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# ARCTIC PLANTS AND TEMPERATURE: DO SPATIAL RELATIONSHIPS PREDICT CHANGE OVER TIME?



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## Abstract

Temperature in the Arctic is increasing rapidly, potentially triggering global climate feedback if the carbon in the Arctic soil is released. Plants are affected by the rising temperature and play crucial roles in ecosystem function and atmosphere-soil interactions, including snow accumulation, soil shading, carbon fluxes and albedo. However, we lack clarity in how the community composition of plants responds to spatial and temporal temperature change. Additionally, it is unclear whether the coarse scale temperature grids commonly used in vegetation studies sufficiently represent the small-scale temperature variations in the Arctic landscape. Here, I explore how the relative abundance of plant functional groups and community temperature affinity are related to temperature to assess if spatial relationships on a microclimate scale can predict changes over time, a method known as space-for-time substitution. The plot-based vegetation and temperature data utilized in this study is obtained from three arctic sites: Svalbard, Disko Island on Greenland and Latnjajaure in northern Sweden. The results show that the relative abundance of plant functional groups and community temperature affinity are strongly correlated with summer air temperature on a spatial microclimate scale across all three sites. In Latnjajaure, change over time in long-term monitoring plots were generally in the same direction as expected given observed spatial temperature-composition relationships, suggesting that recent climate change has caused a community composition shift of plants that is similar to spatial variation in sub-arctic regions. However, on higher latitudes no spatiotemporal relationship could be detected. Temperature does not act in isolation with the changing climate, soil moisture is one other driver closely connected to vegetation response, namely in shrubs. This study supports the view that plant communities, across the Arctic region as a whole, will have a heterogeneous response to climate change.

## Sammanfattning

Temperaturen i Arktis ökar snabbt, vilket kan utlösa en global återkoppling för klimatet om kolen i den arktiska jordmånen släpps ut. Växter påverkas av den stigande temperaturen och spelar en avgörande roll för ekosystemets funktion och i interaktionen mellan jordmån och atmosfär, specifikt så påverkar växter snöansamling, markskuggning, kolflöden och albedo. Vi saknar dock klarhet i hur växternas sammansättning reagerar på rumsliga och tidsmässiga temperaturförändringar. Dessutom är det oklart om de grovskaliga temperaturmätningarna som vanligtvis används i vegetationsstudier motsvarar de småskaliga temperaturvariationerna i det arktiska landskapet. I denna studie används relativ abundans av växters funktionella grupper och termofilisering i koppling till temperatur för att bedöma om rumsliga samband på en mikroklimatskala kan förutsäga förändringar över tid, en metod som kallas rum-för-tid-substitution. Vegetations- och temperaturdatat som används i denna studie kommer från tre arktiska lokaler: Svalbard, Disko Island på Grönland och Latnjajaure i norra Sverige. Resultaten visar att termofilisering och relativ förekomst av funktionella grupper är kopplad till lufttemperaturen under sommaren på en rumslig mikroklimatskala i alla studieområden. En spatiotemporal jämförelse visar potential i att använda sommarlufttemperatur och relativ förekomst på mikroklimatskala för att förutsäga riktningförändringen av relativ förekomst över tid på en makroklimatskala i Latnjajaure. På högre breddgrader kunde dock inget spatiotemporalt samband upptäckas. Det är tydligt att temperatur inte är den enda faktorn inblandad i arktiska växters respons på klimatförändringarna och att vi inte kan förvänta oss en homogen respons från Arktis i sin helhet.

## **Introduction**

### **The arctic and global change**

Climate change is causing an global increase in temperature (IPCC, 2022) and the rate of warming is nearly four times faster in the arctic (Rantanen et al., 2022). The increasing temperature is causing a shift in arctic plant communities (Elmendorf et al., 2015), which can in turn influence carbon storage and surface albedo (Myers-Smith et al., 2011; Post et al., 2019). Since arctic soils hold twice the amount of carbon compared to the current levels in the atmosphere (Schuur et al., 2008; Tarnocai et al., 2009) vegetation associated feedbacks may have global consequences for the climate system (Pearson et al., 2013).

The large-scale tundra vegetation change observed is often called the greening of the arctic. It has been observed with the help of satellites and scale-wise it is one of the world's most important ecological responses to climate change (Myers-Smith et al., 2020). However, the trends observed are variable and complex. In recent years, a slowing or even reversal of the greening, sometimes termed browning, has been observed in some regions indicating heterogenic vegetation response (Myers-Smith et al., 2020). In warmer regions with increased summer temperature and soil moisture greening is more likely to occur, while browning occurred more frequently in colder regions (Berner et al., 2020). It has also been shown that different satellite datasets do not always correspond at a given location (Guay et al., 2014). Furthermore, the most common vegetation index (normalized difference vegetation index, NDVI) used from satellites records were not developed with a polar context in mind (Benedetti & Rossini, 1993). NDVI is a proxy of photosynthetic activity and not a direct measure of biological productivity, therefore vegetation changes linked to greening could mean different things, some examples include encroachment of vegetation on previously non-vegetated land, changes in community composition and changes in plant traits such as height, leaf area or phenology (Myers-Smith et al., 2020). Furthermore, it is often unclear how in situ observations and satellite-derived vegetation indices correspond to each other. In situ observations can provide a powerful source of data for understanding Arctic vegetation change, but there is also a clear need for a more geographically widespread and comprehensive monitoring effort, especially in the high arctic (Bjorkman et al., 2020).

### **In situ observations of vegetation in the arctic: functional groups, shrubification and thermophilization**

Functional groups (sometimes called growth forms) are plants that share similar function and form. For the arctic four larger groups are usually distinguished among the vascular plants: woody plants separated into (1) deciduous shrubs (thinner leaves that seldom are kept during winter) and (2) evergreen shrubs (thicker leaves that are usually kept during winter), (3) graminoids (the grass-like families Poaceae, Cyperaceae and Juncaceae) and (4) forbs (herbaceous non-woody plants). These groups co-exist across several bioclimatic zones (Walker et al., 2005) and are commonly used in vegetation studies (Elmendorf et al., 2015; R. Scharn et al., 2022).

Using the paleo-record to reconstruct historical vegetation patterns in the high arctic reveals that the relative abundance of shrubs were higher during the warm mid-Holocene compared to the present (Bigelow et al., 2003). Presently in the arctic, a change in vegetation composition known as shrubification seem to point in the same direction as the historical records. Shrubification consists of increase in woody plant growth, increase of their relative abundance and shrub encroachment across the circumpolar arctic (Elmendorf et al., 2012b; García Criado et al., 2020; Myers-Smith et al., 2011). The changes are in part linked to climate warming but there are other drivers as well, e.g. snow accumulation, soil moisture, disturbance, and herbivory (Martin et al., 2017). Shrubification seems to occur primarily where there are tall deciduous shrubs, especially

in warmer arctic regions (Elmendorf et al., 2012b) and the trait height seems to have the strongest positive correlation to warming (Bjorkman et al., 2018). There are still pieces missing in the story of arctic vegetation response to recent climate change. However, compared to other functional groups, shrubs (especially deciduous shrubs) appear to have the most strong and consistent response. Nevertheless, forbs have been shown to increase in abundance with summer temperature, but only on sites with near-surface permafrost (Elmendorf et al., 2012b). There is a knowledge gap when it comes to the large-scale response of graminoids to climate warming. However, in Latnjajaure, northern Sweden, graminoids decrease with time on wet sites, likely due to competition from deciduous shrubs. In contrast, graminoids increase over time with experimental warming in dry habitats (R. Scharn et al., 2022).

Another way to infer changes in the vegetation is by the process known as thermophilization, whereby cold-adapted species decline and/or warm adapted species increase (Gottfried et al., 2012). On a continental scale, it has been shown that European alpine summits have an ongoing thermophilization with recent climate change (Gottfried et al., 2012). In the arctic, increasing temperature leads to thermophilization in plant communities consistently across different methods (Elmendorf et al., 2015).

### **Microclimate and Macroclimate**

There is discrepancy between coarse spatial scales, such as global datasets of temperature, and fine spatial scale at which most organisms respond to climatic variation. Understanding this is important for assessing species vulnerability to climate change (Potter et al., 2013). Many temperature time series used in vegetation studies originate from extrapolated grids based on climate stations with loggers two meters above ground (Moritz & Agudo, 2013). Within the arctic landscape there is variation on much smaller scales due to topography, sun exposure with slope direction, vegetation, and snow accumulation, so macro-scale temperatures often do not reflect the plants' experienced temperature. For instance, the microclimate on leaves can be 10 °C warmer or colder than surrounding air (Potter et al., 2009). Furthermore, extinction risk from climate change can be reduced by microclimatic buffering, especially for species adversely affected and in areas experiencing a high level of warming (Suggitt et al., 2018). In a coastal grassland, colder slopes, often northward facing, acts as a refuge for some species within plant communities. In short, topography can enable species with low temperature requirements to persist in an ecosystem even under climate warming (Maclean et al., 2015).

One study conducted in the arctic concluded that some aspects of microclimate could be related to vegetation. High vegetation cover was associated with colder soil temperature but not canopy-level temperature during the growing season. Extended snow cover duration during winter and low vegetation cover during summer were associated with warmer soils (von Oppen et al., 2022). Another study showed similar results, the inclusion of vegetation significantly improved models of soil temperature and soil moisture on a fine spatial scale (Aalto et al., 2013).

### **Space-for-time substitutions**

Ecological processes can occur over long timescales, sometimes too long for conventional experiments or observations. One commonly used method to overcome this problem is to extrapolate temporal dynamics from spatial variation. Space-for-time substitutions has been applied to project impacts of future changes in climate to species, functional groups and plant communities (Elmendorf et al., 2015; Fukami & Wardle, 2005; Pearson et al., 2013). There has been some concern regarding projection of spatial models across time for individual species (Dobrowski et al., 2011). Thus, using collective biodiversity properties or compositional turnover is suggested as a more robust approach (Algar et al., 2009; Ferrier & Guisan, 2006). Furthermore, spatial variation can reflect ecological relationships established over long time frames and that

can prove problematic when inferring impacts of contemporary climate change (Wiens et al., 2009). There is a possibility that the extrapolation fails to account for temporal lags such as soil development, migration, and biophysical limitations (La Sorte et al., 2009; Shaver et al., 2000). To assess this in arctic vegetation, Elmendorf et al (2015) compared the thermophilization response to recent climate change using long-term monitoring, experimental warming, and spatial gradients. All three methods showed that a synthetic index based on species thermal niche (community thermophilization index, CTI) increased with warming over time or space. However, the magnitude of change in CTI per °C was greater for the spatial gradient. It is hypothesized that the disparities in response magnitude stem from a lag in biotic response to recent climate warming, but slower processes such as soil development might be involved as well (Elmendorf et al., 2015).

## Aim

Understanding vegetation shifts in the arctic is an important matter for present policymaking connected to climate change and for helping us improve models predicting future changes. We have established that there is an ongoing arctic vegetation shift and that one of the drivers behind it is climate warming. However, there is also evidence for heterogeneous vegetation response co-correlation with other drivers such as soil moisture and snow dynamics. Furthermore, on a microclimatic scale there is evidence for buffering capacity and resilience. Here, temperature variation on spatial microclimate-scales and temporal macroclimate-scales are used to predict arctic plant community composition in terms of thermophilization and abundance of plant functional groups. The aim is to explore if we can predict vegetation shifts with recent climate change using temperature variation on a smaller spatial scale, a method called space-for-time substitution. Across the recent decades plot-based temperature and vegetation cover data has been collected from three different arctic regions (Svalbard, Greenland, and Northern Sweden). Using this data, the following question will be explored:

- How does two **community thermophilization indexes** (CTI) change with a spatial and temporal summer air temperature gradient in Latnjajaure?
- How does the **relative abundance** of plant functional groups change with spatial and temporal temperature gradients on Svalbard, Disko Island and in Latnjajaure?
- Can we predict vegetation change over time from spatial temperature-composition relationships?

## Methods

### Description of the study sites

#### *Latnjajaure*

Situated in northern Scandes, Sweden (68.35°N, 18.49°E, figure 1), Latnjajaure field station has a history of plant ecology research dating back to 1989. The bedrock mainly consists of Cambro-Silurian mica-garnet schists but there are also intrusions of acidic granites and limestone (Kulling, 1964). Deglaciation occurred 8000-10000 years ago (André, 1995) and the post-glacial modification is regarded as low (Beylich & Laute, 2017). The mean annual temperature at Latnjajaure increased significantly (0.3 °C per decade) during the period 1992-2019. However, the mean growing season (May-August) temperature increase of 0.2 °C per decade is not statistically significant (Ruud Scharn et al., 2022). Average annual precipitation is 850mm and over the same period there is no changing trend (Callaghan et al., 2010). Outside snow beds the snow depth varies between 10-50 cm (Björkman et al., 2010). Within the area you can find a mosaic of different plant communities, mainly explained by factors such as soil moisture content

and nutrients, snow accumulation and pH. Typical dominant species in the area are *Cassiope tetragona*, *Carex bigelowii* and *Dryas octopetala* (R. Scharn et al., 2022). The subsites of the long-term plots are situated close to the eastern shores of the lake Latnjajaure (Figure 1)

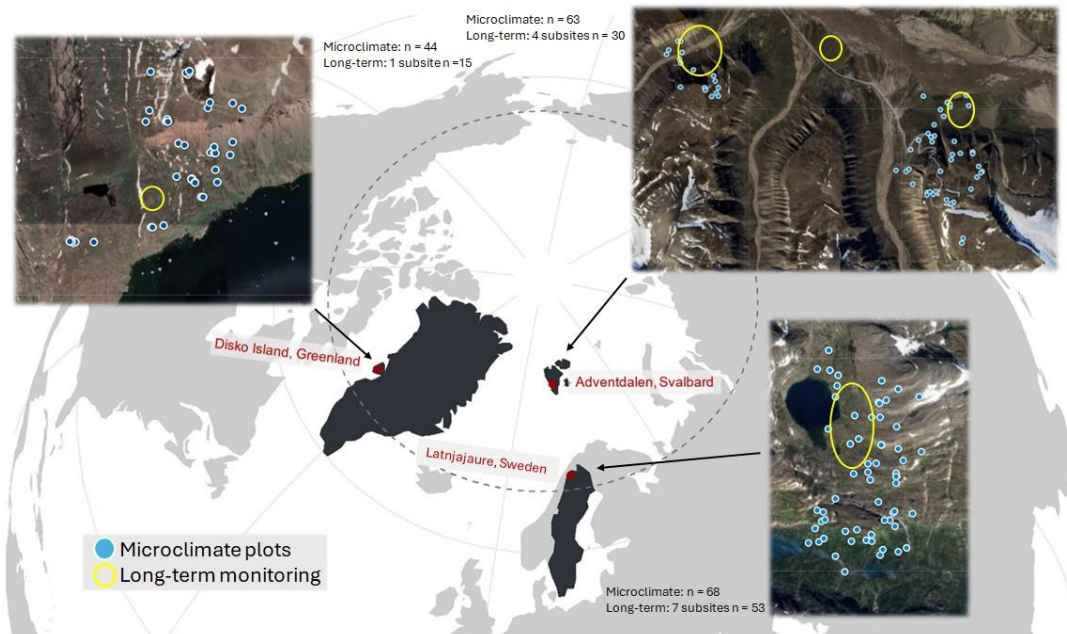
### Svalbard

The high Arctic island of Svalbard has two study areas close to Longyearbyen (78°11' N, 15°45' E), Breinosa to the east and Endalen to the west. On lower elevations there is a dense vegetation cover mainly composed of species such as *Cassiope tetragona*, *Dryas octopetala* and *Salix polaris*. Higher up the vegetation is patchy and, on some microclimate plots, almost non-existent. The subsites of long-term plots are all in the lower parts of the landscape and are divided into four subsites (Figure 1).

### Disko Island

Disko island is located on western Greenland (69°16'N, 53°28'W) and the Arctic station run by Copenhagen university was established in 1906. The area has, from a Greenlandic perspective, a rich biodiversity of plants. This is because of the diverse landscape, maritime climate, rich soils and the presence of homothermic springs. The bedrock is mainly basalt made of volcanic lava, this has produced a soil that is dark and rich in iron (Xu et al., 2021). The vegetation in the area is classified as prostrate to erect dwarf shrub tundra (Raynolds et al., 2019). Common species that dominate the vegetation cover are *Dryas integrifolia*, *Betula nana*, *Empetrum hermaphroditum*, *Salix glauca* and *Vaccinium uliginosum*.

The microclimate plots cover parts of the western slope of Blæsedalen valley (figure 1). The long-term plots are all situated close to each other within one subsite on the lower parts in the valley (Figure 1).



**Figure 1. Map of the study sites.**

The red circles show the three study sites. The spatial data comes from the microclimate plots (blue circles). The temporal vegetation data comes from plots nested within subsites inside the yellow ellipses. Note that the satellite maps are on slightly different scales. n = number of plots.

### Spatial data

During the summers, primarily July, of 2020-2023 logging of temperature and estimation of plant species cover was done in the three arctic sites. Originally there are around 90 plots at each site,

but I only used plots that had plants in them, plot vegetation surveys had been conducted and plots with properly acquired temperature data. The final number of plots analysed are 44 for Disko Island, 63 for Svalbard and 68 for Latnjajaure (Figure 1 shows the plot layout on satellite maps of the different sites). The plots and loggers were distributed using a stratified random sampling strategy within each site (von Oppen et al., 2022). The idea behind the strategy is to be as unbiased as possible but also capture biotic and abiotic variation in an optimal way using a limited number of loggers. The stratification is based on elevation and two different satellite derived indexes, Normalized Difference Vegetation Index (NDVI) and Normalized Difference Water Index (NDWI). The indexes provide a rough proxy of vegetation productivity, leaf area and soil moisture.

One plot consists of a two-meter radius circle with a TMS logger in the middle measuring both temperature (soil, surface, air) and moisture with five-minute intervals. Only air (15cm above surface) and soil (6 cm below surface) temperature measurement are used here. The summer gradients are consisting of mean temperatures during the month of July. Ideally it would have been longer, but the choice had to reflect a period where all three sites overlapped with loggers working consistently. The gradient should reflect changing temperature and not the number of loggers measuring temperature properly and with that in mind, only using July was the best compromise. The winter temperature is a mean of minimum temperatures for each plot (5% quantile between 1/10 – 2022 and 1/4 2023).

Estimation of plant cover on Svalbard and Latnjajaure was done with a fixed estimated percentage for each species and on Greenland with percentage categories. The categories are as follows: 2.5 = 0-2.5% cover, 7.5 = 2.5-7.5%, 15 = 7.5-15%, 25 = 15-25%, ..., 95 = 85-95%. Plant species were separated to one of four functional groups (deciduous shrub, evergreen shrub, forb or graminoid) according to classification from ITEX (Henry & Molau, 1997).

### **Temporal data**

Across the arctic the International Tundra Experiment (ITEX) has repeatedly monitored vegetation plots since 1991 (Henry & Molau, 1997). Here, time series from Svalbard, Disko Island and Latnjajaure collected between the years 1991 and 2019 are used. These plots are the control plots to warming experiments using Open Top Chambers. However, with recent climate change they are now after 30 years starting to provide useful insights in their own right. The vegetation has been monitored using a point framing method developed by Walker (1996). It consists of using a 100-point grid at plots with the size of 75cm x 75cm at Svalbard and 100 cm x 100cm at Disko and Latnjajaure. Permanent markers were put down for the corners of each plot, ensuring that the grid can be reinstalled above the canopy in the same position and orientation year after year. At each point in the grid a small stick is lowered down towards the vegetation noting all contacts (AC) with species at Svalbard or the top and bottom (TB) contact at Disko and Latnjajaure (Walker, 1996). The TB-method was developed to make the field work less time consuming. However, it has been shown that TB significantly underrepresent total vegetation cover compared to AC (May & Hollister, 2012). To make them more comparable relative abundance is used here.

The point framing in Latnjajaure was conducted in the period 1994-2016 during the following years: 1994, 1995, 1996, 1997, 1998, 1999, 2001, 2006, 2007, 2008, 2013, 2014 and 2016. The point framing on Svalbard was conducted in the period 2003-2015 during the following years: 2003, 2005, 2009, 2014 and 2015. The point framing on Disko Island was conducted in the period 1991-2019 during the following years: 1991, 1994, 2002 and 2019.

Temperature over time was acquired from gridded data from the Climatic Research Unit (CRU). These time series are an extrapolated grid based on weather station loggers two meters above

ground. The in-data used here consists of one monthly mean value for each site. The summer temperatures are a mean of July (due to comparability to the spatial data) each year and the winter temperature a mean of November, December, January and February each year. The winter temperature is only used in figure 3 for visualization of temperature change over time. It was excluded from any further analysis due to the logger being two meters above ground and not reflecting the plants experienced temperature during winter, which is generally warmer due to the insulating effect of snow cover.

The July temperature used is a mean of the year the vegetation survey was conducted and the previous three years. This is to capture sensitivity to recent local temperature changes before each survey occasion, capturing the fluctuations within a longer trend. Other studies show that using this method is better than just using the temperature of the year the vegetation survey was done (Elmendorf et al., 2012b; Gottfried et al., 2012).

### **Creating community thermophilization indexes**

Two community thermophilization indexes (CTI) were created using a list of ecological indicator and trait values for Swedish vascular plant (Tyler et al., 2021). Each plant species within Sweden has been assigned a value both for their cold and heat requirement that is based on their distribution. The value represents each species' thermal niche in relation to either cold or warm climate; the indices are thus very similar but reversed. The difference between them is that the distribution was based on data coming from slightly different sources. Examples of the distribution sources included are the cultivation zones defined by the Swedish national horticultural society and altitudinal limits of the alpine species. The cold requirement is 20-degree scale were 1 = *annual minimum rarely below 10 °C (subtropical/tropical regions)* and 20 = *confined to the high-alpine/arctic zone*. The heat requirement is a 14-degree scale were 1 = *reaching the high-alpine/arctic zone* and 14 = *at present not reproducing/resident in Sweden due to climatic constraints*. See appendix 2 for full listing of the scales (Tyler et al., 2021).

The species present within the vegetation surveys were assigned a value both for heat requirement and cold requirement. In the spatial vegetation survey around 10% of the registration were only possible to identify to genera. Since some genera have species with vastly different heat and cold requirement the decision was made to exclude those 10% from this part of the analysis. A community weighted mean for both heat and cold requirement was calculated to make sure that the mean reflects, to some extent, the evenness of species distribution within each plot. If a species has a high relative abundance in a plot its' number on the cold and heat requirement will carry more weight towards the CTI for that plot.

### **Statistical analysis**

Mean air and soil temperature for summer and winter were calculated for each microclimate plot. Linear regressions are used to determine the relationships between CTI (only summer air) and relative abundance of functional groups with the spatial temperature gradients. The R package "tidyr" (Wickham, Vaughan, et al., 2023) was used to extract the estimates, confidence intervals and p-values.

The long-term plots are clustered into multiple subsites on Svalbard and in Latnjajaure, to account for this variance a mixed model (generalized for the relative abundance data and linear for the CTI) was used for these sites using the R package "lme4" (Bates et al., 2015). Subsite are added as a random effect within these models. Years is also added as a random effect for all sites to avoid within-year pseudo-replication of temperature values. The sampling of the temporal data was not made in a uniform way among the three sites. Each site is sampled in a different period, not all subsites are surveyed every year, and the number of plots differ, see figures in Appendix 3. To account for this, a within-subsite centering of the temporal temperature gradient was done: the

mean of the temperature gradient was subtracted from the gradient within each subsite (van de Pol & Wright, 2009). Slopes and confidence intervals were calculated post hoc using the R package “emmeans” (Lenth, 2024).

All abundance data was converted to relative abundance. The main reason behind this is comparability between the spatial and temporal temperature gradients, but also among-site comparability for the temporal gradients. The direction of the spatial and temporal changes was compared by extracting the slope coefficients from each given model, due to discrepancies in the models used here it is not possible to compare the magnitude of change. Every analysis was done in R-studio version 4.2.2 (31<sup>st</sup> October 2022). All basic handling of the data was done in the R package “dplyr” (Wickham, François, et al., 2023) and figures were created with the R package “ggplot2” (Wickham, 2016).

## Results

### Setting the stage: temperature means and gradients across time and space

There is interannual variation in both summer and winter temperature (Figure 3)

#### *Latnjajaure temperature gradients*

The mean summer air temperature (July of 2023) of all plots along the spatial gradient in Latnjajaure was 10.92 °C, ranging from a minimum of 7.77 °C and maximum of 13.67 °C. The mean summer soil temperature was 10.8 °C, ranging from a minimum of 6.09 °C and maximum of 15.56 °C. The mean of the temporal gradient (1994, 1995, 1996, 1997, 1998, 1999, 2001, 2006, 2007, 2008, 2013, 2014 and 2016) during summer is 9.22 °C, with a minimum of 8.42 °C and maximum of 10.52 °C (Figure 2). The mean 5% quantile winter air temperature (mean temperature the 5% coldest days for each plot between 1/10 – 2022 and 1/4 2023) of all plots along the spatial gradient in Latnjajaure was -12.58 °C ranging from a minimum of -20.78 °C and maximum of -2.35 °C. The mean soil temperature during winter was -6.69 °C, ranging from a minimum of -14.27°C and maximum of 0.07 °C. The mean of the temporal gradient during winter was -10.88 °C with a minimum of -11.81 °C and maximum of -9.74 °C (Figure 2).

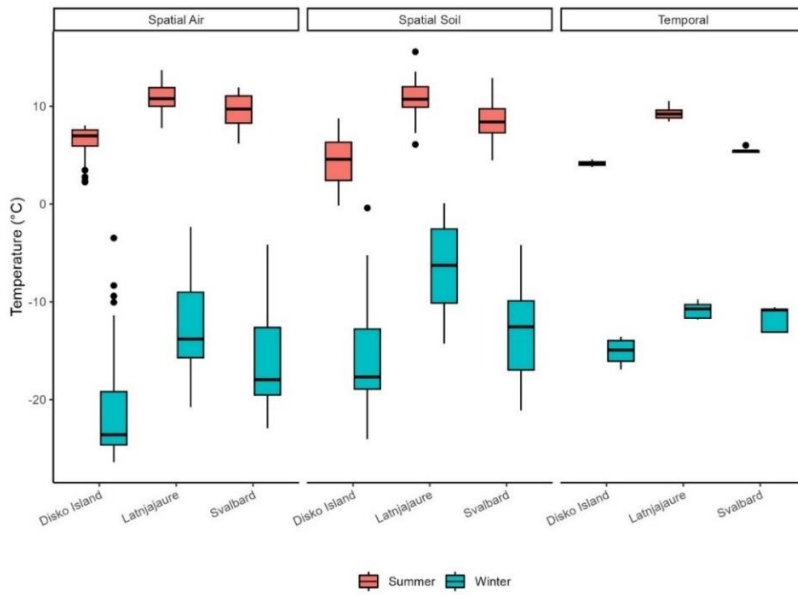
#### *Svalbard temperature gradients*

The spatial gradients mean air temperature on Svalbard during the growing season (July 2023) is 9.58 °C ranging from a minimum of 6.2 °C and maximum of 11.9 °C. The mean soil temperature during growing season is 8.52 °C ranging from a minimum of 4.46 °C and maximum of 12.9 °C. The mean of the temporal gradient (2003, 2005, 2009, 2014 and 2015) during summer is 5.43 °C with a minimum of 5.3 °C and maximum of 6 °C (Figure 2). The spatial gradients mean air temperature on Svalbard during winter (mean temperature the 5% coldest days for each plot between 1/10 – 2022 and 1/4 2023) is -16.17 °C ranging from a minimum of -22.92 °C and maximum of -4.15 °C. The mean soil temperature during winter is -13.01 °C ranging from a minimum of -21.09 °C and maximum of -4.2 °C. The mean of the temporal gradient during winter is -11.56 °C with a minimum of -13.09 °C and maximum of - 10.54 °C (Figure 2).

#### *Disko Island temperature gradients*

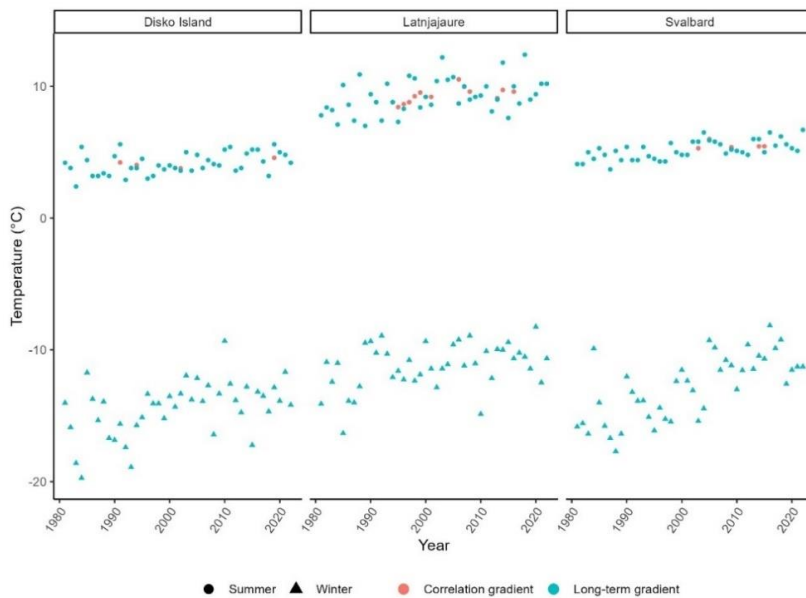
The spatial gradients mean air temperature on Disko Island during the growing season (July 2023) is 6.35 °C ranging from a minimum of 2.25 °C and maximum of 8 °C. The mean soil temperature during the same period is 4.55 °C ranging from a minimum of -0.15 °C and maximum of 8.75 °C. The mean of the temporal gradient (1991, 1994, 2002 and 2019) during summer is 4.15 °C with a minimum of 3.77 °C and a maximum of 4.57 °C (Figure 2). The spatial gradients mean air temperature on Disko Island during winter (mean temperature the 5% coldest days for each plot between 1/10 – 2022 and 1/4 2023) is -20.86 °C ranging from a minimum of -26.38 °C and maximum of -3.48 °C. The mean soil temperature during winter is -15.76 °C

ranging from a minimum of  $-24\text{ }^{\circ}\text{C}$  and maximum of  $-0.4\text{ }^{\circ}\text{C}$ . The mean of the temporal gradient during winter is  $-15.08\text{ }^{\circ}\text{C}$  with a minimum of  $-16.91\text{ }^{\circ}\text{C}$  and maximum of  $-13.15\text{ }^{\circ}\text{C}$  (Figure 2).



**Figure 2. Means of spatial and temporal temperature gradients**

Spatial summer: mean air and soil growing season temperature (July 2023) of all plots. Spatial winter: mean air and soil temperature of all plots for the 5% coldest days between 1/10 – 2022 and 1/4 2023. Temporal summer: mean temperature of July for the temporal gradients. Temporal winter: mean temperature of winter (November, December, January and February) for the temporal gradients.

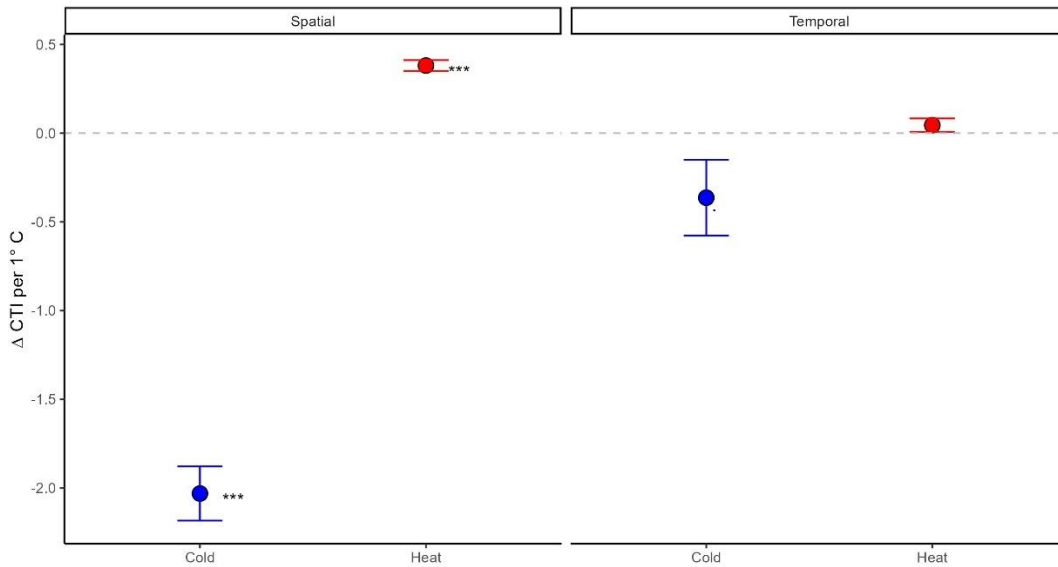


**Figure 3. Temperature change over time.**

Circles: mean temperature in July each year. Triangles: mean temperature of November, December, January and February. Blue colour: long term changes (1980-2022) of July and winter temperature. Red colour: the temperature gradient used in the different models here. Each value is a mean of the survey year and the previous three years to capture sensitivity to recent local temperature variation.

## CTI change with growing season air temperature gradients in Latnjajaure

There were significant relationships between spatial summer air temperature and CTI (figure 4). The CTI based on the cold requirement scale had a negative relationship with summer air temperature (estimate = -2.03 per °C,  $p < 0.0001$ ). The CTI based on the heat requirement scale had a positive relationship with summer air temperature (estimate = 0.38 per °C,  $p < 0.0001$ ). CTI was not significantly related to temperature variation over time (figure 4). However, CTI based on the cold requirement had a declining trend with summer air temperature over time (estimate = -0.36,  $p = 0.08$ ). CTI based on the cold requirement scale for the functional group evergreen shrubs had a significant decrease with summer air temperature both across time and space (Appendix 4).



**Figure 4. CTI change with growing season temperature gradients in Latnjajaure.**

Y-axis: CTI change per 1°C for a spatial temperature gradient (mean growing season temperature in July 2023 for each plot in Latnjajaure) and a temporal temperature gradient (mean temperature of July in Latnjajaure for each year). Cold/Heat = The two different scales reflecting the plant communities thermal niche within each plot. The spatial points are slope coefficients from a linear regression. The temporal points are slope coefficients from a linear mixed model with subsites as a random effect. P-value: no star = non-significant correlation, \*\*\* < 0.001. The small dot after CTI cold on the temporal gradient means that it was close to significant. Error bars show standard error. Number of plots: Spatial: 68 plots, Temporal: 53 plots within 7 subsites.

## Abundance changes of functional groups with spatial temperature gradients

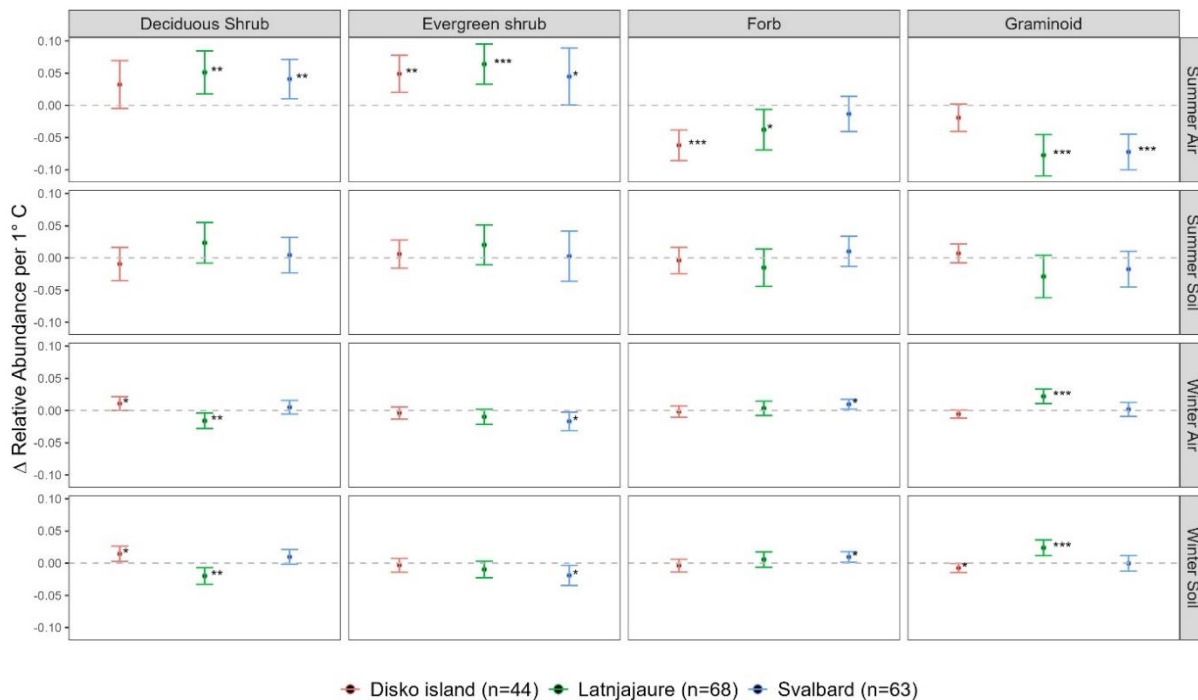
The 48 separate linear regressions between relative abundance of functional groups and spatial temperature gradients resulted in 20 significant relationships (figure 5). Summer soil temperature was not significantly related to abundance of functional groups among all three sites.

On Disko Island, summer air temperature was positively related to the relative abundance of evergreen shrubs (estimate = 0.049 per °C,  $p = 0.001$ ) and negatively related to the relative abundance of forbs (estimate = -0.062 per °C,  $p < 0.001$ ). In Latnjajaure, summer air temperature was positively related to the relative abundance of deciduous- (estimate = 0.051 per °C,  $p = 0.003$ ) and evergreen shrubs (estimate = 0.064 per °C,  $p < 0.001$ ) and negatively related to the relative abundance of forbs (estimate = -0.038 per °C,  $p = 0.019$ ) and graminoids (estimate = -0.077 per °C,  $p < 0.001$ ). On Svalbard, summer air temperature was positively related to the relative abundance of deciduous- (estimate = 0.041 per °C,  $p = 0.01$ ) and evergreen shrubs

(estimate = 0.045 per °C,  $p < 0.048$ ) and negatively related to the relative abundance of graminoids (estimate = -0.072 per °C,  $p < 0.001$ ).

On Disko Island, winter air temperature was positively related to the relative abundance of deciduous shrubs (estimate = 0.011 per °C,  $p = 0.049$ ). In Latnjajaure, winter air temperature was positively related to the relative abundance of graminoids (estimate = 0.022 per °C,  $p < 0.001$ ) and negatively related to the relative abundance of deciduous shrubs (estimate = -0.016 per °C,  $p = 0.01$ ). On Svalbard, winter air temperature was positively related to the relative abundance of forbs (estimate = 0.010 per °C,  $p = 0.012$ ) and negatively related to the relative abundance of evergreen shrubs (estimate = -0.17 per °C,  $p = 0.024$ ).

On Disko Island, winter soil temperature was positively related to the relative abundance of deciduous shrubs (estimate = 0.015 per °C,  $p = 0.017$ ) and negatively related to the relative abundance of graminoids (estimate = -0.007 per °C,  $p = 0.033$ ). In Latnjajaure, winter soil temperature was positively related to the relative abundance of graminoids (estimate = 0.024 per °C,  $p < 0.001$ ) and negatively related to the relative abundance of deciduous shrubs (estimate = -0.020 per °C,  $p = 0.003$ ). On Svalbard, winter soil temperature was positively related to the relative abundance of forbs (estimate = 0.010 per °C,  $p = 0.024$ ) and negatively related to the relative abundance of evergreen shrubs (estimate = -0.019 per °C,  $p = 0.019$ ).



**Figure 5. Abundance changes of functional groups with spatial temperature gradients.**

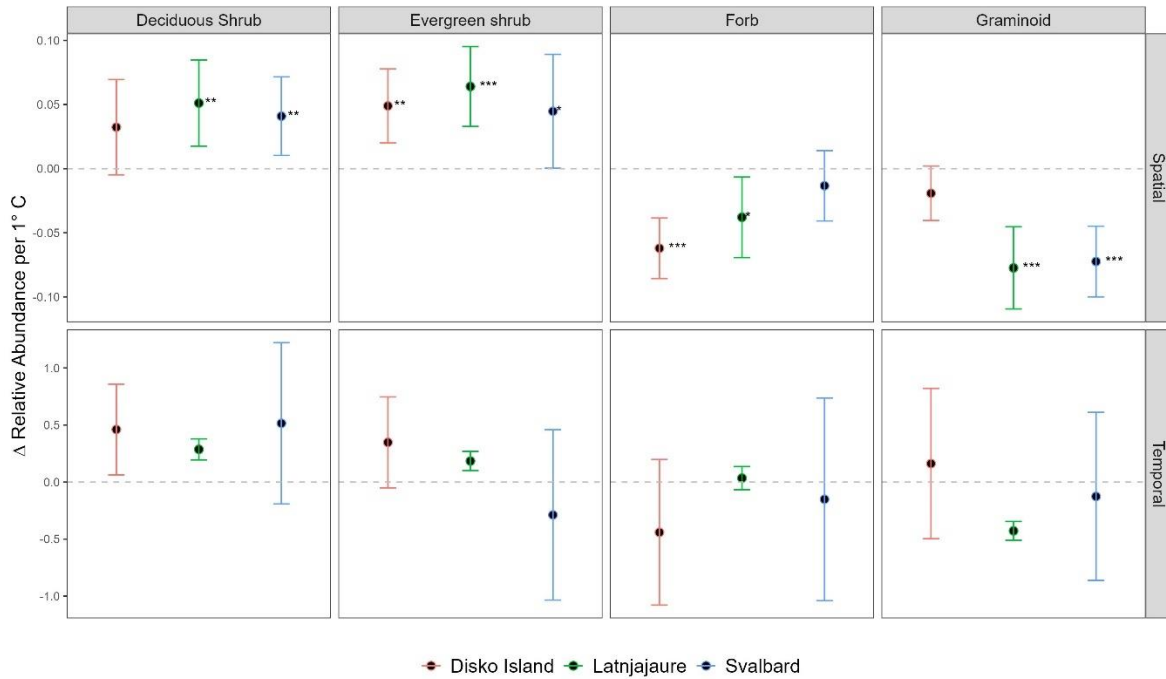
Y-axis: Relative abundance changes per 1°C during summer air and soil temperature (mean temperature in July 2023 for each plot) and winter air and soil temperature (mean temperature for the 5% coldest days between 1/10 – 2022 and 1/4 2023 for each plot). Each point is a slope coefficient from a linear regression. P-value: no star = non-significant correlation, \* = 0.01-0.05, \*\* = 0.001-0.01, \*\*\* < 0.001. Error bars show 95% confidence interval. n = number of plots.

### Change over time and spatiotemporal comparisons

In Latnjajaure, summer air temperature over time was positively related to the relative abundance of deciduous- (estimate = 0.29, 95% CI: low = 0.19, high = 0.38) and evergreen shrubs (estimate = 0.18, 95% CI: low = 0.1, high = 0.27) and negatively related to the relative abundance of

graminoids (estimate = -0.43, 95% CI: low = -0.51, high = -0.35). On Disko Island, summer air temperature over time was positively related to the relative abundance of deciduous shrubs (estimate = 0.46, 95% CI: low = 0.06, high = 0.86).

In Latnjajaure, summer air temperature on a spatiotemporal scale was, in terms of direction, positively related to the relative abundance of deciduous shrubs and evergreen shrubs and negatively related to the relative abundance of graminoids (compare the rows “spatial” and “temporal” in Figure 6). On Disko Island and Svalbard, summer air temperature on a spatiotemporal scale showed no similar directional change of the relative abundance of any plant functional groups (Figure 6).



**Figure 6. Comparison of temporal and spatial changes with summer air temperature.**

The top row (spatial) is a copy of the row summer air in figure 4 to illustrate the comparison with the temporal gradient. The bottom row shows extracted slope coefficients from the generalized linear mixed-effects models for each functional group and site. Note that the y-axis is scaled differently on the rows of the facet grid. All error bars show 95% confidence interval.

## Discussion

The results here show that relative abundance of plant functional groups and temperature affinity of plant communities are sensitive to summer air temperature across space and to a lesser extent time (Figure 4, 5, 6). In Latnjajaure, these results also indicate that temperature-community relationships measured at a microscale can correspond to those on a macroscale (Figure 6). The close relationship between CTI and summer air temperature in Latnjajaure (Figure 4) indicates that both the loggers are likely working and that the temperature indicator values used here (Tyler et al., 2021) are accurate. Despite the strong relationship between temperature and CTI across space, CTI did not increase significantly with warmer temperatures over time, though the trend was in the expected direction (Figure 4). This could be related to too much interannual variation in temperature (Figure 3) or the lack of significant warming trend in Latnjajaure (R. Scharn et al., 2022). This result differs from an earlier study of CTI over time using multiple study sites (Elmendorf et al., 2015), which found a small but significant increase in CTI over time. Furthermore, the increase of CTI over time was of smaller magnitude than the CTI increase with

space. Extrapolating 10 years into the future from the model used in that case could reproduce effect for CTI over time similar to that over space. However, that would be inappropriate interpretation of a linear trend since it is implausible to expect warming to have increasing effects indefinitely (Elmendorf et al., 2015). Nevertheless, even if the results here (from one site only) did not show a strong temporal relationship between CTI and temperature, it is likely that with Arctic amplification and future climate warming we should expect a vegetation shift of declining cold affiliated species and increasing warm affiliated species (Elmendorf et al., 2015; Gottfried et al., 2012).

The relative abundance of shrubs is positively related to summer air temperature across space and to a lesser extent (only in Latnjajaure and only deciduous shrubs on Disko Island) time (figure 6). For the temporal analysis in Latnjajaure, there is evidence supporting the result here using the same data (R. Scharn et al., 2022). They concluded that, in most subsites, shrubs are expanding and outcompeting forbs and graminoids. Soil moisture determined if the expansion was by evergreen or deciduous shrubs. On dry sites, evergreen shrubs dominate the expansion and on wet sites it shifts to deciduous shrubs, suggesting that responses to warming in Latnjajaure are likely mediated by edaphic characteristics (R. Scharn et al., 2022). Shifting focus to a larger Arctic perspective Elmendorf et al (2012b) showed in a comprehensive review that deciduous shrubs were most positively associated with warming over time on wet sites. They also found that warming had a positive effect on total abundance of shrubs in locations that were already warm to begin with, primarily driven by strong positive responses of deciduous shrubs. Compared to Svalbard and Disko Island, Latnjajaure is more southern (figure 1) and warmer (figure 2 and 5) which could in parts explain why a shrub response was detected there. On Disko Island, relative abundance of deciduous shrubs increases over time (Figure 6). Another study did a snapshot comparison of vegetation status between 1967 and 2009 on Disko Island (Callaghan et al., 2011). Their results were presented with species specific responses the comparison isn't ideal, but they found significant increases of the two common shrub species *Dryas integrifolia* (evergreen) and *Vaccinium uliginosum* (deciduous) and decreases of the forb *Saxifraga tricuspidata* and the graminoid *Luzula arctica*. They also note that the conditions for their study sites were considerably drier in 2009 and that could in part explain the abundance change (Callaghan et al., 2011). Increases of shrubs species over time (Callaghan et al., 2011) in combination with relative abundance increase of deciduous shrubs with temperature over time (figure 6) suggests that shrubs on Disko Island might increase with climate warming. In contrast, deciduous shrubs on Disko Island showed no change with the spatial summer temperature, instead, there was a positive relationship with winter temperatures (Figure 5). Nevertheless, the general pattern is that summer air temperature across space has a positive relationship with relative abundance of shrubs on all sites (Figure 5). Does that mean we can expect shrubs to do well with potential future summer warming? One thing to consider is that the summer air temperature is influenced by landscape features that do not change with time, at least not a temporal perspective relevant for climate change, such as elevation. Elevation is connected to temperature but also to soil depth, soil stability and wind exposure. In summary, shrubs could do well in warmer parts of the landscape due to other reasons than temperature. However, there is evidence of a positive direct effect of temperature on shrubs in the arctic from warming experiments, although only in region with high ambient temperature (Elmendorf et al., 2012a).

Across all sites the relative abundance changes with spatial winter soil and air temperature gradients are similar, both in terms of direction and magnitude (figure 4). In Latnjajaure, snow depth varies between 10-50 cm (Björkman et al., 2010) so one could assume that most plots have a snow cover deeper than 15 cm, i.e. a depth that encapsulates the whole TMS-logger during winter. This snow cover provides an insulating effect, suggesting that the air temperature measured by our loggers should be similar to soil temperature during winter. However, even

though no statistics were made in that regard there still seems to be some difference between winter air and soil temperature (Figure 2) even though the relationship with relative abundance is similar (Figure 5). Another aspect of the winter temperature gradients is that the significant relationships of relative abundance was varied for different functional groups and on different sites. Likely the responses detected are due to site-specific characteristics and/or species-specific differences more related to snow accumulation and soil moisture than temperature. Suggesting again that temperature does not act in isolation as driver for Arctic plant community composition (Martin et al., 2017), and maybe especially during winter.

Relative abundance is showing which functional groups that are abundant within the plant community, but you lose information on total vegetation cover. The microclimate plots, across all three sites, span areas with high, close to 100% total cover, to areas with almost no cover at all. Total cover is important regulator for summer soil temperature due to shading (von Oppen et al., 2022) and soil moisture (Aalto et al., 2013) but it seems that relative abundance of functional groups is not among the variables capturing that relationship.

## **Conclusion**

The results here hints at the possibility of using spatial temperature-composition relationships to predict change over time. However, there is a substantial among-site variability and before space-for-time substitution can be used as a robust methodology there are many other aspects that needs to be explored, most importantly the co-occurrence of other drivers than temperature, both across space and time. Additionally, the results here support previous evidence of a non-uniform response of Arctic plant communities to climate change, especially the fact that high-arctic seems remarkably resilient. We observe rapid change in the abiotic parts of the Arctic ecosystem, such as thawing permafrost, melting sea ice, melting glaciers, and increasing temperatures with potential impacts to the carbon cycle, the climate system, and ecosystem function. The Arctic plant communities have a part to play in this story and, now more than ever, we need to continue with our monitoring efforts to uncover the patterns of change today so we can plan for a better tomorrow.

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# Appendix 1. Popular science summary

## Arctic plants and temperature – a journey through space and time

Written by Nicklas Albertsson

The first thing that comes to people's minds when they hear the word arctic is rarely plants. Other aspects of the arctic is often the primary association, such as: ice, snow, polar bears, melting glaciers and northern lights. You might be thinking, does the arctic even have plants? The answer is a resounding yes, just on Greenland alone there are around 500 species of plants!



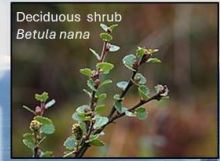
The arctic is the northernmost region in the world. Vast and varied with an annually melting and freezing ocean, landmasses covered with glaciers and permanently frozen soil. But there are also things that are not frozen. The **short summers** have pleasantly warm periods with temperatures up to 15-20 °C, especially areas situated on lower elevation. These lowland areas with summer-thawed soil are home to the majority of arctic plants. Here, we find small, low stature plants such as the evergreen shrub *Cassiope tetragona* or the small tussock growing graminoid *Phippsia algida*.

### Arctic plants might affect your future!

The Arctic is warming fast with climate change, potentially releasing large amounts of trapped carbon in the soil. Arctic vegetation is also changing and plays an important role in the carbon cycle. Taller plants results in more accumulated snow during winter leading to warmer soil due to insolation. In contrast, more vegetation cover or a different composition of plants can lead to cooling of the soil in summer due to shading. This is two examples exemplifying the complex interplay between atmosphere, vegetation and the soil. We need understand the vegetation shift going on right now in the arctic, with that we can improve our future predictions of the impacts of climate change.

### Arctic plants and temperature: do spatial relationships predict change over time?

Since the plant cover consists of so many species it can be hard to draw conclusions from measuring temperature and connect that to each specific plant species. Instead, we categorize the plants in groups that share similar function and form, **functional groups**. The four different groups used here are shown on the pictures. My research has concluded that, spatially in the landscape, air temperature of summer describes the relative abundance of these functional groups across three arctic sites. In the most southern site, Latnjajaure in Sweden, summer air temperature also describes the relative abundance over time. In the two more northern sites, Greenland and Svalbard, there is no relative abundance change with time. Those two sites are part of the high arctic, perhaps one of the most extreme ecosystems on earth when it comes to annual variation in temperature, even if we don't take climate change into consideration. It might be that the plant communities there are inherently resilient towards changing temperature. Or maybe enough time hasn't passed yet. We also need to consider that more things than temperature is changing with climate change, such as snow cover and soil moisture, those factors may also affect the plants. The full story of how arctic plant will respond to climate change is still not uncovered, but since we humans are causing it, it is also our responsibility to reveal the impacts it will have. With that knowledge my hope is that we can, as a civilization, embrace collective decisions that will shape a better future for us and ecosystems alike.



Deciduous shrub  
*Betula nana*



Evergreen shrub  
*Cassiope tetragona*



Forb  
*Arabis alpina*



Graminoid  
*Phippsia algida*

## Appendix 2. Cold and heat requirement scales

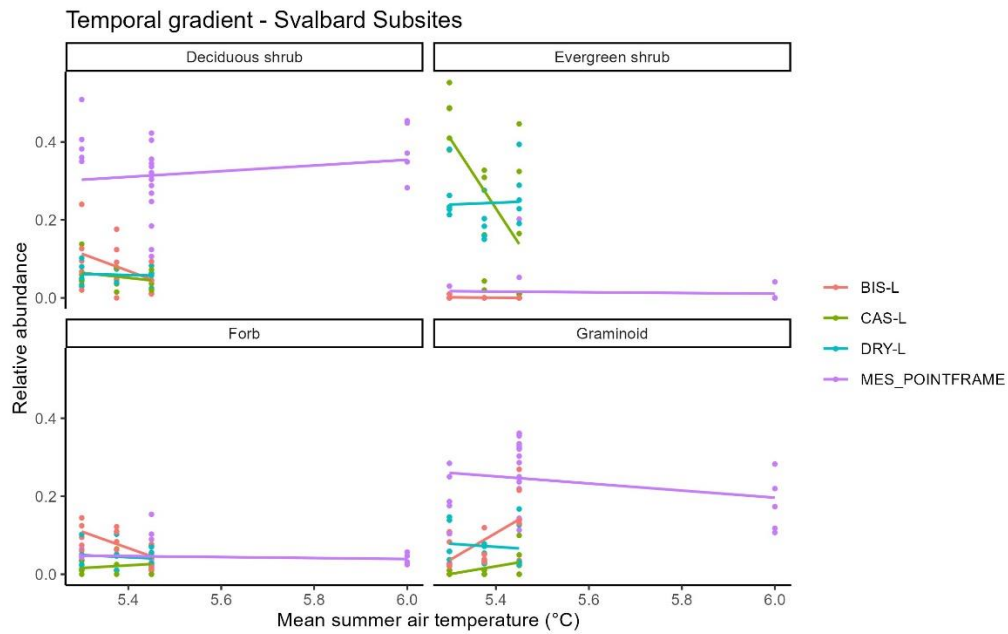
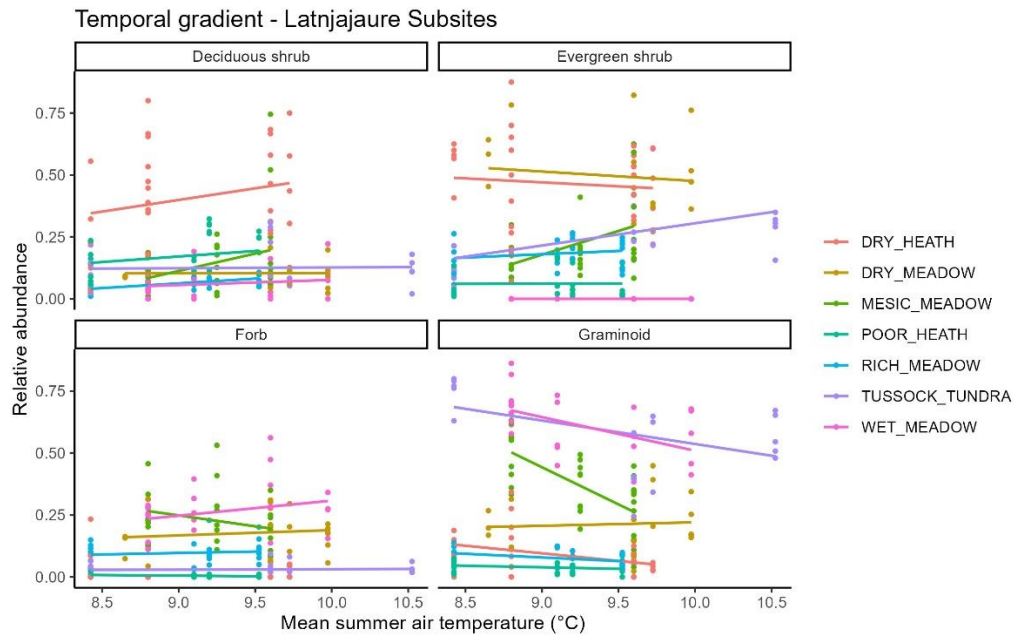
The cold requirement is a 20-degree scale that translates as follows (Tyler et al., 2021):

- 1 = annual minimum rarely below 10 °C (subtropical/tropical regions)*
- 2 = annual minimum rarely below 5 °C*
- 3 = annual minimum rarely below 0 °C*
- 4 = temperatures below 0 °C occasional, but annual minima not below –5°C*
- 5 = temperatures below 0 °C regular but sporadic, annual minima rarely below –10 °C*
- 6 = winter temperatures typically below 0°, but during less than three months and annual minima not below –15 °C*
- 7–16 = the Swedish cultivation zones 1–9*
- 17 = descending to the timberline (uppermost subalpine zone)*
- 18 = descending to the low-alpine zone*
- 19 = descending to the mid-alpine zone*
- 20 = confined to the high-alpine/arctic zone*

The heat requirement is a 14-degree scale that translates as follows (Tyler et al., 2021):

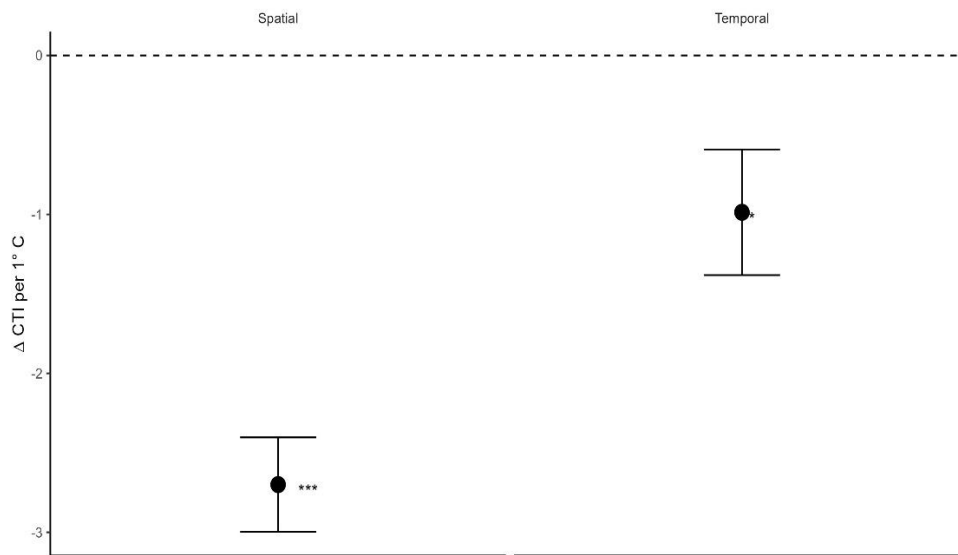
- 1 = reaching the high-alpine/arctic zone*
- 2 = reaching the mid-alpine zone*
- 3 = reaching the low-alpine zone*
- 4 = reaching the timberline (uppermost subalpine zone)*
- 5 = reaching the subalpine zone (cultivation zone 9), but only at sites with a favorable microclimate*
- 6 = reaching cultivation zone 8*
- 7 = reaching cultivation zone 7*
- 8 = reaching cultivation zone 6*
- 9 = reaching cultivation zone 5*
- 10 = reaching cultivation zone 4*
- 11 = reaching cultivation zone 3*
- 12 = reaching cultivation zone 2*
- 13 = reaching cultivation zone 1*
- 14 = at present not reproducing/resident in Sweden due to climatic constraints.*

### Appendix 3. Variability of Subsites



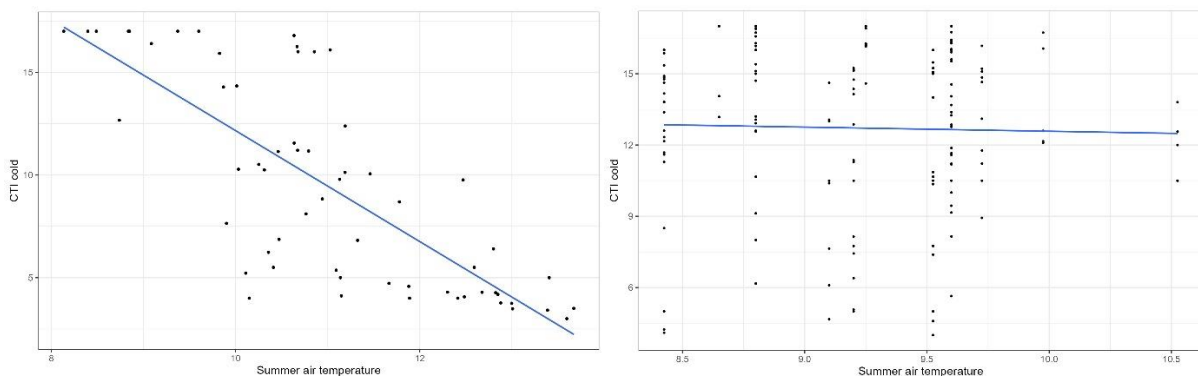
## Appendix 4. CTI within functional groups

A last-minute approach to the CTI analysis. Instead of looking at temperature affinity turnover for the whole plant community this analysis was done within the functional groups. With this method the group evergreen shrubs had a significant result over time for the CTI based on the cold requirement scale. CTI for all functional groups showed significant change with spatial summer air temperature. Since evergreen shrubs in Latnjajaure consists of rather few species a species-specific turnover can be revealed from this approach. With increasing temperature, both across space and time there is an compositional turnover from more alpine specialist species (*Dryas octopetala*, *Phyllodoce caerulea*, *Diapensia lapponica*, *Harrimanella hypnoides*, *Rhododendrom lapponicum*, and *Cassiope tetragona*, these species have 16 or 17 on the cold requirement scale) to species that are distributed on a much wider temperature range (*Vaccinium vitis-idaea* and *Empetrum nigrum*, 4 and 5 on the cold requirement scale).



### Spatiotemporal comparison of CTI change within evergreen shrubs.

CTI based on the cold requirement scale. Spatial analysis – linear regression. Temporal analysis – linear mixed effect model with subsite as random effect. Spatial:  $p < 0.0001$ , temporal:  $p = 0.013$



Raw data for evergreen shrubs. Left: spatial data. Right: temporal data