb the long-wave radiation emitted by the ground, instead of losing it to the atmosphere. Then, the canopy re-radiates it back, warming the air beneath it and reducing the radiative cooling of the soil (Grimmond, Robeson, & Schoof, 2000). On the other hand, in deserts, shrubs are usually sparsely distributed in patches surrounded by bare soil. A larger cover of bare soil means that soils present great heat fluxes and, also, reach high soil temperatures. This heat is often stored in the soils as thermal energy. During the night this stored energy is released as long-wave radiation causing the warming of the air beneath and around the shrub canopy, this effect being more pronounced when there is minimum air velocity and an absence of cloud cover (D'Odorico et al., 2010; He et al., 2010). It is believed that the increase of woody plants in alpine and tundra environments as a consequence of climate change will in turn raise temperatures of these ecosystems because of their lower albedo (Aartsma et al., 2020). In a recent study Aartsma et al. (2020) found that lichens presented a higher albedo, fluctuating from 0.227 to 0.284, in comparison to shrubs, fluctuating from 0.115 to 0.148, which has implications for the atmospheric heating. In a following study, Aartsma et al. (2021) reported a difference in atmospheric heating between lichens and shrubs of  $3.35 \text{ MJ d}^{-1}$  in a mountain area in Norway during the growing season, which means that if shrubs keep increasing their cover and lichens keep decreasing their cover an increase in atmospheric heating will occur as well as a rise in air temperature.

The effects of lichens on microclimate has been less studied but some studies have investigated the insulation ability of lichen mats, the high albedo effect of light colored lichens that cover large areas in alpine and tundra environments and their capacity to alter moisture (Aartsma et al., 2020; Asplund et al., 2017; Den Herder, Kytöviita, & Niemelä, 2003; Porada, Ekici, & Beer, 2016; van Zuijlen et al., 2020). It is important to study and understand these effects because microclimate modification by an organism can also lead to changes in ecosystem processes for example in the soil (van Zuijlen et al., 2020) and this will also affect other neighboring organisms. This modification can make the conditions of the site more favorable or unfavorable for those organisms, leading to positive or negative biotic interactions and changes in community dynamics by driving recruitment or death of organisms (Blonder et al., 2018; Graae et al., 2011). Marsman et al. (2021) found that for pine the microclimatic factors do not seem to be important for germination and recruitment, however Nystuen et al. (2019) found that lichen mats buffered the temperatures and, in turn, increased seedling recruitment rates in lichen mats compared to on bare soil.

There are many ways used to record temperatures at a finer scale, such as thermocouples, thermistors, PT sensors, or "button" type stand-alone data loggers (Körner et al., 2018; Sklenář et al., 2016; Strimbeck, Johnson, & Vann, 1993). In recent years the use of thermal imaging has helped to investigate plant temperatures (Dietrich & Körner, 2014; Gersony et al., 2016). All objects at temperatures above 0K emit electromagnetic radiation. Thermal imaging records the emitted mid- to long-wave infrared radiation, usually  $2 - 14 \mu\text{m}$ , as thermo-photographs allowing estimation of surface temperatures (Harrap et al., 2018; Lloyd, 2013). This method can be used to record the surface temperature of the different plant and lichen species and soil at a finer scale, detects small changes in temperature, is relatively easy to use, is a non-invasive technique and a relative fast way to record temperatures (Tattersall, 2016).

Most studies concerning microclimate and surface temperature have focused on vascular plants, with only a few studies on bryophytes (Block, Lewis Smith, & Kennedy, 2009; Casanova-Katny & Cavieres, 2012; Lett et al., 2018; Perera-Castro et al., 2020; Van Tooren, During, & Lensink, 1985)

and even fewer on lichens (Aartsma et al., 2021; Mallen-Cooper, Graae, & Cornwell, 2021; Nystuen et al., 2019) despite them being an important component in some communities. It is important to know how the different functional groups of organisms affect microclimate. Changes in microclimate can lead to shifts in the community and in turn lead to changes in the macroclimate as has already been proposed in other studies (Aartsma et al., 2021; Myers-Smith et al., 2011). Understanding if there are differences in microclimate between the different organisms in a community will give us a clearer picture of the community dynamics, how they work and how they will react under a changing climate.

In this project, I study and describe the microclimate/surface temperature of four different plant community types: willow shrub, meadow, heath, and lichen ridge tops, through the use of thermal imaging. More specifically, (1) The difference between the surface temperature of the four different communities: heath, lichen ridgetop, meadow and willow will be explored, (2) I will attempt to understand how the different environmental variables explain the decoupling of plot temperature with air temperature. (3) I will explore the surface temperature of the different functional types of vascular plants (deciduous shrubs, evergreen shrubs, forbs and graminoids) and lichens (fruticose and foliose) will be compared, and (4) the difference in surface temperature between the most abundant lichen species.

For the abovementioned questions the following hypothesis will be tested. (1) There will be differences in the surface temperatures of the different communities due the difference in environmental conditions in the sites where the communities are located and the different species that form these communities. The lichen ridgetop will present the lowest temperature because the dominant lichens in these sites have bright colours and high wind speeds, followed by the willow shrub, the meadow and the heath will have the highest temperature. (2) A highest light intensity will cause a higher heating in the surface temperature in all the vegetation making the surface temperature higher than the air temperature and a higher wind speed will reduce the heating of the surface temperature making it be closer to air temperature. (3) There will be differences in the surface temperatures of the different functional types because of the different in albedo, height, and surface roughness. Functional types with a higher roughness (deciduous shrubs) will have a lower temperature in comparison to the other functional types (4) There will be differences between the surface temperature of the different lichen species because the species present different colouration and growth form. The lichens with a darker colouration will present higher surface temperatures. Lichens with a fruticose growth form will present a higher temperature because of its highest complexity.

## Methods

### Study site

The study was conducted in the Dovrefjell mountains in Central Norway (62°00'00" N, 9°00'00" E), in low-alpine vegetation around 1100 m. The area presents a continental and dry (298 mm during the growing season) climate with cold winters and relatively warm summers (Johansen, 2004; Nystuen et al., 2019; Sørensen, 2018; Sørensen et al., 2018a). At Hjerkin, the closest meteorological station at 1012 m from the study sites, the mean annual temperature was 0.6°C in the year 2021. The same meteorological station reports a mean air temperatures of 10.6 °C and 13.3 °C in the months of June and July 2021 respectively (Norwegian Centre of Climate Services).

### Study design

In the study site, plots of 50 x 50 cm were installed as part of the ECOshrub project in 2013 (Sørensen et al., 2018a). The plots were installed in three sites on two mountains, Hjerkinshøe (1288 m) and Armodshøkollen (1274 m) located next to each other (Sørensen, 2018). The sites represent three different community types: a heath dominated by dwarf shrubs, a meadow dominated by graminoids and forbs, and a willow shrub community dominated by *Salix*. The willow and the meadow site on Hjerkinshøe on the west and east respectively, and the heath at Armodshøkollen (Nystuen, 2020). The shrub and heath communities were south facing and the meadow south-west facing (Sørensen, 2018). Each site had 16 plots, for a total of 48. Plastic seed traps were already present in these plots, as well as metal tubes which marked the corners of the plot before taking the pictures. Additionally, these plots vary in vegetation and their species composition and vegetation structure are well-described with data from 2020.

Additionally, new plots on ridge tops with a clear dominance of lichens were added to the study design. In order to do so, a stick was tossed to mark a random start point on the crown of the ridge. From the selected starting point a transect running downhill perpendicular to the ridge was established, with stops every 10 steps. A compass was used to maintain a constant direction. At each point, two plots of 50 x 50 cm were established on opposite sides (W-E or N-S), on each side of the line. The plots were framed with bamboo sticks. Furthermore, plots mostly dominated by the most abundant and common lichen species (*Cladonia stellaris*, *Flavocetraria nivalis*, *Alectoria ochroleuca*, *Bryocaulon divergens*, *Cladonia* cf. *arbuscula*, *Cladonia* cf. *rangiferina* and *Stereocaulon paschale*) were selected. A total of 7 plots for each species were selected. The plots were selected using a bamboo frame of 25 x 25 cm, to ensure that the plot was mostly dominated by only one species. These plots were established to give a clearer picture of the surface temperature in vegetation covered by the most common and abundant lichen species.

## Thermography

The thermographs were taken using a FLIR E8-XT Wifi camera (FLIR systems, Estonia). In each plot, a tripod with an extension arm was positioned facing south. In the extension arm of the tripod, the FLIR camera was firmly attached with two straps. The plots were framed using four bamboo sticks of 50 x 50 cm previously measured. The lens of the camera was positioned in a way so that it would be as parallel to the ground as possible and at a distance of 100 cm ( $\pm 5$ cm) from the center of the plot, in the 25 x 25cm plots the distance was slightly shorter (65cm,  $\pm 5$ cm). Two thermographs were taken in each plot — one with and another without a reference plant (see below)— and, additionally, a RGB picture was taken for reference with a Canon camera (Appendix, Figure 8). The parameters of the FLIR camera were set before taking the images. The emissivity was set at 0.95 and the reflected temperature was established based on the air temperature.

Before taking the thermograph, the following weather conditions were recorded in a field sheet: air temperature ( $^{\circ}\text{C}$ ), humidity (%RH), wind speed ( $\text{m}/\text{s}$ ), light intensity (PAR, photosynthetic active radiation,  $\mu\text{mol}/\text{m}^2/\text{sec}$ ). The air temperature, and wind speed were measured in the first period with a Kestrel 2000 anemometer (Kestrel meters, USA) and in the second with a Skywatch Atmos anemometer (Skyview weather, UK). To measure air temperature, the anemometer was hung on the tripod for a couple of seconds, and then the value was recorded. The humidity was only recorded during the second period of the field season because the first anemometer did not have the capacity to record humidity. The wind speed was measured at two positions above the ground. First, the anemometer was held 15cm above the ground, and secondly right above the plot (5cm). In both cases, the average was recorded after 30 seconds.

The light intensity was measured with a Skye PAR 215 quantum sensor (Skye Instruments Ltd, UK) with particular attention to avoid shadowing the sensor and hereby erroneous measurements.

Additionally, a brief weather description (Sunny, Cloudy), the time (hh:mm), GPS coordinates (Decimal degrees, DD), the orientation from which the tripod was positioned, and the picture code were also recorded. In a different field sheet, the most abundant species in each plot were also recorded.

### Reference plants:

A reference plant was constructed to see how the surface temperature of a simple surface is affected by the different environmental variables. The reference plants consisted of circles made of green construction paper with a diameter of 3 cm, impaled on 8cm bamboo skewers. The reference plants were placed outside the 50x50cm plots and the 25 x 25 cm plots. Before placing, it was brushed with water using the fingertips so that the paper became damp, but not droopy. After placing the reference plant, a minute was allowed for its acclimation before taking the thermal picture. However, because lack of a thermo-photograph with a reference plant with a dry surface at the end it was decided not to use them in the analysis.

The field season was divided in two parts, the first one from the 21<sup>st</sup> of June to the 2<sup>nd</sup> of July and the second from the 12<sup>th</sup> to the 22<sup>nd</sup> of July. During this time the willow, meadow and heath

plots were photographed several times throughout the different days, but the lichen plots were not permanent, so each plot was a new plot.

## Temperature extraction

To extract the temperatures of the different thermal photographs two types of software were used, ImageJ (Schneider, Rasband, & Eliceiri, 2012) and FLIR Tools (FLIR Systems, 2021). Two different temperature extractions were made. The first one was to extract the mean temperature (°C) of each plot and the second one to extract the mean temperature (°C) of areas dominated by a single species. The plot extraction was done in ImageJ with the package ThermImageJ (Tattersall, 2019). Before extracting the mean temperatures of each plot, areas covered with seed traps had to be eliminated from the picture. To do so, the seed trap was selected and eliminated which turned it black and the temperature extracted from there became 0°C. The tool “polygon selection” was used to form a square that encloses the plot. Then the pixel values were extracted from this area of interest with the tool ROI that created a matrix with those values. Afterwards this table was imported to R (R Core Team, 2021) the values equal lower or equal to 0 were excluded using the function filter() of the package dplyr (Wickham et al., 2022) and a new matrix was created, from which the mean temperature was calculated. The exclusion of values lower than 0 was done because the presence of metal tubes used to mark the corners of the plot was adding temperatures below 0 °C. Because of the warm conditions during the field season there was not a risk of excluding relevant information when excluding the values lower or equal to 0, but to be sure every time the minimum temperature found in a plant was checked.

The extraction of the mean temperatures for areas dominated by a single species was done with FLIR tools. A line was drawn in the area of interest with the tool “Add line measurement” of the FLIR software which gives the minimum, maximum and mean temperature in the area through which the line passes. The line was drawn in a way so that it covers the longest possible distance of the area dominated by a species.

## Functional types and Functional traits

Plants were classified by functional types (deciduous shrub, evergreen shrub, forb and graminoids) and lichen by growth form and colour (Table 1). Lichen colour characterization was done in a similar way as in the study of van Zuijlen et al. (2020). However, because *Cetraria cf. ericetorum* and *Flavocetraria cucullata* had very few measurements in comparison to the other species (four and eight respectively), they were not taken into account for the statistical analysis.

<b>Species</b>	<b>Growth Form</b>	<b>Colour</b>
<i>Flavocetraria nivalis</i>	Foliose	Bright-coloured
<i>Alectoria ochroleuca</i>	Fruticose	Bright-coloured
<i>Cladonia stellaris</i>	Fruticose	Bright-coloured
<i>Cladonia cf. arbuscula</i>	Fruticose	Intermediate
<i>Cladonia cf. rangiferina</i>	Fruticose	Intermediate
<i>Stereocaulon paschale</i>	Fruticose	Intermediate
<i>Bryocaulon divergens</i>	Fruticose	Dark-coloured
<i>Cetraria cf. ericetorum</i>	Fruticose	Dark-coloured
<i>Cetraria islandica</i>	Foliose	Dark-coloured
<i>Flavocetraria cucullata</i>	Fruticose	Intermediate

Table 1. Lichen Functional Traits

## Statistical Analysis

Three data sets were constructed to answer the three different research questions. All of them had the environmental variables measured in the field: Air temperature, wind speed and light intensity, as well as the date when the measurement was done, the time when the picture was taken and the community where the plots were located. In the first data set the mean plot temperature was added. In the second data set the species-specific mean temperatures and the functional type in the case of plant species or growth form in the case of lichen species were added. Finally, in the third data set only the lichen species were filtered and a column with the colour category was added. An additional variable that contained the difference in temperature between air temperature and mean plot temperature or species mean temperature was added in all data sets, from now on called difference in temperature ( $\Delta T$ ). For the different analysis only, variables measured since the beginning and throughout the field season were used. Variables like wind speed measured at 5cm above the ground and humidity were not used for the different analysis because were not recorded since the beginning.

## ANOVA

To explore the difference between the temperature in the different communities, the different functional types of vascular plants and lichens, and between lichen species an analysis of variance (ANOVA) was performed and then, if the differences were significant, a post hoc test was done to see more clearly the differences between the groups.

To see if the difference between the plot temperatures in the different communities was statistically significant a two-way ANOVA was performed with mean temperature of the plots as a response variable and the communities and the date as explanatory variables. Before conducting the function `gvlma()` of the package “gvlma” (Pena & Slate, 2019) was used to see if the model fulfilled the assumptions of ANOVA. Additionally, the normality of the residuals was tested using a quantile-quantile plot and the Shapiro-wilk test using the functions `plot()` and `shapiro.test()` in `r`, respectively. It was decided to use a type III sum of squares because of the unbalanced design, this was specified using the `anova()` function of the “cars” package (Fox, Weisberg, & Price, 2021). Afterwards, a Tukey HSD test using the `HSD.test()` function of the “agricolae” package (de Mendiburu, 2021) in `r` was used to compare the different communities.

In order to see if there were significant differences between the surface temperature of the functional types a nested ANOVA was performed. To do the nested ANOVA the function `lmer()` of the package “lme4” (Bates et al., 2022) was used. The mean temperature was used as the response variable, functional type as a fixed effect and species within community as a random effect. In this analysis the soil and moss surface temperature were also considered. Afterwards, to compare the different functional types the function `emmeans()` of the package “emmeans” was used (Lenth, 2022). The same procedure was done to see if there were significant differences in the decoupling with air temperature between the different lichen species, growth forms and colors. A model was created with the difference in temperature ( $\Delta T$ ) of the lichen species with air temperature as the response variable, species were added as a fixed effect and species within community as a random variable.

### Linear mixed effect models

To see how the environmental variables, light intensity and wind speed, affected the decoupling from the air temperature in the plots of the different communities two linear mixed models were created with the `lmer()` function. In the first model the difference in temperature ( $\Delta T$ ) was used as a response variable, community, wind speed and air temperature as fixed effects, and light intensity as a random factor. In the second model community, light intensity and air temperature were fixed factors and wind speed a random factor. In both cases AIC was used to select the best model that explained the data, the function `aictab()` of the package “AICcmodavg” was used to do so. The tables with the candidate models and their AICc values can be found in the appendix (Table 4; Table 5). All the different candidate models were tested to see if their residuals were normally distributed with the `Shapiro.test()` function and also visually assessed by creating two graphs one with the functions `qqplot()`, `qqline()` and a histogram with the function `hist()`.

Additionally, two models were created with the functional traits of lichens one with the colour category and the other with lichen growth form. These models were created to see if the growth form and colour of the lichens could explain the difference in temperature with the air. In both models “difference of temperature ( $\Delta T$ )” was used as the response variable. In the first model colour, light intensity and wind speed as fixed factors and in the second one growth form replaced colour. In both models “species within community” were added as a random factor. In the first model an interaction between “colour” and “light intensity” was added to the model and in the second one an interaction between “growth form” and “wind speed”. Afterwards, if significant differences were found between the colours an estimated marginal means (`emmeans`) test was conducted to see the differences.

## Results

### Difference in surface temperature in the different communities

#### Environmental variables and plot surface temperature in the different communities

The community that registered the highest mean air temperature during the field period was the lichen ridge top and the community that registered the lowest was the heath. The values registered for mean plot surface temperature were in all the communities higher than the air temperature. The community that registered the highest mean plot surface temperature was the lichen ridge top, followed by the meadow, then the willow and the community with the lowest mean plot surface temperature was the heath (Figure 1A; table 2).

The community which recorded the highest mean wind speed was the heath, followed by the lichen ridge and the meadow and willow presented an equal mean wind speed (Figure 1B; table 2). The lichen ridge top was the community which experienced the highest mean light intensity followed by the willow, then the heath and the community that received the lowest light intensity was the meadow during the field season (Figure 1C; table 2). The daily environmental conditions can be found in the appendix (Appendix, Figure 9).

<b>Community</b>	<b>Mean air temperature (°C)</b>	<b>Mean plot surface temperature (°C)</b>	<b>Mean Wind speed (m/s)</b>	<b>Mean light intensity (μmol/m<sup>2</sup>/sec)</b>
<b>Heath</b>	13.4 ± 0.3	18.9 ± 0.8	2.7 ± 0.2	1136.7 ± 52.6
<b>Lichen ridge top</b>	19.4 ± 0.2	25.3 ± 0.4	2.1 ± 0.1	1253.8 ± 34.4
<b>Meadow</b>	17.5 ± 0.3	21.1 ± 0.6	1.2 ± 0.1	1017.3 ± 50
<b>Willow</b>	18.3 ± 0.4	20.6 ± 0.4	1.2 ± 0.1	1241.8 ± 47.2

*Table 2. Mean air temperature and standard error registered by the anemometer, mean plot surface temperature and standard error extracted from the thermo-photograph, mean wind speed measured at 15cm above the ground and its standard error, and mean light intensity and its standard error during the field season in the different communities*

The ANOVA showed that the mean plot surface temperatures between the communities were significantly different ( $p$ -value<0.005) from each other (Appendix table 6). The Tukey HSD test revealed that the heath and the lichen ridge top were significantly different from each other and from the meadow and the willow, but the meadow and the willow were not significantly different from each other (Figure 1A; Appendix table 7).



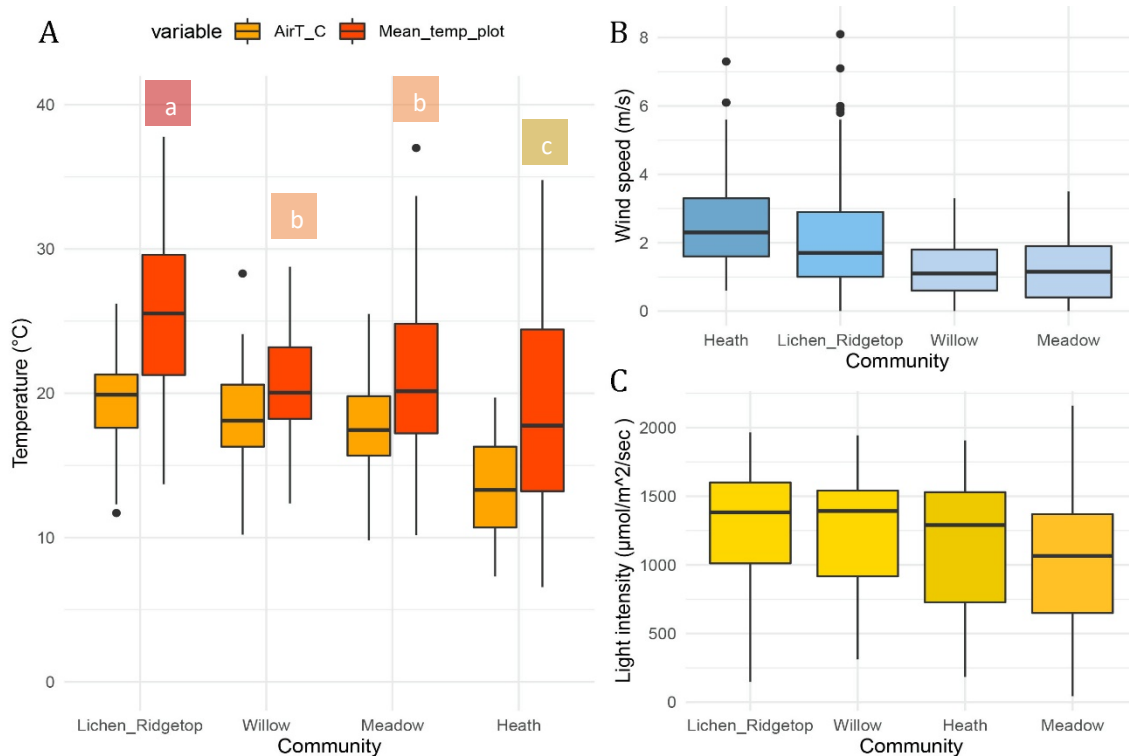


Figure 1. A) Air temperature recorded with the anemometer, and mean plot surface temperature extracted from the thermo-photographs in the different communities.. The letters above the boxes represents the grouping done by Tuckey HSD test. If the communities have a different letter, it means that they are significantly different from each other, if they share the same letter, they are not significantly different from each other. B) Wind speed measured at 15cm above the ground in the different communities during the field season. C) Light intensity in the different communities during the field season.

## How the environmental variables explain the decoupling of plot temperature with air temperature

### Decoupling of vegetation temperature from the air temperature

The wind speed had a significant effect in  $\Delta T$  (p-value < 0.001). However, the air temperature did not have a significant effect in  $\Delta T$  (p-value= 0.14). The interaction between air temperature and the different communities had also a significant effect on  $\Delta T$  (p-value < 0.001), as well as the interaction between the air temperature and the different communities (p-value < 0.05), and the interaction between wind speed and air temperature was not significant (p-value= 0.06). The variance in  $\Delta T$  explained by the light intensity was 3.7. In general, the  $\Delta T$  decreases in all communities when the wind speed increases. The  $\Delta T$  decreases by 0.36 °C in the heath, by 0.26 °C in the lichen ridge top, by 0.04 °C in the meadow, and by 0.14 °C in the willow when the wind speed increases by 0.1 m/s and at a mean air temperature (Figure 2).

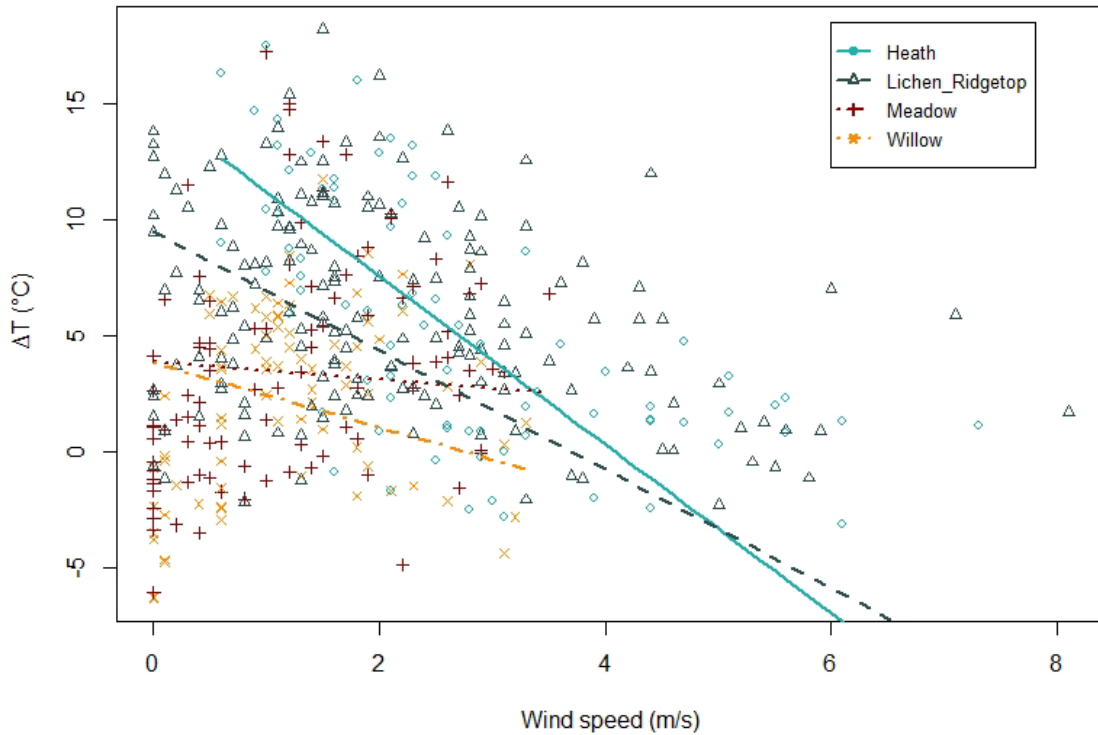


Figure 2. Linear mixed model of difference in temperature between the air temperature and the mean plot temperature ( $\Delta T$ ), and wind speed. The different line types and its colours represent the different communities, and the points represent each plot. The shape and colours of the points represent in which community these plots are from.

The light intensity had a significant effect on  $\Delta T$  ( $p$ -value  $< 0.001$ ), as well as the air temperature ( $p$ -value  $< 0.01$ ). The interaction between the light intensity and the different communities was significant ( $p$ -value  $< 0.05$ ), and the interaction between light intensity and air temperature was also significant ( $p$ -value  $< 0.001$ ). The variance of the  $\Delta T$  explained by wind speed was 2.2. In general,  $\Delta T$  increases in all communities with an increase in light intensity. It increases by  $0.008$  °C in the heath, by  $0.006$  °C in the lichen ridge top, by  $0.005$  °C in the meadow, and by  $0.003$  °C in the willow when the light intensity increases by  $1 \mu\text{mol}/\text{m}^2/\text{s}$  and at a mean air temperature (Figure 3).

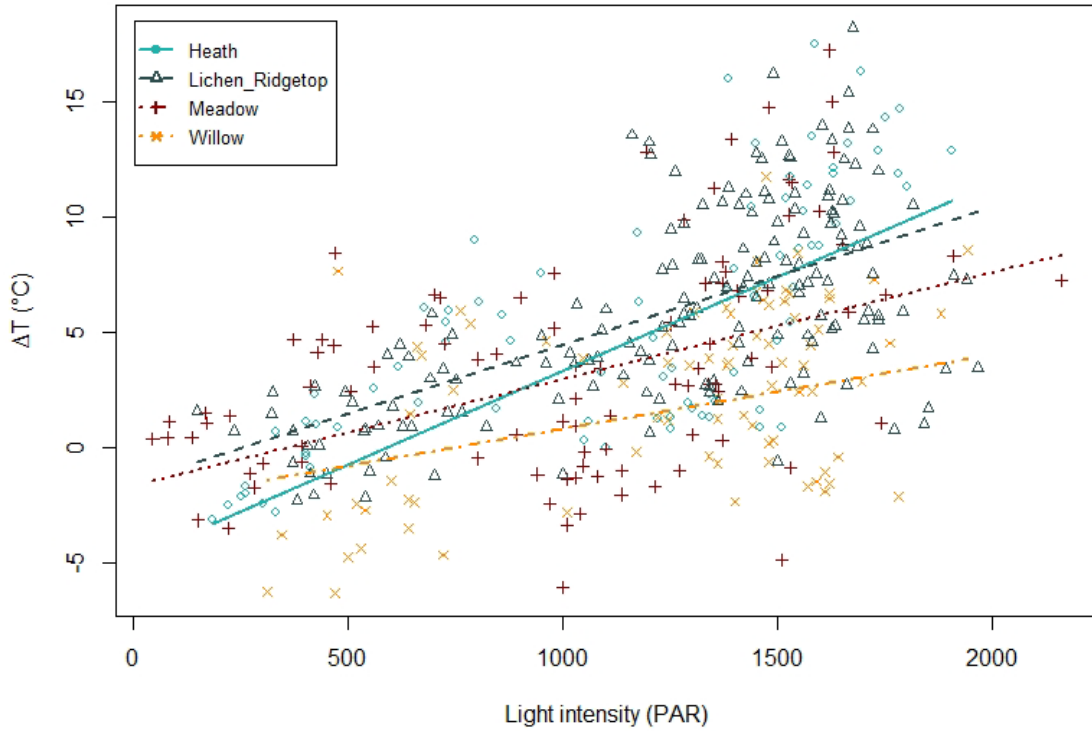


Figure 3. Linear mixed model of difference in temperature between air temperature and plot temperature ( $\Delta T$ ) with light intensity. The different line types and its colours represent the different communities, and the points represent each plot. The shape and colours of the points represent in which community these plots are from.

## Functional types of vascular plants and lichens

### Surface temperature of the different functional types of vascular plants and lichens

Both lichen growth forms presented a higher temperature than all the functional types of vascular plants. Mosses had the highest surface temperature. Lichens presented a higher mean surface temperature than bare soil. Of the vascular plants the graminoids had the highest surface temperature and the deciduous shrubs presented the lowest surface temperature (Table 3).

Functional type	Mean surface temperature (°C)
Moss	26.0 ± 0.7
Foliose lichen	25.8 ± 0.7
Fruticose lichen	25.5 ± 0.4
Soil	24.8 ± 1
Graminoids	21.1 ± 0.5
Forb	19 ± 0.3
Evergreen shrub	18.8 ± 0.5
Deciduous shrub	18.2 ± 0.3

Table 3. Mean surface temperature and its standard error extracted from the thermo-photographs of the functional types

The difference between the mean surface temperature of the different functional types was significant ( $p$ -value $<0.001$ ). The estimated marginal means (emmeans) comparison showed that deciduous shrubs were significantly cooler than foliose lichens ( $p$ -value  $< 0.001$ ), fruticose lichens ( $p$ -value  $< 0.001$ ), graminoids ( $p$ -value $<0.01$ ), moss ( $p$ -value $<0.001$ ) and soil ( $p$ -value $<0.001$ ), but they were not significantly cooler than forbs ( $p$ -value= 0.95) and evergreen shrubs ( $p$ -value= 0.19). The evergreen shrubs were significantly cooler than foliose lichens ( $p$ -value $<0.05$ ), fruticose lichens ( $p$ -value $<0.05$ ), moss ( $p$ -value $<0.05$ ) and soil ( $p$ -value  $< 0.05$ ), but they were not significantly cooler than forbs ( $p$ -value=0.86) and graminoids ( $p$ -value = 0.96). The forbs were significantly cooler than foliose lichens ( $p$ -value  $< 0.001$ ), fruticose lichens ( $p$ -value  $<0.001$ ), moss ( $p$ -value $<0.001$ ) and soil ( $p$ -value  $< 0.001$ ), but they were not significantly cooler than graminoids ( $p$ -value = 0.13). Graminoids were significantly cooler than fruticose lichens ( $p$ -value  $< 0.05$ ), moss ( $p$ -value  $< 0.05$ ) and soil ( $p$ -value  $< 0.05$ ) but they were not significantly cooler than foliose lichens ( $p$ -value= 0.15). The surface temperature of fruticose and foliose lichens was not significantly different from each other ( $p$ -value= 1), from moss ( $p$ -value = 0.95;  $p$ -value = 0.99, respectively) and from the soil ( $p$ -value= 0.82;  $p$ -value= 0.95, respectively). The surface temperature of soil and moss was not significantly different from one another ( $p$ -value= 0.99; Figure 4, Appendix table 8).

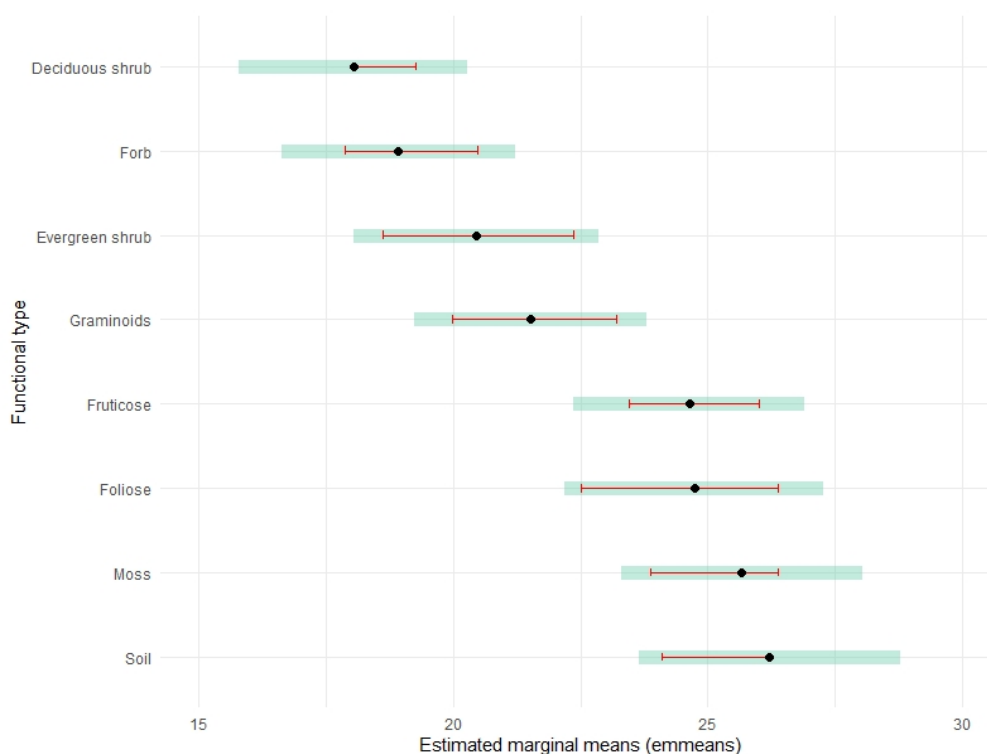


Figure 4. Estimated marginal means comparison between the different functional types. The blue transparent lines represent the confidence intervals. If the red lines overlap, it means that they are not significantly different.

## Lichen species and functional traits

### Surface temperature of the different lichen species

There was not much variation between the lichen species surface temperature. The species that presented the highest mean surface temperatures was *Cladonia cf. rangiferina* followed by *Cladonia cf. arbuscula* and the species that presented the lowest temperatures were *Flavocetraria cucullata* and *Cetraria cf. ericetorum* (Figure 5; Appendix table 9). However, the ANOVA showed that there were not significant differences between the surface temperature of the lichen species ( $p$ -value  $> 0.05$ ).

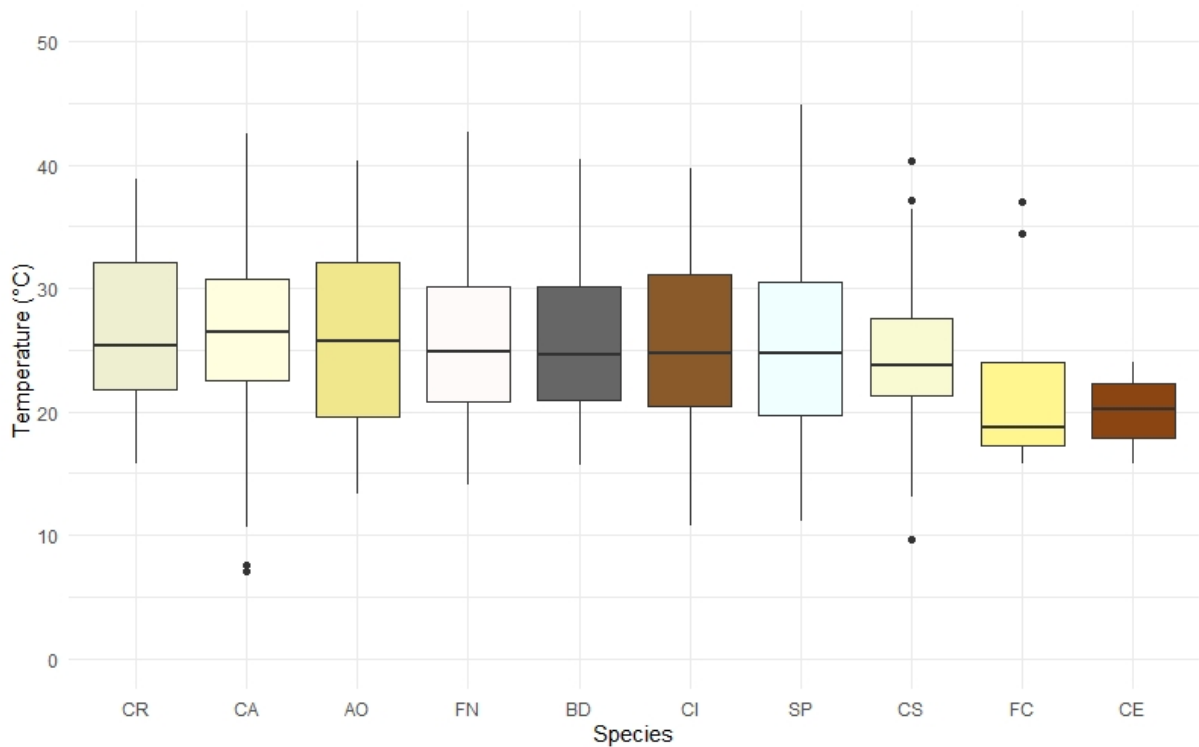


Figure 5. Lichen species surface temperature. The codes represent the different species AO- *Alectoria ochroleuca*, BD- *Bryocaulon divergens*, CA- *Cladonia cf. arbuscula*, CE- *Cetraria cf. ericetorum*, CI- *Cetraria islandica*, CR- *Cladonia cf. rangiferina*, CS- *Cladonia stellaris*, FC- *Flavocetraria cucullata*, FN- *Flavocetraria nivalis* and SP- *Stereocaulon paschale*.

### Decoupling of surface temperature from the air temperature explained by lichen functional traits

#### Lichen Colouration

The model showed a significant effect of light intensity ( $p$ -value $<0.001$ ) and wind speed ( $p$ -value $<0.001$ ) in the decoupling from air temperature of the lichens ( $\Delta T$ ). The interaction between light intensity and intermediate-coloured lichens was significant ( $p$ -value= 0.02). In all the cases  $\Delta T$  increased with an increased in light intensity. The increase was faster in the intermediate colour lichens, it increased by 0.009 °C with an increase of 1 unit in light intensity and with a mean wind speed.  $\Delta T$  in the bright-coloured increased by 0.006°C, and dark-coloured

lichens increased by 0.007 °C with an increase of 1  $\mu\text{mol}/\text{m}^2/\text{s}$  in light intensity and with a mean wind speed (Figure 6).

### Lichen growth form

The model showed that the effect of wind speed was significant ( $p\text{-value}<0.001$ ) as well as the effect of light intensity ( $p\text{-value}<0.001$ ) in the decoupling from air temperature of the lichens ( $\Delta T$ ). However, the interaction between wind speed and growth form was not significant ( $p\text{-value}=0.68$ ), as well as the effect of growth form ( $p\text{-value}=0.79$ ) (Appendix, Figure 10).

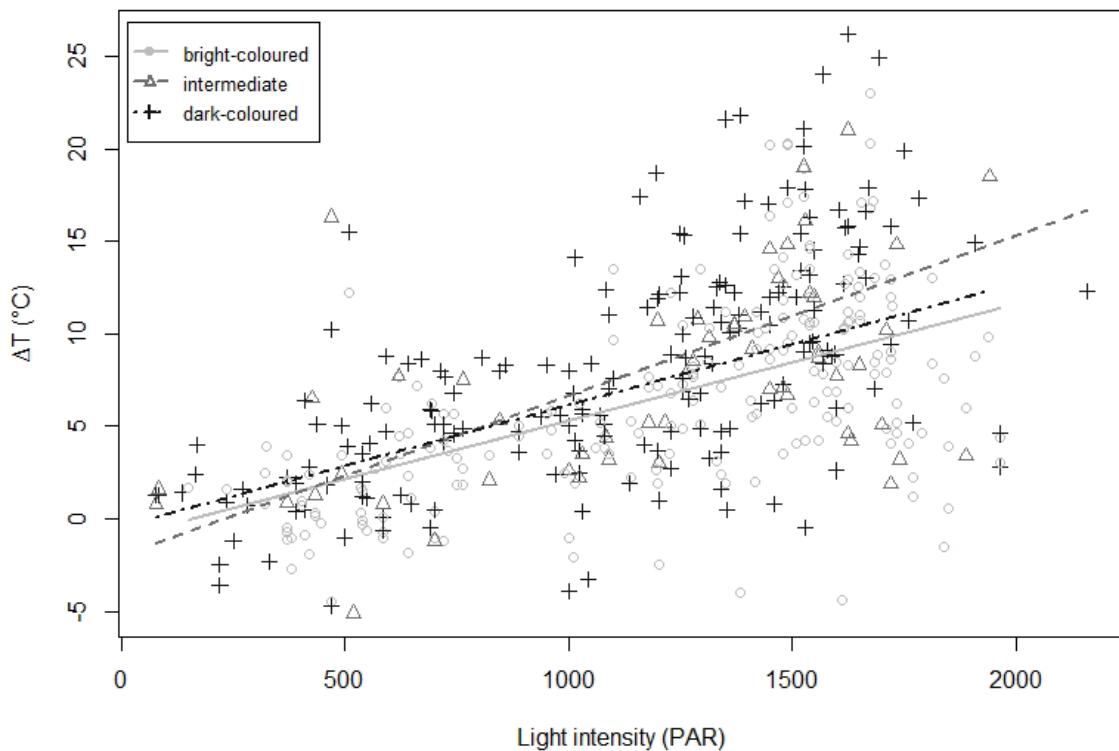


Figure 6. Linear mixed model of the difference in temperature between air and mean plot temperature ( $\Delta T$ ) with light intensity. Each line type and its colour represents the different colorations of the lichen species. The points are the different lichen species within the colour category.

The emmeans test showed that there is not a significant difference between bright-coloured lichens and intermediate colour lichens ( $p\text{-value}=0.56$ ), between bright-coloured and dark-coloured lichens ( $p\text{-value}=0.57$ ) and between dark colour and intermediate-coloured lichens ( $p\text{-value}=0.46$ ; Figure 7; Appendix table 10).

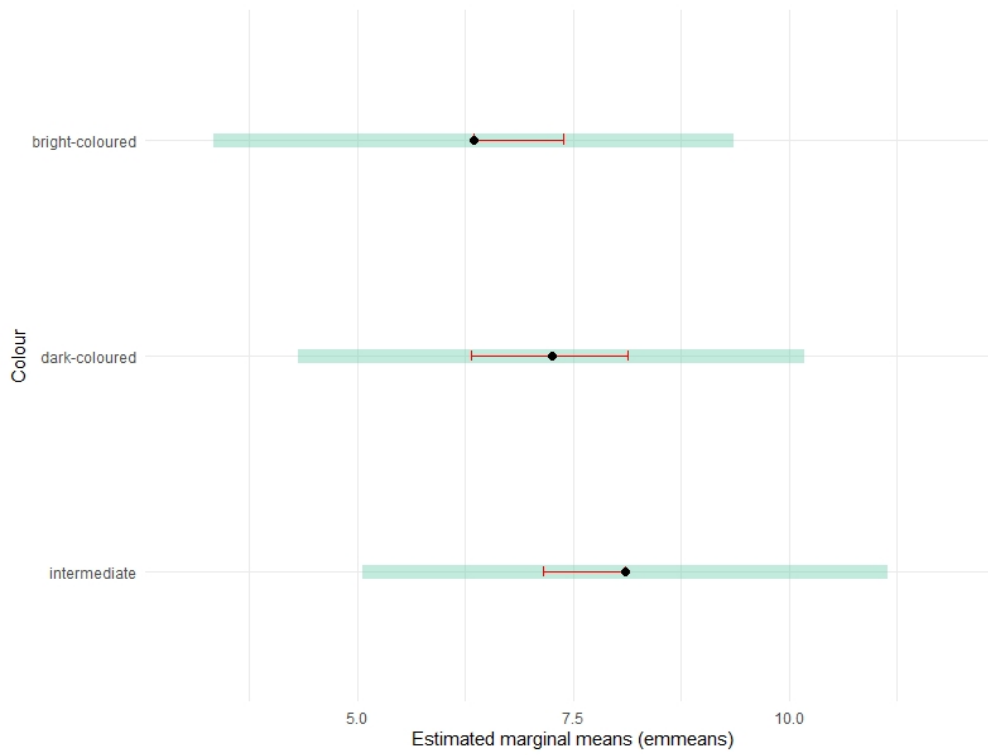


Figure 7. Estimated marginal means comparison between the difference in temperature ( $\Delta T$ ) in the different colorations of the lichens.

## Discussion

### Difference in surface temperature in the different communities

#### Environmental variables and plot surface temperature in the different communities

The surface temperature of the plots in all the communities was higher than the air temperature. This decoupling of vascular plants and lichens temperature with air temperature has been reported in several studies (Aartsma et al., 2021; Dietrich et al., 2014; Gauslaa, 1984; Gersony et al., 2016; Larcher, 2012; Scherrer & Körner, 2010; Sklenář et al., 2016; Strimbeck et al., 1993). Many alpine plants have a high heat tolerance because it is common in the alpine communities to experience high temperatures during the growing season with a clear, warm sunny day (Gauslaa, 1984; Körner, 2021c). Decoupling from air temperature is an adaptation of these plants to cold conditions. This decoupling is due to the amount of solar irradiation absorbed by these organisms and the boundary layer of air adjacent to their surfaces. The boundary layer affects both the sensible and latent heat loss of the organisms and therefore affects their temperature. A thicker boundary layer means a bigger area where turbulence is reduced and, thus, a bigger area where heat and mass transfer occurs mainly by molecular diffusion (Schuepp, 1993). The thickness of the boundary layer decreases the heat exchange between the organism and the environment because air is not a good heat conductor (Albrecht et al., 2020; Defraeye et al., 2013); it also affects evaporative cooling because the layer of calm air traps more humidity reducing water loss (Albrecht et al., 2020; Bunce, 1985; Grace, 1974). The thicker the boundary layer of the organism the more decoupled from the environment it will be (Larcher, 2003a; Nobel, 2009). The thickness of boundary layer depends on wind speed and on the size and form of the surface, leaf or thallus. The boundary layer has an effect in the overall vegetation surface of a community as well as in individual leaves and/or thallus.

There were significant differences in the surface temperature of the different communities that is in agreement with the first hypothesis, however, the heath rather than lichen ridgetop was the community that registered the lowest mean plot surface temperatures. The heath is located in an exposed site where the vegetation receives a lot of wind and light. The highest wind velocities and the lowest air temperatures were recorded in the heath, which would explain the low temperatures of the plots. The wind speed model showed that an increase in wind velocity decreases  $\Delta T$ , in accordance with the second hypothesis, and this effect was more pronounced in the heath. A higher wind speed reduces the thickness of the boundary layer causing heat transfer by forced convection to become more prominent. Forced convection occurs when the heated air conducted outside the boundary layer is removed mechanically by the wind (Nobel, 2009; Schuepp, 1993).

Nevertheless, the vegetation in the heath was still on average 5.5°C higher than the air temperature registered there. The heath is mainly dominated by evergreen dwarf shrubs like *Empetrum nigrum*, *Arctostaphyllum uva-ursi*, *Vaccinium vitis-idaea* and small deciduous shrubs like *Vaccinium uliginosum*, which because of their small size, are in close proximity to the ground. When plants grow close to the ground they tend to accumulate heat in their canopy allowing them to become more decoupled from the air temperature in comparison to taller plants (Körner, 2021b). Dwarf shrubs have a clonal growth, plants growing one very close to the next one, making them have a high canopy density and acting as a single surface which gives



these plants and this community a thicker boundary layer (Grace, Allen, & Wilson, 1989; Körner, 2021b). Additionally, low values of maximum leaf stomatal conductance have been reported for species of the genera *Empetrum* and *V. vitis-idaea*, 127 and 155 mmol/m<sup>2</sup>s, respectively (Körner, 1995). Gauslaa (1984) reported high cuticular diffusion resistances for *Empetrum nigrum*, 85.5 ± 26.2 s/cm, and *Arctostaphyllum uva-ursi*, 62.7 ± 10.9 s/cm. This means that these species have lower transpiration rates and, hence, a lower evaporative cooling in comparison to other plants. Even though the vegetation in the heath experience high wind speeds and low temperatures, which led to their plots having the lowest surface temperatures, they are highly decoupled from air temperature (high ΔT) because they are dominated by dwarf shrubs that are good at trapping heat and have a low latent heat loss.

The vegetation in the meadow was on average 3.6 °C higher than the air temperature. In the wind speed model, ΔT in the meadow seemed to have a very slow response to the increase in wind speed. The wind speed measured at 15cm above the ground was rather slow (1.2 m/s). Additionally, the meadow is mainly dominated by forbs and graminoids that are small plants growing close to the ground and the wind speed that they are experiencing is even slower (mean wind speed measured at 5cm above the ground 0.43 m/s), making the effect of the wind not as important as for other communities. Therefore, it might be possible that latent heat exchange is more important in this community. In a study done in the Rocky Mountains, *Deschampsia caespitosa*, one of the most dominant species in this community, reported a stomatal conductance of 408 ± 75 mmol/m<sup>2</sup>s for this species, which is relatively high (Bowman, Theodose, & Fisk, 1995). Additionally, other species present in this community like *Carex bigelowi* and *Solidago virgauraea* were reported to have cuticular diffusion resistances of 31.3 ± 10.3 and 48.8 ± 10.6 s/cm, respectively (Gauslaa, 1984), lower values than the ones from the species that are present in the heath. The wind speed seemed not to be such an important factor for the decoupling of the vegetation in the meadow with air temperature (ΔT) because of the low wind speeds registered in this site, but the relatively high latent heat loss could explain why there is no bigger difference between plot and air temperature (low ΔT).

The vegetation in the willow was on average 2.3°C higher than the air temperature and in the light intensity model, it was shown that an increase in light intensity meant an increase in ΔT supporting the second hypothesis. The slope of the willow community in this model was the least steep showing a slower decoupling from air temperature. The dominant species in the willow are deciduous shrubs, specially species of the genera *Salix* which are rather tall in comparison to the vegetation present in the other communities (Sørensen et al., 2018b). The height of these shrubs creates a shadow over the smaller size vegetation and the soil beneath them and gives this community a rougher surface. Rougher surfaces generate more turbulence because they slow air flow and turbulence facilitates sensible heat exchange (Bonan, 2016a). This turbulence is created above the shrubs canopy but a layer of relatively still air is present between the surface of the soil and the top of the canopy. This would make the leaves to have a higher sensible heat exchange but the surface of the soil and the smaller vegetation under the shrubs will have a lower heat exchange. However, the shadow cast over the soil surface and the smaller vegetation will lower the temperature to those close to the air temperature (Sørensen et al., 2018b). Dietrich et al. (2014) in a study in the alps showed that shading the alpine plants during sunny days will make them lose heat in 2 to 3 minutes and the temperature will be closer to that of the air temperature.

Additionally, the species of the genera *Salix* are known to have high evapotranspiration rates (Frédette et al., 2019; Přibáň & Ondok, 1986). *Salix glauca* and *Salix lapponum*, species found

in this community, have a low cuticular diffusion resistance,  $23.6 \pm 2.1$  and  $19.9 \pm 4$  s/cm, respectively (Gauslaa, 1984), and it has been reported that the stomatal conductance of *S. glauca* varies between 150-700 mmol/m<sup>2</sup>s (Bush, Berke, & Jacobson, 2017) which would mean that they have higher evaporative cooling rates as well. The leaves of the *Salix* species found in this site have a silver color and pubescence giving them a higher reflectance (Gauslaa, 1984; Nobel, 2009). This would provoke that even though the irradiation increases they manage to regulate their temperature by evaporative cooling and by reflecting the shortwave radiation.

The plots in the lichen ridge top had the highest temperature of all the communities. The vegetation in the lichen ridgetop was in average 5.9°C higher than the air temperature. This can be explained because these plots were mainly dominated by lichens which were the organisms that presented the highest surface temperatures. An important factor in the recorded lichen surface temperature is that the lichens were dry during the field season and would have little to not latent heat loss (as will be discussed in more detail in the next section). The vascular plant with a bigger presence in this community was *Betula nana* that has been reported to have a rather low stomatal conductance of 129 mmol/m<sup>2</sup>s (Gamm et al., 2018) and a high cuticular diffusion resistance of  $58.9 \pm 6.1$  s/cm (Gauslaa, 1984), which would give this community a very low latent heat loss. Furthermore, these communities were located in exposed sites where they received more light and wind in comparison to the other communities, and the registered mean air temperatures were also the highest. In addition, as shown in the light intensity model, an increase in light intensity increases  $\Delta T$ . It is worth mentioning that the light intensity measured in this study were only 400-700nm that is the photosynthetic active radiation (PAR), so the effect might be more intense if the whole spectrum would be measured. The higher light intensity and higher temperatures in addition to the dominance of lichens in the lichen ridgetop community created a higher surface temperature and the highest decoupling from air temperatures of all the communities.

## Functional types of vascular plants and lichens

### Surface temperature of the different functional types of vascular plants and lichens

There were significant differences between the different functional types which is in accordance with the third hypothesis. Within the vascular plants the graminoids presented the highest and deciduous shrubs the lowest surface temperature. This is similar to the findings of Gersony et al. (2016) in a study in an arctic tundra where they use thermography to study leaf temperature and reported that deciduous shrubs presented the lowest and graminoids the highest surface temperature. Chapin, van Cleve, and Chapin (1979) also found that graminoid tussocks in arctic communities had a temperature of 6-8°C higher than surrounding areas between the tussocks. The higher surface temperature of graminoids can be explained partially because tussocks have a protruding and bulbous structure which allows them to capture more low angle radiation (Chapin et al., 1979; Gersony et al., 2016). Furthermore, as the leaves get old in graminoids the stomata become rigid causing the loss of control of their water balance. This makes that the plant transpires constantly, even when there is no more available water in the soil, until the leaves desiccate (Larcher, 2003b). These dry dead leaves which are still part of their tussocks can be heated similarly to the poikilohydric lichens and mosses (Körner, 2021b). It is important to mention that while there are graminoids that do not form tussocks in the study sites, the

majority of graminoids from which the surface temperatures were extracted were forming tussocks. This because of their bigger size and more evident cover in the plots, making it easier to spot in the thermos-photographs.

The deciduous shrubs' surface temperature (18.2 °C) seemed to be more coupled with air temperature (17.6°C mean air temperature during the whole field season) than the other functional types. This can be explained by the height and the roughness of these plants since they are relatively taller in comparison with the other functional types and their branches make them rougher. A taller plant receives more wind reducing the thickness of the boundary layer and, in turn, loses more heat. Heat is first conducted across the air boundary layer and then convected away in the moving air stream (Körner, 2021b; Nobel, 2009; Sklenář et al., 2016). The structure of the plant can also influence to make the surface temperature be closer to air temperature. The air is decelerated and redirected around the leaves and branches of the plant creating more turbulence and forming eddies that can help in the transfer of heat from the plant to the air by convection (Bonan, 2016b; Gersony et al., 2016; Nobel, 2009). This has been reported by several studies (Gauslaa, 1984; Sklenář et al., 2010; Sklenář et al., 2016; Squeo et al., 1991). Sklenář et al. (2010) in a study done in the Antisana volcano in Ecuador reported that leaves of shrubs and herbs were colder than the air while leaves of smaller functional types as cushions and rosettes were higher than air temperature.

Both lichen growth forms presented a higher surface temperature in comparison to all the functional types of vascular plants. This result is in agreement with other studies that have studied lichen and vascular plant surface temperature. Aartsma et al. (2021) found in their study that even though lichens have a higher albedo they had a lower long wave radiation emission, which implies that lichens have a higher surface temperature in comparison to shrubs. The results of the present study can be explained in part because during the field season there were mostly sunny and dry conditions (Appendix, Figure 9). Lichens are poikilohydric organisms which means that they passively change their water content in response to water availability until eventually reaching a hydric equilibrium with the environment (Kappen & Valladares, 1999). Lichens do not have roots so they do not depend on the water of the soil and must withstand period of desiccation (Crittenden, 2000). This means that they depend completely on the water provided by the environment and because the conditions were dry, they were also dry and crisp during the measurements. In this conditions lichens had no water to lose as evaporative heat while vascular plants, because they can control their evaporative loss by closing and opening the stomata, have water to lose as evaporative heat (Larcher, 2003b; Nobel, 2009). Additionally, the reflectance also gets affected by the dryness of the lichen. Gauslaa (1984) found in a study where the reflectance in the wavelengths 400-1400 nm of 24 lichen species was measured that wet lichens reflect less sunlight than dry lichens. This is consistent with a study done in Alaska where surface and subsurface temperature of lichens and mosses was measured on dry and rainy days. In this study it was reported that the surface temperature of the lichen *Cladonia rangiferina* was greater in sunny and dry conditions (Stoy et al., 2012).

Even though the lichen species presented different colouration and growth forms their surface temperature was not significantly different from one another which did not support the fourth hypothesis. However, intermediate colour lichens presented a marginally higher surface temperature (Appendix table 11) and with an increasing light intensity their decoupling from the air temperature ( $\Delta T$ ) occurred faster in comparison to bright and dark-coloured lichens. This is rather surprising and, once again, not in accordance with the fourth hypothesis. It would be expected that bright-coloured lichens with a higher albedo reflect more radiation and,

therefore, have lower temperature and that dark-colour lichens absorb more radiation and a higher temperature. In a study Kershaw (1975) compared the temperatures of the white lichen *Thamnolia vermicularis* painting some individuals in black and leaving untouched others. It was found that in general the thalli painted in black had a higher temperature. In another study conducted by Gauslaa (1984) the temperatures of *Alectoria ochroleuca* and *Bryocaulon divergens*, light colored and dark color lichens respectively, were measured and it was found that the thallus of *B. divergens* was as much as 20°C higher than *A. ochroleuca*. However, van Zuijlen et al. (2020) found the different lichen colour categories did not alter the soil temperature beneath them suggesting that colouration only affects lichen surface temperature. The discrepancy of the results in this study with other studies could be explained because the number of dark-coloured lichens used in this study was lower than the number of bright- and intermediate-coloured lichens. Furthermore, only one species of dark colour lichen was used while several species were used in the bright- and intermediate-coloured lichens because of the low cover and presence the other potential species of dark colour lichens presented.

The lichen growth forms were not significantly different from each other but from the model it seems that the surface temperature of fruticose lichens is less affected by wind speed (Appendix, Figure 9) which is in accordance with the fourth hypothesis that stated that fruticose lichens will present a higher decoupling from air temperature because of their structure. Fruticose lichens like the species of *Cladonia* would behave as vertical cylinders similar to conifer needle shoots creating a thicker boundary layer that makes the decoupling from environment bigger (Gates & Benedict, 1963; Martin et al., 1999; Nobel, 2009; Smith & Carter, 1988; Strimbeck et al., 1993).

Soil and mosses presented a very high surface temperature which is explained once again by the dry conditions during the field season. Like lichens, many mosses are poikilohydric organisms that cannot do evaporative cooling when the conditions are dry. Stoy et al. (2012) reported that the moss *Pleurozium schreberi* reached temperatures over 55°C in a transition zone between taiga and tundra ecosystems in Alaska. Perera-Castro et al. (2020) found that hydration of arctic mosses had a significant effect on moss surface temperature, with the dry mosses reaching higher maximum temperatures than the wet mosses. Moss surface temperature in the middle of the day was 16.2°C higher than the mean air temperature. Likewise, soils under high radiation reach very high temperatures. Wundram, Pape, and Löffler (2010) reported that subsurface soil temperature in central Norway can reach as much as 45.6°C. Soils have a high heat capacity and absorption and emission of radiation of the soil usually takes place in the upper few millimeters of the soil. In order to see how these processes would work in a simple flat surface as a control the use of the reference leaf would have been useful. However, in the present study because only pictures with wet reference leaves were taken such analysis was not possible.

## Conclusion

The various characteristics of the different functional types of the plant and lichen species that compose the different communities make that each of them presents a difference in surface temperature. In addition to air temperature other environmental variables like the light intensity and wind velocity affect the surface temperature of plants and lichens. A higher light intensity increases the decoupling of the organisms to the air temperature while a higher wind speed decreases it. Dry lichens and mosses present high surface temperatures due to the lack of control of their water loss and an apparent higher absorbance of light during sunny dry days. Even though graminoids can regulate their water loss the accumulation of dead leaves can lead them to be heated by the sun more than other vascular plants. The deciduous shrubs of this study because of their height, roughness and morphology of their leaves are more couple to air conditions than the other growth forms.

## Acknowledgement

I would like to start thanking my supervisors Richard Strimbeck (NTNU) and Bente Jessen Graae (NTNU) for all the guidance and help provided during the realization of the thesis. Rick for always been present, answering my many questions, clarifying my doubts, and guiding me through the whole process, and Bente for her comments and suggestion, and introducing me to the fantastic group with whom I made my thesis with. I would also like to thank Benjamin Blonder (UC Berkeley) and Courtney Ray (UC Berkeley) for their useful comments in the methodology and statistical methods. Similarly, I would like to thank the people who help me during the field work, Ronja and Hanne that help me with all the setup for taking the measurements, the identification of the Norwegian flora but specially were an amazing company during the field season. I would also like to thank my friends and family, especially my mom and my sister who are always there for me and inspire me to keep going when things are difficult, without them traveling to a new country to study a master's degree, with all the challenges and opportunities that comes with it, would not have been possible.

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## Appendix

### Figures

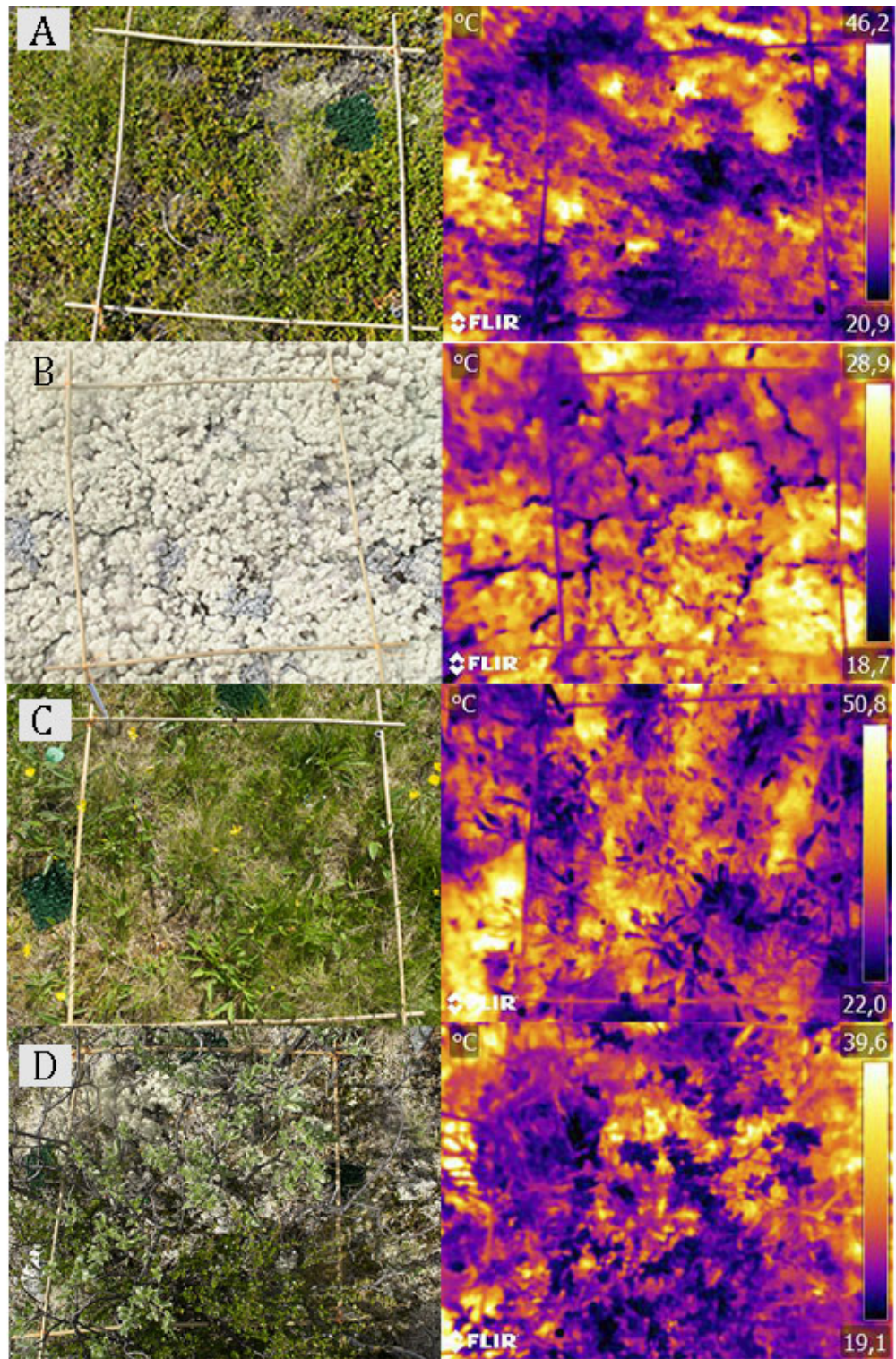


Figure 8. Example of RGB pictures and a thermo-photographs of A) a plot in the heath, B) a plot in the lichen ridge top, C) a plot in the meadow and D) a plot in the willow.

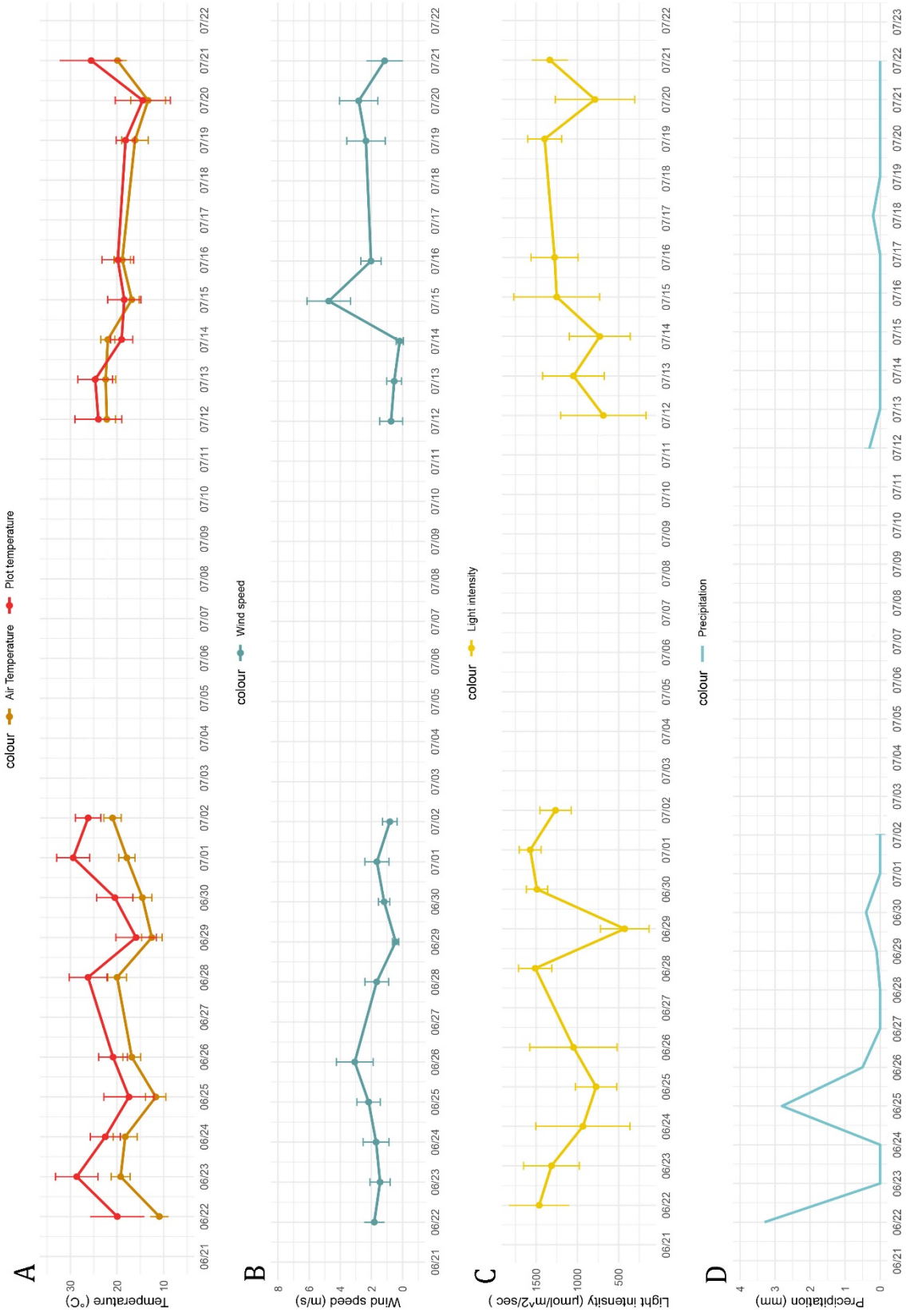


Figure 9. Daily environmental measures during the field season. A) Daily mean air temperature (red line) extracted from the thermos-photographs and daily mean air temperature (golden line) measured with the anemometer. B) Daily wind speed measured with the anemometer. C) Daily light intensity measured with PAR sensor. D) Daily precipitation



reported by Hjerkin the closest meteorological station at 1012 m from the study sites (Norwegian Center of Climate services).

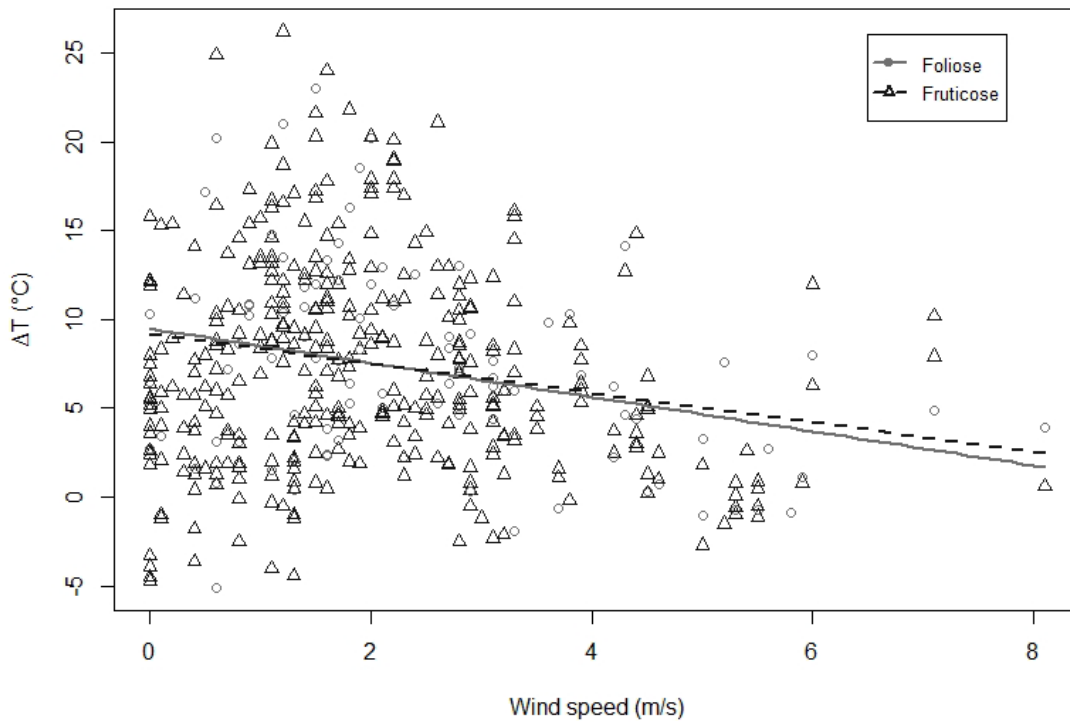


Figure 10. Linear mixed model of the difference in temperature between air and mean plot temperature ( $\Delta T$ ) and wind speed. The lines represent the growth form of the lichen species.

## Tables

		AICc	AICcWt
<b>ModA6</b>	Diff_temp ~ Community + Wspd_50cm_ms.1 + AirT_C + Community: AirT_C + Community: Wspd_50cm_ms.1 + AirT_C: Wspd_50cm_ms.1 + (1 Light_level)	2374.02	0.82
<b>ModA</b>	Diff_temp ~ Community * AirT_C * Wspd_50cm_ms.1 + (1 Light_level)	2377.04	0.18
<b>ModA2</b>	Diff_temp ~ Community * Wspd_50cm_ms.1 + (1 Light_level)	2398.93	0.00
<b>ModA4</b>	Diff_temp ~ Community * Wspd_50cm_ms.1 + AirT_C + (1 Light_level)	2400.87	0.00
<b>ModA1</b>	Diff_temp ~ Community * AirT_C + Wspd_50cm_ms.1 + (1 Light_level)	2420.13	0.00
<b>ModA3</b>	Diff_temp ~ Community + Wspd_50cm_ms.1 + (1 Light_level)	2441.25	0.00
<b>ModA5</b>	Diff_temp ~ Community + Wspd_50cm_ms.1 + AirT_C + (1 Light_level)	2443.09	0.00

Table 4. AICc Wind speed

		AICc	AICcWt
<b>ModL5</b>	Diff_temp ~ Community + Light_level + AirT_C + Community: Light_level + Community: AirT_C + Light_level : AirT_C + (1 Wspd_50cm_ms.1)	2270.89	0.54

<b>ModL4</b>	Diff_temp ~ Community * Light_level + AirT_C + (1 Wspd_50cm_ms.1)	2271.54	0.39
<b>ModL1</b>	Diff_temp ~ Community * AirT_C * Light_level + (1 Wspd_50cm_ms.1)	2276.23	0.04
<b>ModL2</b>	Diff_temp ~ Community * Light_level + (1 Wspd_50cm_ms.1)	2276.32	0.04
<b>ModL</b>	Diff_temp ~ Community * AirT_C + Light_level + (1 Wspd_50cm_ms.1)	2282.53	0.00
<b>ModL3</b>	Diff_temp ~ Community + Light_level + (1 Wspd_50cm_ms.1)	2284.34	0.00

Table 5. AICc Light Intensity

	Summ of squares	Df	F-value	P-value
<b>Intercept</b>	16075	1	983.047	<0.001***
<b>Community</b>	663.3	3	13.520	<0.001***
<b>Date</b>	6449.1	19	20.757	<0.001***
<b>Residuals</b>	6508.2	398		

Table 6. Analysis of variance of mean plot temperature and type III test

Comparison	P-value
<b>Heath - Lichen ridge top</b>	<0.001
<b>Heath - Meadow</b>	<0.01
<b>Heath - Willow</b>	<0.05
<b>Lichen ridge top - Meadow</b>	<0.001
<b>Lichen ridge top - Willow</b>	<0.001
<b>Meadow - Willow</b>	0.85

Table 7. Comparison between the different communities, with a tuckey HSD

Comparison	P-value
<b>Deciduous shrub – Evergreen shrub</b>	0.19
<b>Deciduous shrub – Foliose</b>	<0.001
<b>Deciduous shrub – Forb</b>	0.95
<b>Deciduous shrub – Fruticose</b>	<0.001
<b>Deciduous shrub – Graminoids</b>	<0.01
<b>Deciduous shrub – Moss</b>	<0.001
<b>Deciduous shrub – Soil</b>	<0.001
<b>Evergreen shrub – Foliose</b>	<0.05
<b>Evergreen shrub – Forb</b>	0.86
<b>Evergreen shrub – Fruticose</b>	<0.05
<b>Evergreen shrub – Graminoids</b>	0.96
<b>Evergreen shrub – Moss</b>	<0.05
<b>Evergreen shrub – Soil</b>	<0.05
<b>Foliose – Forb</b>	<0.001
<b>Foliose – Fruticose</b>	1.00
<b>Foliose – Graminoids</b>	0.15
<b>Foliose – Moss</b>	0.99
<b>Foliose – Soil</b>	0.95

<b>Forb – Fruticose</b>	<0.001
<b>Forb – Graminoids</b>	0.13
<b>Forb – Moss</b>	<0.001
<b>Forb – Soil</b>	<0.001
<b>Fruticose – Graminoids</b>	<0.05
<b>Fruticose – Moss</b>	0.95
<b>Fruticose – Soil</b>	0.82
<b>Graminoids – Moss</b>	<0.05
<b>Graminoids – Soil</b>	<0.05
<b>Moss – Soil</b>	0.99

Table 8. Estimated marginal mean comparison with tuckey

<b>Species</b>	<b>Mean surface temperature (°C)</b>
<i>Cladonia cf. rangiferina</i>	27.1 ± 1.03
<i>Cladonia cf. arbuscula</i>	26.4 ± 0.84
<i>Alectoria ochroleuca</i>	26.0 ± 1.04
<i>Bryocaulon divergens</i>	25.8 ± 1.1
<i>Flavocetraria nivalis</i>	25.8 ± 0.8
<i>Cetraria islandica</i>	25.6 ± 1.9
<i>Stereocaulon paschale</i>	25.3 ± 0.9
<i>Cladonia stellaris</i>	24.4 ± 0.61
<i>Flavocetraria cucullata</i>	22.4 ± 2.95
<i>Cetraria cf. ericetorum</i>	20.0 ± 1.8

Table 9. Mean surface temperature and its standard error extracted from the thermo-photographs of the different lichen species

<b>Comparison</b>	<b>P-value</b>
<b>(Bright-coloured) – (dark-coloured)</b>	0.62
<b>(Bright-coloured) - intermediate</b>	0.18
<b>(Dark-coloured)- intermediate</b>	0.67

Table 10. Estimate marginal mean comparison of lichen colour categories surface temperature.

<b>Lichen colour category</b>	<b>Mean surface temperature (°C)</b>
<b>Bright-coloured</b>	25.3 ± 0.45
<b>Intermediate-coloured</b>	25.9 ± 0.52
<b>Dark-coloured</b>	25.4 ± 0.94

Table 11. Mean surface temperature and its standard error of the different lichen colour categories

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