The effect of climate warming to vegetation composition and functionality across three different vegetation types in the low-Arctic

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View over Blæsedalen and Skarvefjæld (Qeqertarsuaq, Greenland) - 2021, by: Hanne Tjoflot

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ABSTRACT

The Arctic tundra is experiencing climate warming at twice the rate of lower latitudes. Rapid warming has profound effects on plant diversity and functionality of arctic plant communities. Investigating change in species composition and functional traits of plant communities in the Arctic, is an approach to understand responses of tundra ecosystems to increasing temperatures. Taxonomic and functional plant responses can either mitigate or amplify climate change through direct and indirect processes, and quantifying these changes can provide an insight of the future state of the Arctic.

In this study, I quantified how background warming affected the composition and functionality of plant communities in three widespread vegetation types within the low-Arctic. In the summer of 2021, I resurveyed plant community and trait data from 2008 at Disko Island, Greenland. I conducted vegetation analyses from twelve semi-permanent plots and collected individuals of vascular plant species to calculate and compare four different functional traits: plant height, leaf area, specific leaf area (SLA), and leaf dry matter content (LDMC). To investigate the importance of both species-turnover and within species diversity, I used a methodology that both accounts for intra- and interspecific trait variation.

I found larger changes in species compositions than change within plant functional groups than at the plant community level. Plant strategies varied between vegetation types, but overall warming is driving functional changes within plant communities towards more productive and resource acquisitive strategies. Trait variation within species has decreased through time, indicating that some species within the Arctic tundra is facing an increasing extinction risk.

A warming Arctic is leading to shifts in species distribution and abundance, as well as changes in plant community functioning. Shifts can be caused by immigration of species to new habitats, local extinction of individual species, and/or change in trait expression. This study emphasise that plant communities are rapidly changing in low-Arctic, and my findings emphasise the importance of investigating functional groups in plant community ecology.

INTRODUCTION

In the Arctic, annual air temperatures are currently increasing at more than twice the rate of average global warming (Box et al., 2019). Since 2014, the measured temperatures in this circumpolar area has been particularly high (Overland et al., 2019). The increased temperature is a major driver of vegetational changes on the tundra, like shifts in distribution, and changes in composition and abundance (IPCC, 2021; Pearson et al., 2013). These responses are likely to affect tundra ecosystem functions, like plant productivity, and organic matter decomposability, which in turn result in positive feedbacks to global climate (Pearson et al., 2013). Increased vegetation production, for instance, may lead to decreased albedo, and enhanced decomposition of soils which increases CO_2 emissions (McGuire, Chapin Iii, Walsh, & Wirth, 2006; Piao et al., 2020). To make predictions of how climate warming will affect future tundra communities, there is a need to investigate how altered climate affect species composition and community functionality across dominating vegetation types in the Arctic.

Increase in biomass on the arctic tundra, known as “Arctic greening”, is a well-documented large-scale response to climate change, mainly driven by climate warming (Piao et al., 2020). Greening can be related to an extension of the growing season, as well as an increased uptake of CO_2, as the tundra is storing huge quantities of carbon that releases as permafrost is thawing (Ernakovich et al., 2014; Schuur et al., 2009). Increased productivity and expansion of species due to warming is especially observed in shrub vegetation. Common vegetation types in the Arctic does among others consist of shrublands, graminoid tundras, barrens, and wetlands, and change in shrub abundance will alter the structure and composition of tundra ecosystems (Myers-Smith et al., 2011; Walker et al., 2005). Yet, the effect of climate warming and change in vegetation on tundra carbon balance, as well as nutrient and water cycling regimes, remains uncertain. They are all affected by multiple climatic factors and are sensitive to environmental change (Callaghan et al., 2004; Huemmrich et al., 2010). Carbon, nutrient, and water cycles are also closely connected, and as plants are highly linked to these factors, they are likely to dive changes in community compositions as response to change (Tateno & Chapin Iii, 1997). To understand how ecosystem structure and functionality is affected by rapid warming, it therefore necessary to study responses to climate warming of smaller scales within tundra communities (Myers-Smith et al., 2020).

Plant functional traits are morphological, physiological or phenological features of an organism that can be measured on an individual scale, influence the organism's performance, and indirectly impact its fitness (McGill, Enquist, Weiher, & Westoby, 2006; Violle et al., 2007). The measure or value of a trait therefore indicates the strategy of the plant, in which is usually a trade-off between growth and survival. Plant height is a central functional trait that reflects several different factors like growth potential, how it is exposed to light in the vegetation, competition between its surrounding species, and potential life span (Perez-Harguindeguy et al., 2016). A leaf with high specific leaf area (SLA) reflects a strategy that is resource acquisitive (Halbritter et al., 2020). It is often associated with high photosynthetic rates and leaf nitrogen contents. In contrast, leaves with high SLA usually have shorter life spans, including a lower carbon investment in protective secondary compounds (Perez-Harguindeguy et al., 2016). SLA is highly connected with leaf area, where large leaves tend to be less exposed to environmental stressors, such as cold stress, drought stress, and nutrient stress (Perez-Harguindeguy et al., 2016).

A trait that is usually seen as the “inverse” of SLA, is leaf dry matter content (LDMC). LDMC is highly associated with resource use and availability, where high values often are related to tough and resistant leaves with long lifespans, but with low relative growth rates and litter decomposition rates (Perez-Harguindeguy et al., 2016; Wilson, Thompson, & Hodgson, 1999). Leaves with low decomposition rates can potentially increase soil stocks of carbon and nitrogen, and thereby regulate ecosystem carbon balance and limit nutrient flow (Garnier et al., 2004). Knowing that traits respond to both biotic and abiotic surroundings, and thereby influence the surrounding environment of the plant, traits can be used as important links between vegetational change and ecosystem functionality (Myers-Smith, Thomas, & Bjorkman, 2019). Using a trait-based approach in the study of community ecology makes it possible to identify patterns and make predictions of future climate responses (McGill et al., 2006). The value, range, and relative abundance of traits controls ecosystem functions within a community, and a shift in the dominance of a community trait distribution would therefore likely alter properties of that community, leading to climatic feedbacks (de Bello et al., 2010).

Interactions between biotic and abiotic factors are working at the level of the individual, suggesting that changes in values, ranges, and relative abundances of community trait averages due to environmental change, can be caused by intraspecific variability and/or species turnover (Lepš, de Bello, Šmilauer, & Doležal, 2011; Violle et al., 2012). Trait variation among individuals within a species might have significant influence on structure and ecosystem processes in a community as does variation across species, and interspecific variation can therefore at least not be neglected (Albert et al., 2010). Intraspecific variability is also possibly greater in areas where species richness is low and the climate cold, which emphasize the need to include trait variability within species on the tundra (Albert et al., 2010; Siefert et al., 2015).

In this study I investigate plant diversity and intra- and interspecific trait variability in plant communities on the arctic tundra. By resampling functional trait data from 2008, and conducting vegetation analyses in three distinct vegetation types (meadow, dwarf-shrub, and willow shrub) on Disko Island, Greenland, we aim to answer the following questions:

- How has thirteen years of ambient climate warming affected species composition and plant functional change across three different vegetation types on the arctic tundra?
- How important are the ecological effects of intraspecific- relative to interspecific trait variability as response to climate warming in an arctic environment?

MATERIALS AND METHODS

Site description

The field observations of this study were conducted in July 2008 and 2021 in the area around Arctic station, on Disko Island. Disko is located on the west coast of Greenland, where Arctic station is situated about 1 km outside of the town Qeqertarsuaq (69.24´N and 53.54´W) on the southern end of Disko (Figure 1). The study design was conducted in similar ways as it was in 2008 (Table 1), and consisted of twelve locations/plots divided equally by four sites relatively close to Arctic station. An overview of the sites is found in Figure 1. Within each site the plots were distributed in three different vegetation types. These were willow shrubs, meadow vegetation, and heaths of dwarf shrubs. Willow shrubs are often found in southern slopes (Böcher, Holmen, & Jakobsen, 1966), and are in this area characterized by the species *Salix glauca*. The meadows were typically snowbeds with quite moist soils, and consisted of a larger variation of species. Some of the common ones were *Salix herbacea*, *Salix glauca, Vaccinium uliginosum, Bistorta vivipara and Poa alpina*. The dwarf shrubs were relatively dry heaths dominated by the species *Vaccinium uliginosum, Empetrum hermaphroditum*, and *Betula nana*.

Qeqertarsuaq and Arctic station is situated on a bedrock of gneiss, and the landscape around consists of basalt breccia and plateau lava (Nielsen, Hansen, Humlum, & Rasch, 1995). Due to its position in the north, the growing season on Disko is quite short, and the length can vary between locations considering the time of snowmelt locally.

As Disko is surrounded by Baffin Bay in the north, Davis strait in the west and Disko bay in the south-east, the climate of this study area is characterized as arctic maritime (Nielsen et al., 1995). In 2020, Arctic station had a mean annual air temperature of -2.3 °C, and the summer months (June, July, and August) had a mean temperature of 6.5 °C. Total annual precipitation for the same year was 488.2 mm, where 104.6 mm fell during the summer. The relative humidity had an annual percentage of 69.5%, and a mean of 79.8% during the summer (climate data provided from https://data.g-e-m.dk/("Greenland Ecosystem monitoring database,")).

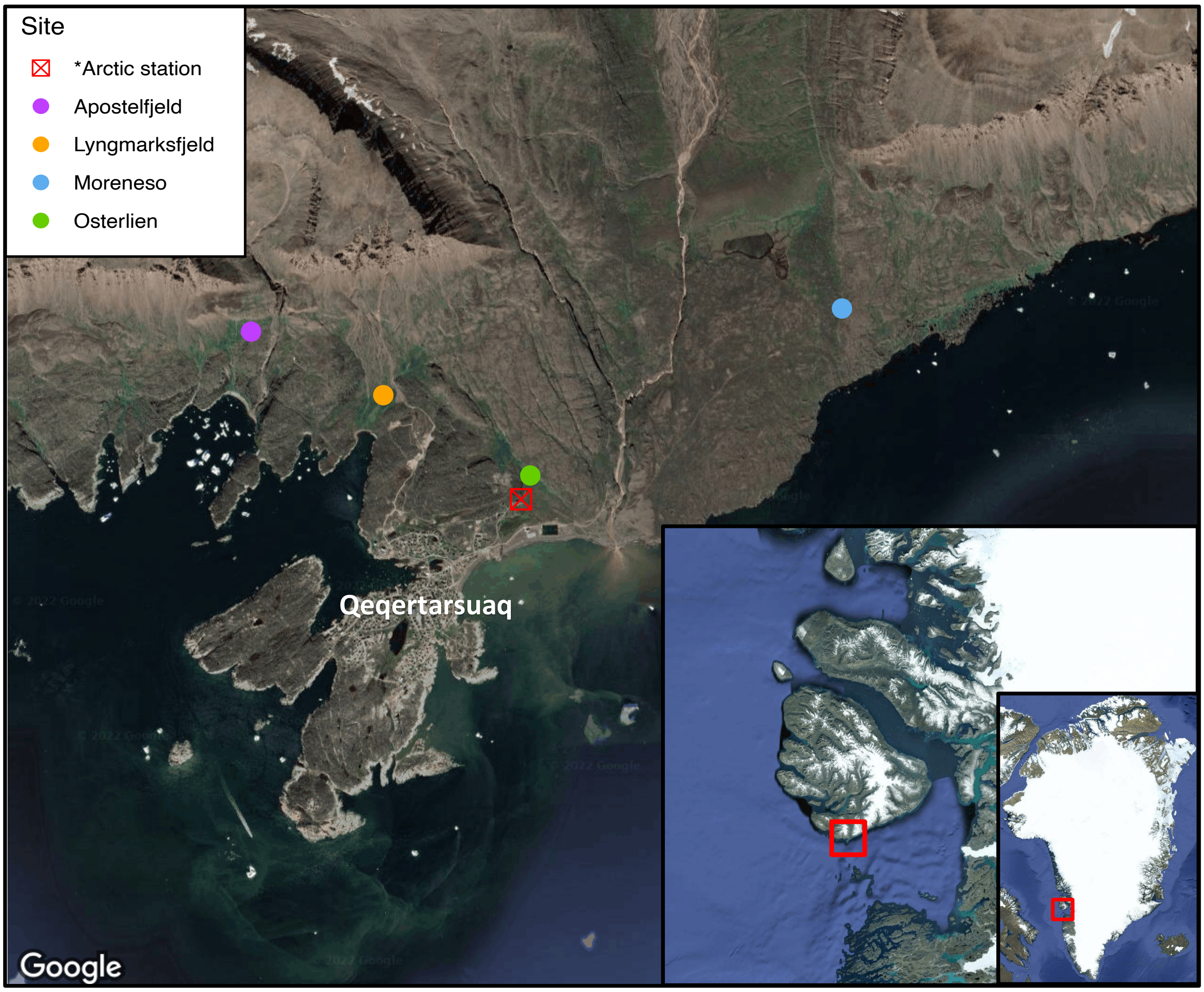

Figure 1: Map visualising the study site areas.

Visualisation of the study sites included in this study (round dots), and their location relative to Arctic station (red crossed square).

Maps are retrievd from Google Maps in R Studio using the «ggmap» and «ggplot2» packages.

Table 1: Comparison the methods used in the study in 2008 and the methods used in the study in 2021, at Disko Island, Greenland.

	2008	**2021**	**Comment**
	Study area and plot information		
Study sites	4 sites: Apostelfjeld, Østerlien, Lyngmarksfjeld, Morenesø	4 sites: Apostelfjeld, Østerlien, Lyngmarksfjeld, Morenesø	The plots from 2008 were divided between different vegetation types based on both vascular plants and the lichen flora. As this

Vegetation types included in the study	5 vegetation types: Willow shrub, meadow vegetation, poor dwarf shrub, rich dwarf shrub, and lichen heaths	3 vegetation types: Willow shrub, meadow vegetation, and dwarf shrub	study mainly focuses on vascular plants, it was decided not to sample from the lichen heaths, and sample from only one of the dwarf shrubs per site to avoid getting an unbalanced study design.
Total amount of plots	20	12	
Area per plot	25 m^2 (5m * 5m)	25 m^2 (5m * 5m)	
Plant groups included in the study	Evergreen shrubs, deciduous shrubs, and forbs	Evergreen shrubs, deciduous shrubs, forbs, graminoids, and pteridophytes	
Vegetation analysis:			
Pinpoint area per plot	1m^2 (0.5m * 0.5 m frame)	2.25 m^2 (0.75m * 0.75m frame)	
Total amount of points per plot	100 - 25 points per subplot	100- 25 points per subplot	
Implementation of pinpoint analysis	Each species that is hit inside a grid point is recorded, but only once per grid point. Plant structures (leaf, stem, flower) are not described, and other types of biomass (lichen, moss, and litter) are not included.	Each species that is hit inside a grid point is recorded, and all hits are included. It is described which plant structure (leaf, stem, flower) that has been hit, and other types of biomass (lichen, moss and litter) are included.	The pinpoint from 2008 recorded a presence/absence of each species hit per point. In 2021 it was also recorded if a species was hit several times inside a grid point to get a three-dimensional image of the distribution.
Functional trait measurements:			
Species included in trait analysis	All species (within the included plant groups) that are present in the plot.	All species (within the included plant groups) that are present in the plot.	
Measured plant traits (calculated traits not included)	Plant height, leaf fresh mass, leaf dry mass, leaf area	Plant height, leaf fresh mass, leaf dry mass, leaf area, leaf thickness, stem length, stem thickness, stem wet mass, stem dry mass	
Replicates per species	10 individuals per species	4 individuals per species	
Leaves measured per individual	1 leaf	Varied per individual	
Plant height measurement	Height of upper leaf	Height of upper vegetative organ	
Other			
Soil moisture measurements included?	No	Yes	

Vegetation analysis

The plots surveyed in 2021 were the exact same as the ones surveyed in 2008. As the plots were not permanently marked, they were all re-located in 2021 using GPS coordinates (Appendix 1). Unfortunately, one of the plots (willow shrub vegetation at Lyngmarksfjeld) had been destroyed since 2008, and this plot therefore had to be replaced in 2021. Each plot was shaped like a square with an area of 5m * 5m (25m^2), and once the plot was marked in the vegetation, all vascular plant species inside the plot were recorded.

Pinpoint analysis

To quantify the abundance of vascular plants, a pinpoint analysis was conducted. For this we used a 75cmx75cm frame, with a grid pattern inside (fig. 2), consisting of 25 squares, or grid points. The frame was placed above the vegetation at four random places (four subplots) in each plot, making the total pin-point area 2,25 m². In plots where the vegetation was very tall, the pinpoint frame was equipped with taller legs to keep the frame steady and avoid it laying over the vegetation.

In each grid point (25 points, totally 100 points for each plot), a pin was inserted slowly towards the ground. For every time the tip of the pin touched a plant structure (leaf, stem, or flower), it was recorded. It was also recorded if a plant structure was hit several times on the same individual, and both the species and the plant structure that was hit was specified. Other types of biomass were also included, like dead plant material (litter), moss, and lichen.

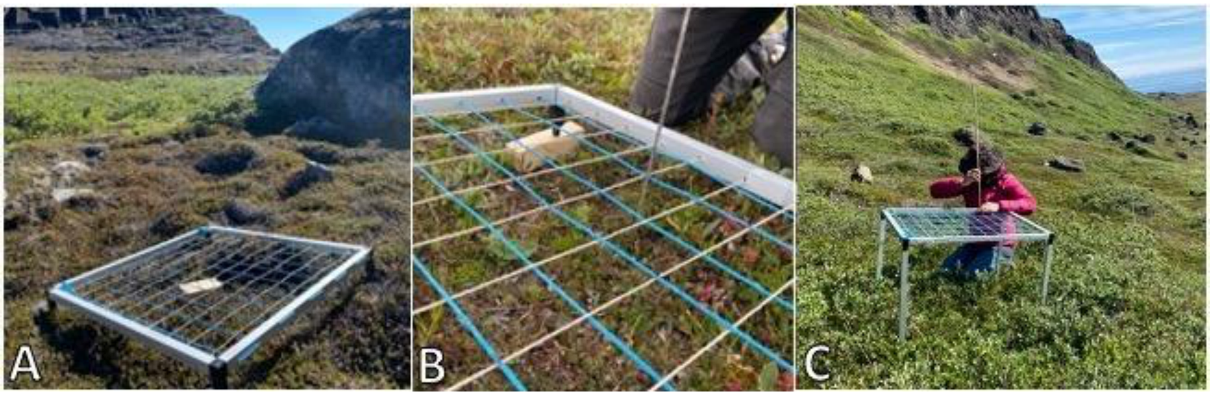

Figure 2: Three pictures illustrating how the pin-point analysis was conducted at Disko Island, Greenland in the summer of 2021.

A: The pinpoint frame used for vegetation analysis, placed above the meadow vegetation at Lyngmarksfjeld. B: A picture that illustrates how the pin was led towards the ground. C: The frame with extended legs in willow vegetation in Østerlien.
Pictures: Hanne Tjoflot

Trait measurements

The traits measured in this study was done according to the methods described in the handbook for measurements of plant functional traits (Perez-Harguindeguy et al., 2016).

Whole plant trait

The height of the plant was measured while collecting the individuals in the field. It was measured from the ground up to the tallest vegetative organ (foliage) (in millimeters), without stretching it out (fig 3). For species with rosette leaves, the height was measured from these, and not from leaves growing on the stem.

***Figure 3**: Measuring plant height and collecting samples of Salix glauca in dwarf shrub vegetation at Lyngmarksfjeld. Pictures: Hanne Tjoflot*

Leaf traits

Before we could measure leaf traits, they had to be collected and brought to the lab.

Four samples from all plant species present in each plot were collected and measured. To minimize the probability of sampling individuals from the same individual, the four individuals were collected as far apart as possible inside the plot. Collected individuals were fully developed, and damaged and very old individuals were avoided. Usually the whole individual was collected, and for larger species, like *Salix glauca*, we sampled whole sections of a twig with the leaves still attached to it (fig.3).

To keep the leaves as fresh as possible, samples were put in sealed plastic bags together with wet paper tissues in the field, before they were brought to the lab where they were kept cold and moist until they were analysed.

To measure leaf traits, leaves from each individual were picked off, including the petiole. As the size of leaves from different species varies, we made sure that there were enough leaves from each individual to get accurate measures. Usually, the leaves would cover at least 2cm^2, but most important was that the chosen leaves were fully developed, and non-damaged. The leaves were put in a paper bag with a unique code to be able to keep track of each sample. The leaves were also wrapped in a wet paper towel to keep them moist. For each leaf sample we measured fresh mass (to calculate LDMC), leaf area (for leaf area and SLA), dry mass (for LDMC and SLA), and thickness (for leaf thickness). Fresh mass from the leaves was measured on a scale with a resolution of 0.001 g +/- 0.0001 g. Excess water was removed from the leaf surfaces before putting them on the scale. The area of the leaves was measured using Canon Lide220 photo scanner. All leaves were scanned, making sure nothing overlapped, and for leaves that were too large for the scanner, like *Angelica archangelica*, we cut them in smaller pieces before scanning them. The pictures were further analysed in “R” to calculate the area, using the “LeafArea” package (Katabuchi, 2015).

Thickness of the leaves was measured using a micrometer (Mitutoyo IP 65 Coolant-proof) with a resolution of 0.001 mm +/- 0.0001. Three leaves from each individual were measured, avoiding measuring the midrib in the leaves. In cases where there were less than three leaves in the sample, one leaf was measured several times in separate parts. The average from the three measurements would later be calculated for further analysis.

To get the dry mass, all leaves were dried in an oven with a temperature between 60 - 70 degrees Celsius for at least 48 hours. Dry mass of the leaves was measured on a finer scale with a resolution of 0.00001g +/-, as some of the samples were very lightweight.

Stem traits

To measure stem specific density (SSD) and stem dry matter content (SDMC), the same equipment for leaf measurements were used. A section of 10-30 mm of the stem was cut off and measured on the wooden plant species. These species included *Salix glauca, Salix herbacea, Betula nana, Vaccinium uliginosum, Phyllodoce caerulea, Rhododendron lapponicum,* and *Empetrum nigrum hermaphroditum (*herafter; *Empetrum hermaphroditum)*. We made sure that the section of the stem we used was growing above ground and was a part of the main stem. To calculate SSD and SDMC, we measured stem length (mm), fresh mass (g), dry mass (g), and thickness. The thickness was measured on the sides and in the middle of the stem (three places), and I used the mean value of these three measurements for data analyses.

Environmental measurements

Soil moisture

Because the plant community also is determined by abiotic factors (McGill, Enquist, Weiher, & Westoby, 2006), the water content of the soil within each plot was measured regularly during the data collection period. The apparatus "Delta T Soil Moisture Kit" was used for this, which measured the moisture of the ground soil in percentage. The soil moisture was measured at ten points within each plot, as illustrated in figure 4, and each plot was measured two or three times in total.

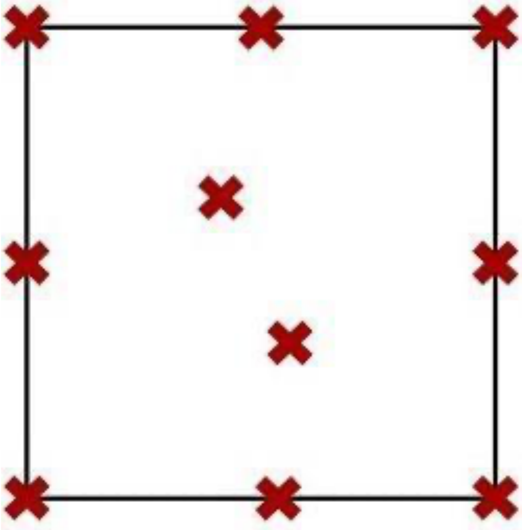

***Figure 4**: Illustration of how the soil moisture points were divided in a plot. The black square illustrates the plot frame, and the red crosses mark the points where soil moisture was measured.*

Data processing and statistical analyses

All statistical processes and analysis were performed using the software R version 4.2.0 (R Core Team, 2022), and RStudio version 2022.02.2.485 (RStudio Team, 2022), and all visualization of the data was performed using the package "ggplot2" (Wickham, 2016).

Processing climate data

Climate data from Arctic station was retrieved from the Greenland Ecosystem Monitoring (GEM) Database (https://data.g-e-m.dk/). The GEM collects climate data from different stations around Greenland, and the data can be accessed by anyone through their website. In this study we used temperature, precipitation, and humidity data from the database, which is raw data that is continuously measured once an hour every day.

For temperature and humidity, annual means and annual monthly means were calculated. Precipitation was summarized for each year, and each month per year. Years that had < 300 measuring days, and months that had < 25 were removed from the dataset. A linear model (lm) was used to visualize the regression.

Soil moisture estimates

Soil moisture was measured once per measuring period in each plot during three periods of 2-4 days. Two of the plots (willow shrub at Apostelfjeld, and willow shrub at Lyngmarksfjeld) were only measured two times (during two periods), because of limitation of time. Values of soil moisture percentage of these plots were therefore estimated using an imputation method.

Processing vegetation data

As the data in 2008 did not include graminoids and pteridophytes, all data from 2021 compared to data from 2008 were filtered from graminoids and pteridophytes before any calculations and analyses were made.

Proportions of each species per plot was calculated using pinpoint-hits per species per plot divided by the total number of hits per plot. When calculating proportions of functional groups, it was done in the same way, but by only calculating with the functional group in question.

Statistical analyses

The models used for statistical analysis were linear mixed effect models (lme) from the packages “lme4” (Bates, Maechler, Bolker, & Walker, 2015) and “lmerTest” (Kuznetsova, Brockhoff, & Christensen, 2017).

To investigate potential taxonomical changes between 2021 and 2008, MDS-ordination of species abundance were made using the package “ggord” (Beck, 2022). Further, species richness, species evenness (Pielou´s index) and species diversity (Shannon´s index) were calculated for all species within each plot, as well as for each functional group within each plot. A model was run for the richness, evenness, and diversity, using year and vegetation types as fixed effects, and site and vegetation types nested in each other as random effects.

For the study of functional changes between the two years, community weighted trait means (CWM) for the traits measured both years (plant height, leaf area, SLA, and LDMC) were calculated for each plot, and for each functional group per plot. These values were also tested using year and vegetation types as fixed effects, and nested site and vegetation type as random effects. For the three most frequent species within each functional group, a model for a species-specific trait value was also tested, using year and vegetation type as fixed effects, and site, vegetation type and individual nested in each other as random effects. MDS-ordination for traits were made using CWM-data, and the package “ggord”.

The importance of intraspecific variability and species turnover when it comes to trait shifts in different vegetation types were investigated by comparing means per species per trait per plot (specific mean) with means per species per trait across all plots (fixed mean).

RESULTS

Climate and environmental conditions

Climate data from Greenland shows an increase in mean annual air temperatures from 1962-2021, with an estimate of 0.029 °C per year and 0.033°C per summer (Figure 5, A and B). Annual air temperature for 2008 was -2.6 °C and 8.2 °C in June-August, and was for 2021 -1.5°C and 6.9°C respectively. The annual relative humidity from 1962-2021 has decreased with an estimate of 0.074 percentage points per year, and 0.034 percentage points per summer (Figure 5, C and D). Annual relative humidity and mean summer humidity for 2008 were 78.0%, and 77.4% respectively, and 74.3% and 83.5% for 2021. Monthly annuals for temperatures and humidity are visualised in Appendix 2. From 1962-1977 and 2011-2020, annual total precipitation has decreased with an estimate of 0.931mm per year, but remained quite stable in the summer months (0.053mm decrease per summer) (Figure 5, E and F). There are no data of the total precipitation for 2008 and 2021, but the total precipitation for 2011 was 340.2 mm, and 169.6mm from June-August. In 2020 the total precipitation was 488.2mm, with a total amount of 104.6mm from June-August.
Soil moisture conditions were measured and are visualised in Appendix 4.

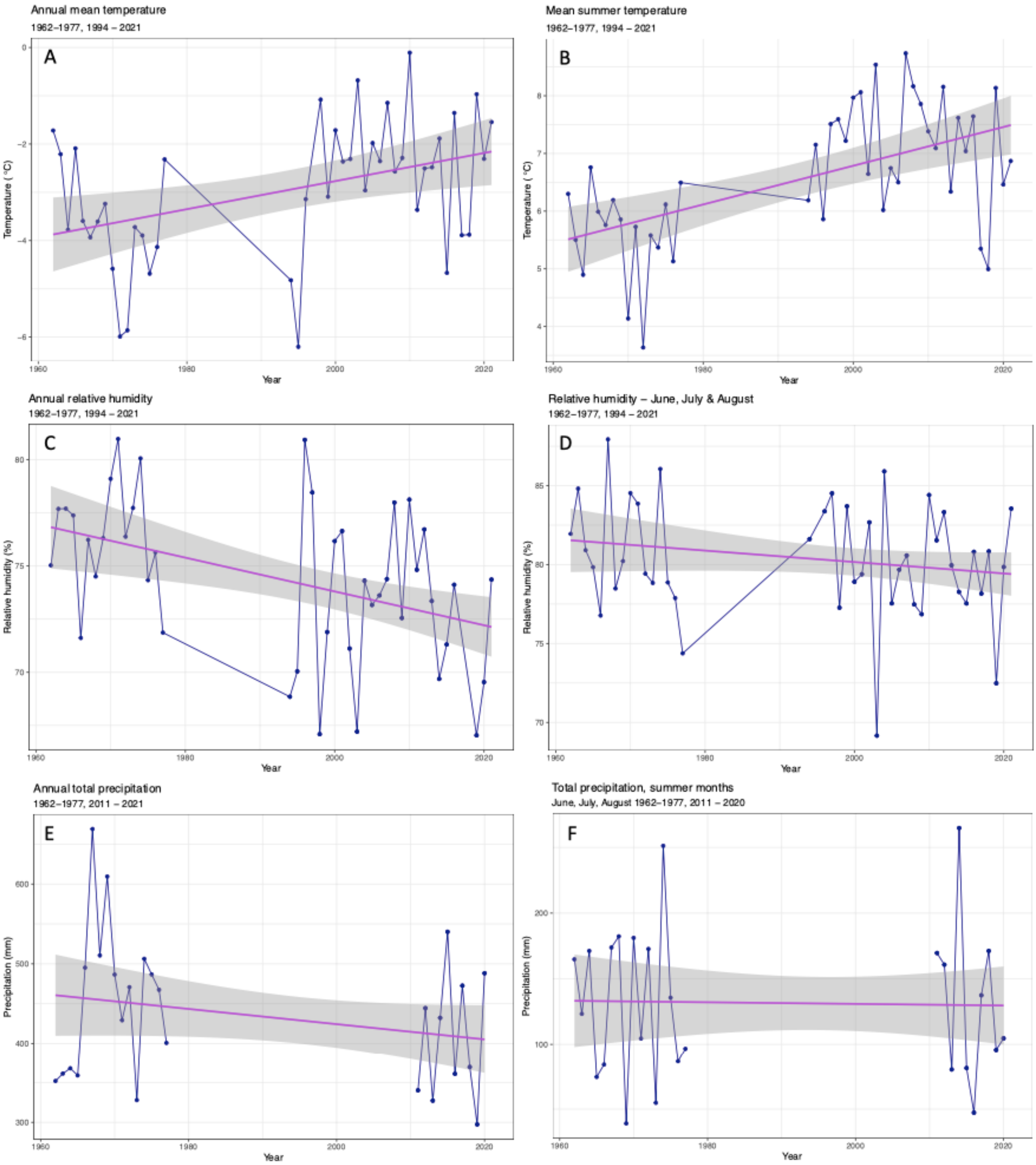

Figure 5: Temperature °C, relative humidity (%) and precipitation (mm) data from Greenland.
The plots are visualising mean annual observations (A, C, and E), and mean annual observations from June - August (B, D, and F). The temperature and humidity data (A, B, C, and D) visualise data from 1962-2021, but lack observations between 1977 – 1994. The precipitation data (E and F) visualise observations between 1962-2020, but does not include observations between 1977 - 2011. Blue lines are connecting annual

observations per year (A and C being significant), and the pink line is a linear regression line with standard errors visualised in grey.

Species diversity and vegetation composition

An overview of all species included in this study are found in Appendix 3.

The MDS ordination (non-metric multidimensional scaling) visualise how the most abundant species (the species hit in the pinpoint analysis) from the study are distributed in the vegetation (Figure 6). There is a clear trend of species clustering within the dwarf shrubs and willow shrubs, while there is a larger spread in the distribution of species within the meadow vegetation. *Salix glauca* is highly participating in the clustering of willow shrubs, while the dwarf shrubs are more driven by the abundance of *Vaccinium uliginosum* and *Empetrum hermaphroditum*. The meadows are more clustered where there is a larger abundance of forb species, like *Bistorta vivipara* and *Sibbaldia procumbens*. *Salix herbacea* is also contributing in the clustering of the meadow vegetation. The stress values (A = 0.12, B = 0.07, and C = 0.06) indicate a good fit for the model.

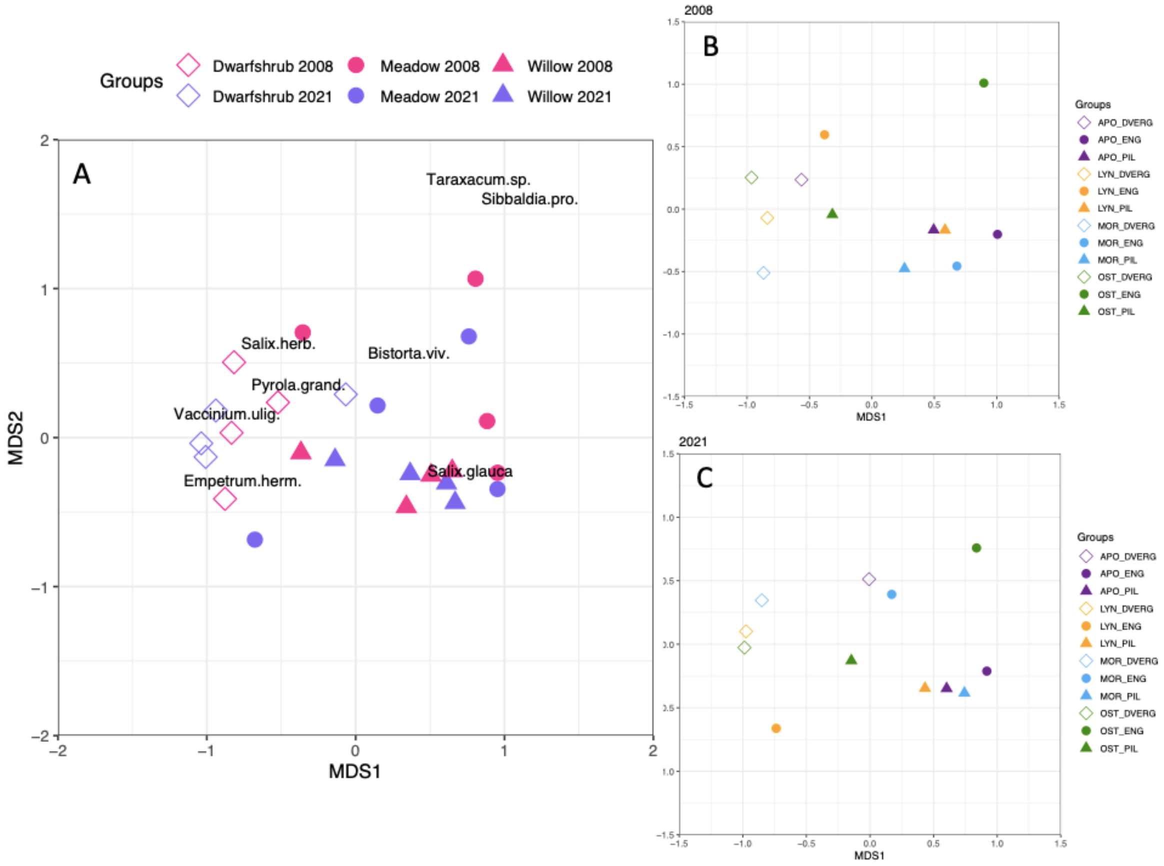

Figure 6: MDS-ordinations visualising species diversity.

Diversity is sampled from species proportions in the vegetation analysis conducted in three vegetation types at Disko Island, in 2008 and 2021 respectively. The Bray-Curtis dissimilarity index is used to calculate the distance for the community composition. Vegetation types are illustrated as different shapes (diamonds = dwarf shrubs, dots = meadow vegetation, and triangles = willow shrubs). The axis ranges from -2, 2 in plot A, while it ranges from -1.5, 1.5 in plot B and C. Plot (A) is visualizing ordination across the three vegetation types, and between the two years (2008 = pink, and 2021 = light purple), and has a stress value = 0.12. Plot (B) and (C) visualize ordination from the vegetation analysis conducted in 2008 (B) and 2021 (C), where shapes illustrate the vegetation types, and colours illustrates the four sites (purple = Apostelfjeld, yellow = Lyngmarksfjeld, blue = Morenesø, and green = Østerlien). The stress value of plot B = 0.07, and stress value for plot C =0.06.

Changes in community composition between vegetation types, as well as between 2008 and 2021, were most distinctive within functional groups, and especially within evergreen shrubs (Table 2). Species richness and species diversity were significantly different between vegetation types. It was overall a significantly higher richness of forbs in meadows, and evergreen shrubs in dwarf shrubs, as well as deciduous shrubs in willow shrubs, where the latter were not significant. Forbs tended to be less even within meadows, and more even within willow shrubs. Species richness increased from 2008 (5.8 +/- 0.56 species per plot) to 2021 (6.3 +/0.45 species per plot), although not significant. Yet, species richness of evergreen shrubs was significantly higher in 2021 (Tukey HSD p = 0.09), and the evenness of the same functional group decreased significantly since 2008 (Tukey HSD p = 0.004).

Table 2: F-values from a linear model explaining variation in community composition variables*.* *Composition variables (richness, diversity (Shannon´s diversity index), and evenness (Pielou´s evenness index)) across three different vegetation types (dwarf shrubs, meadow vegetation, and willow shrubs), and between two different years (2008 and 2021). P values < 0.1 are considered significant, and are reported and highlighted in bold.*

		Richness	**Diversity**	**Evenness**
ALL SPECIES				
	Year	$F_{1,9} = 0.72$	$F_{1,9} = 0.48$	$F_{1,9} = 1.73$
	Vegetation type	**$F_{2,6} = 4.49, p = 0.06$**	**$F_{2,6} = 4.58, p = 0.06$**	$F_{2,6} = 1.67$
	Year:Vegetation type	$F_{2,9} = 0.18$	$F_{2,9} = 1.25$	$F_{2,9} = 1.83$
FORBS				
	Year	$F_{1,17} = 0.003$	$F_{1,17} = 0.026$	$F_{1,13} = 1.23$
	Vegetation type	**$F_{2,17} = 4.3, p = 0.03$**	$F_{2,17} = 1.46$	**$F_{2,13} = 3.4, p = 0.06$**
	Year:Vegetation type	$F_{2,17} = 0.08$	$F_{2,17} = 0.37$	$F_{2,13} = 1.7$
EVERGREEN SHRUBS				
	Year	**$F_{1,8} = 7.15, p = 0.03$**	**$F_{1,5} = 4.85, p = 0.08$**	**$F_{1,2} = 24.14, p = 0.04$**
	Vegetation type	**$F_{2,9} = 6.44, p = 0.02$**	$F_{2,3} = 0.83$	$F_{2,3} = 0.87$
	Year:Vegetation type	$F_{2,8} = 1.62$	**$F_{2,5} = 19.0, p = 0.004$**	**$F_{1,2} = 14.4, p = 0.07$**
DECIDIOUS SHRUBS				
	Year	$F_{1,9} = 3.0$	$F_{1,9} = 0.56$	$F_{1,7} = 1.1$
	Vegetation type	$F_{2,6} = 3.0$	$F_{2,9} = 1.09$	$F_{2,9} = 2.87$
	Year:Vegetation type	$F_{2,9} = 0.75$	$F_{2,9}= 1.79$	$F_{2,7} = 0.6$

Plant functional change

Community weighted means (CWM) were used to investigate trait change across the vegetation types, and between 2008 and 2021 (Figure 7). There are significant differences in both plant height and LDMC between years, where communities were tallest in willow shrubs, with a mean of 372.1 mm (SE: +/- 52.5) (Tukey HSD p = 0.004), and dwarf shrubs tended to be the shortest, with a mean of 62.7 mm (SE: +/- 5.2) (table 3). LDMC were significantly lower in meadow vegetation compared to dwarf shrubs (Tukey HSD p = 0.005).

There has been a positive trend with increasing community height since 2008, and with communities having individuals with significantly lower LDMC (Tukey HSD p = 0.076).

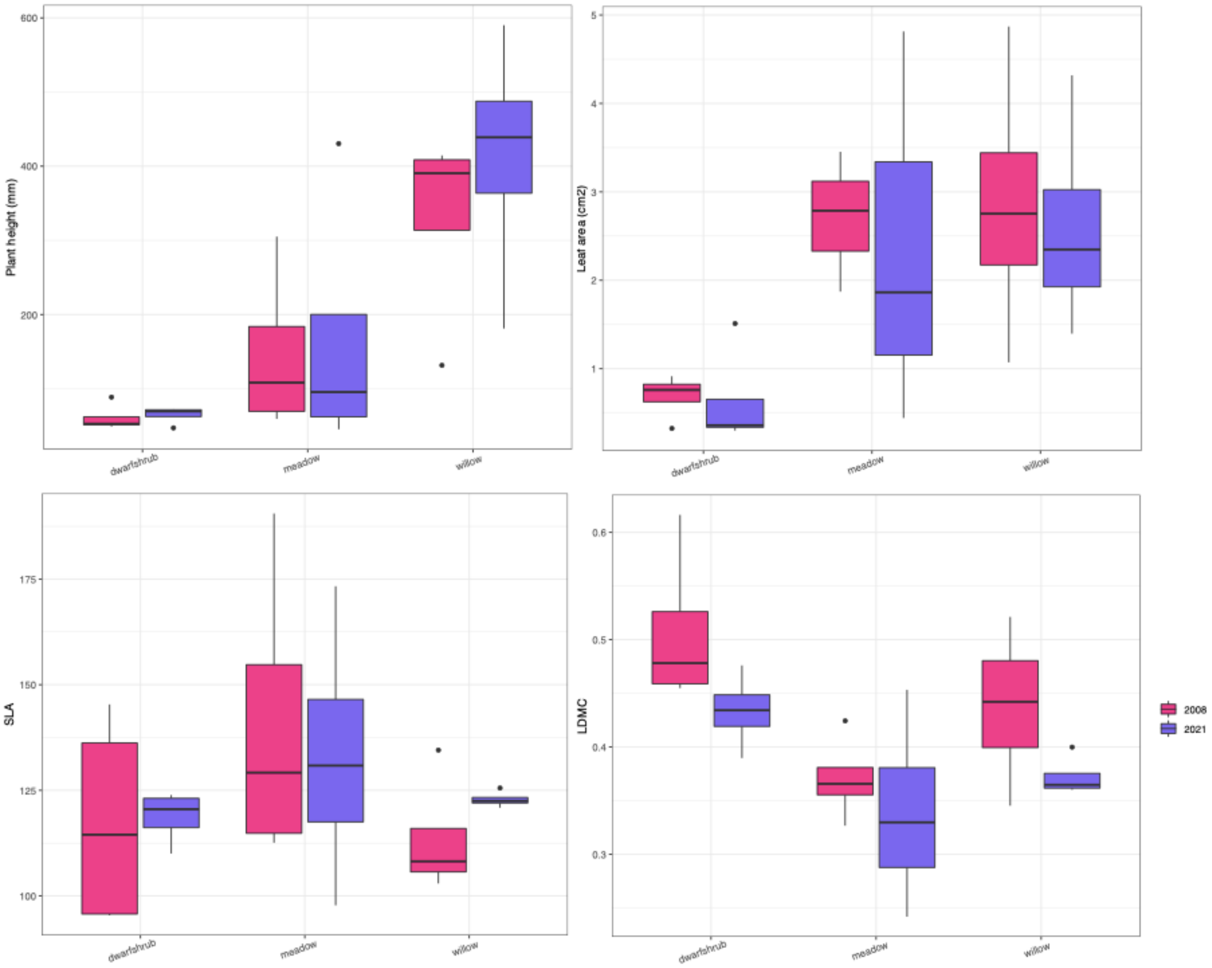

Figure 7*: Four boxplots visualising the community weighted trait means (CWM) (y-axis) for four different traits (plant height - mm, leaf area – cm^2, SLA – cm^2/g, and LDMC), and how they change across vegetation types (x-axis) and between years (pink = 2008, light purple = 2021). Each box represents CWM for four different plots in the vegetation type, divided by four sites (Apostelfjeld, Morenesø, Østerlien, and Lyngmarksfjeld). The replicate for leaf area from the meadow vegetation at Apostelfjeld is removed from the dataset as this plot contained a species, Angelica archangelica, with much larger leaves than the othes species within the same plot. Traits were sampled from vegetation plots in Disko Island, Greenland, in 2008 and 2021.*

Lower LDMC were also significant within both forbs (Tukey HSD p = 0.054) and deciduous shrubs (Tukey HSD p = 0.014) (Appendix 5). SLA within deciduous shrubs has become higher since 2008, while SLA and leaf area in evergreen shrubs have decreased since 2008, but not significantly. Leaf area within deciduous shrubs were smallest within dwarf shrubs (Tukey HSD p = 0.001), with a trend of being largest within willow shrubs.

Table 3: F-values from a linear model explaining community weighted trait means (CWM).
CWM (plant height (mm), leaf area (cm^2), SLA (cm^2/g), and LDMC) across three different vegetation types (dwarf shrubs, meadow vegetation, and willow shrubs), and two different years (2008 and 2021). The model is calculated for CWM for all species within the data set, and within three functional groups: forbs, evergreen shrubs, and deciduous shrubs. P values < 0.1 are considered significant, and are described and highlighted in bold.

		Height (mm)	Leaf area (cm^2)	SLA (cm2/g)	LDMC
ALL SPECIES					
	Year	**$F_{1,9}$ = 4.9, p = 0.05**	$F_{1,9}$ = 0.94	$F_{1,9}$ = 0.03	**$F_{1,9}$ = 6.21, p = 0.03**
	Vegetation type	**$F_{2,9}$ = 6.89**	$F_{2,6}$ = 1.17	$F_{2,6}$ = 1.3	**$F_{2,9}$ = 6.13, p = 0.02**
	Year : Vegetation type	$F_{2,9}$ = 2.11	$F_{2,9}$ = 0.98	$F_{2,9}$ = 0.44	$F_{2,9}$ = 0.31
FORBS					
	Year	$F_{1,17}$ = 1.55	$F_{1,17}$ = 0.93	$F_{1,8}$ = 0.38	**$F_{1,17}$ = 5.44, p = 0.03**
	Vegetation type	$F_{2,17}$ = 2.13	$F_{2,17}$ = 0.96	$F_{2,8}$ = 0.93	**$F_{2,17}$ = 4.89, p = 0.02**
	Year : Vegetation type	**$F_{2,2}$ = 2.93, p = 0.08**	$F_{2,17}$ = 0.92	$F_{2,8}$ = 0.94	$F_{2,17}$ = 0.36
EVERGREEN SHRUBS					
	Year	$F_{1,5}$ = 0.31	**$F_{1,4}$ = 5.07, p = 0.095**	**$F_{1,8}$ = 3.99, p = 0.08**	$F_{1,11}$ = 0.65
	Vegetation type	$F_{2,6}$= 3.36	$F_{2,4}$ = 1.07	$F_{2,10}$ = 1.49	**$F_{2,11}$ = 13.91, p < 0.001**
	Year : Vegetation type	$F_{2,5}$ = 0.23	$F_{2,4}$ = 1.84	$F_{2,8}$ = 1.2	$F_{2,11}$ = 1.1
DECIDIOUS SHRUBS					
	Year	$F_{1,9}$ = 0.77	$F_{1,9}$ = 0.51	**$F_{1,9}$ = 6.86, p = 0.03**	**$F_{1,9}$ = 15.5, p = 0.003**
	Vegetation type	**$F_{2,9}$= 7.06, p = 0.01**	**$F_{2,9}$ = 4.88, p = 0.04**	$F_{2,6}$ = 0.6	**$F_{2,9}$ = 3.6, p = 0.07**
	Year : Vegetation type	$F_{2,9}$ = 1.51	$F_{2,9}$ = 0.11	$F_{2,9}$ = 0.09	$F_{2,9}$ = 0.99

The trait distribution of the community weighted trait means (CWM) are visualised in the MDS-ordination in figure 8. There is a clear clustering of willow shrubs, where plant height has the largest values (Figure 8, A). The dwarf shrubs are also clustered, with a trend of having high LDMC- values. Meadow vegetation is less clustered, but has a small cluster where SLA tends to be higher. Leaf area is highly driven by one observation from meadow vegetation in 2021, which is the meadow vegetation at Apostelfjeld (Figure 8, C).

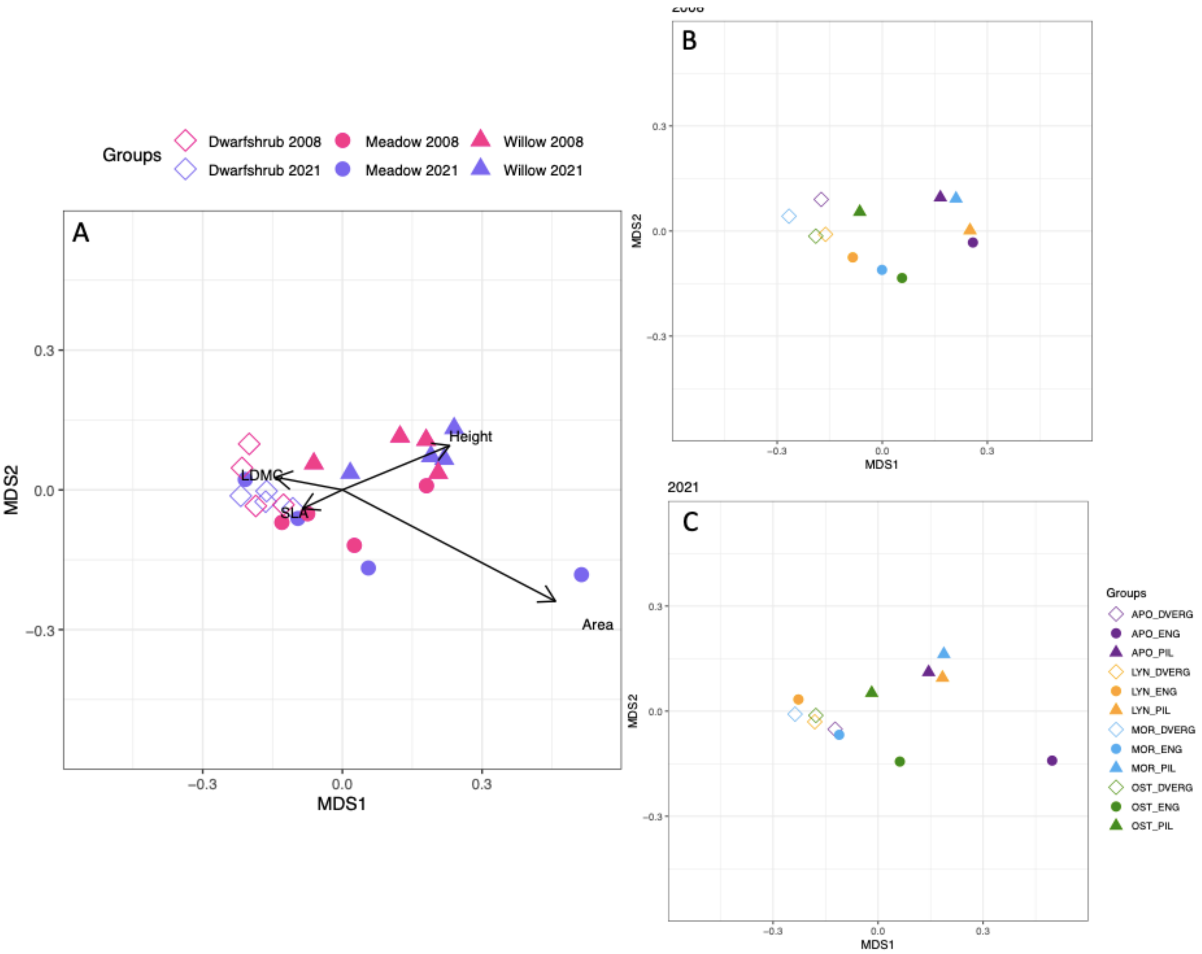

Figure 8: MDS-ordinations visualizing community weighted trait diversity (CWM)

CWM with four different traits (plant height (mm), leaf area (cm^2), SLA (cm^2/g), and LDMC) sampled from three different vegetation types at Disko Island, in 2008 and 2021 respectively. The Bray-Curtis dissimilarity index is used to calculate the distance for the community composition. Vegetation types are illustrated as different shapes (diamonds = dwarf shrubs, dots = meadow vegetation, and triangles = willow shrubs). Plot (A) is visualizing ordination across the three vegetation types, and between the two years (2008 = pink, and 2021 = light purple), and has a stress value = 0.03. Plot (B) and (C) visualize ordination of trait values from 2008 (B) and 2021 (C), where shapes illustrate the vegetation types, and colours illustrates the four sites (purple = Apostelfjeld, yellow = Lyngmarksfjeld, blue = Morenesø, and green = Østerlien). The stress value of plot B = 0.004, and for plot C = 0.0001.

Intraspecific trait variation and species turnover

Intraspecific trait variability has decreased from 2008 to 2021 (Figure 9). Intraspecific variation in 2008 (Figure 9, A) ranged from 17% (leaf area in dwarf shrub vegetation) – 66% (leaf area in willow shrub vegetation) of the total variation. In 2021 (Figure 9, B) the proportion of intraspecific variation ranged from 1% (leaf area in meadow vegetation) – 59%

(height in willow shrub vegetation) of the total variation. Plant height and stem dry matter content (SDMC) were the most plastic traits in 2021.

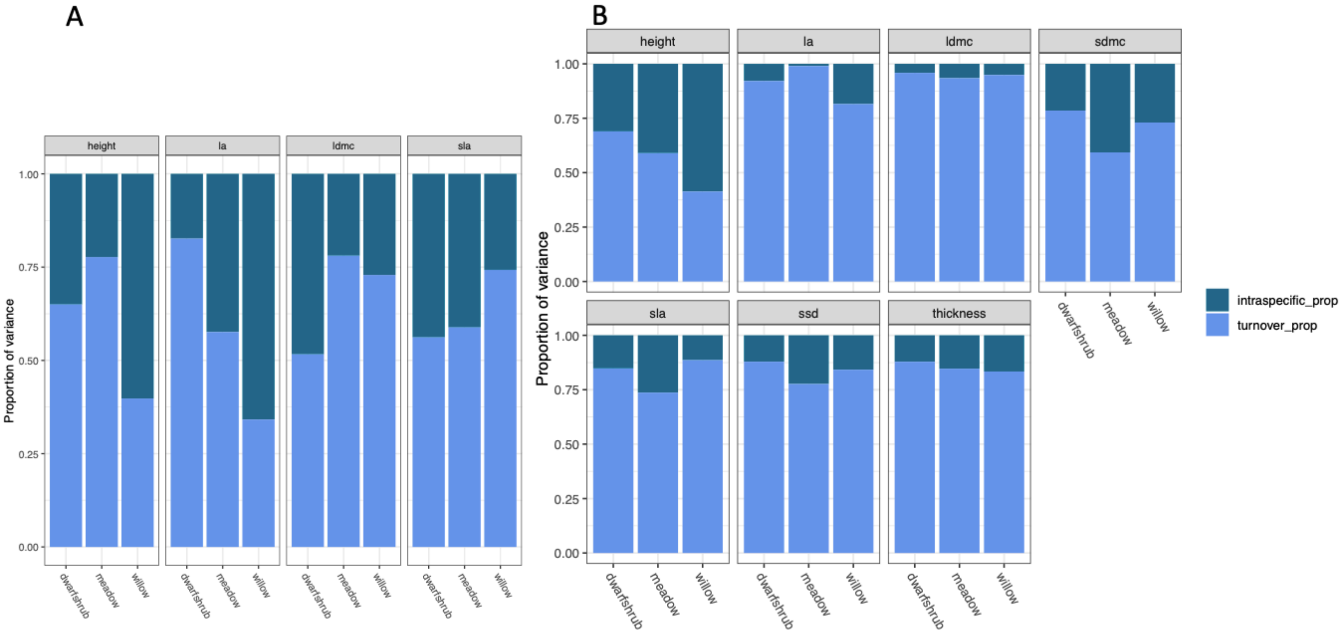

Figure 9: Proportion of trait variance:

Proportion of intraspesific trait variance (dark blue) to interspecific (species turnover) trait variance (light blue) in totally seven different traits (plant height (mm), leaf area (cm^2), SLA (cm^2/g), and LDMC, SDMC, and SSD (g/cm^3)) between three different vegetation types (x-axis: dwarf shrub, meadow, and willow shrub). (A) visualise the proportion of variance of traits measured in 2008, and (B) visualise proportion of variance of traits measured in 2021. All traits were sampled at Disko Island, Greenland.

The distribution of LDMC, leaf area, plant height and SLA within the most common species within each functional group are compared between 2008 and 2021, and visualised in figure 10. There are similar trends between forbs and deciduous shrubs, while evergreen shrub species differs more between the other two. The three deciduous shrubs species (*Vaccinium uliginosum, Salix glauca,* and *Betula nana),* as well as all the forb species (*Pyrola grandiflora*, *Cerastium alpinum*, and *Bistorta vivipara*) have all significantly lower LDMC in 2021 than in 2008 (Figure 10 and table 4), and three of the same species does also have significantly higher SLA in 2021 than 2008 (*Salix glauca, Betula nana* and *Bistorta vivipara).* The evergreen shrub species (*Phyllodoce caerulea, Cerastium alpinum,* and *Cassiope tetragona)* did not have a significant change in LDMC between the two years. Still, the density shows a trend of a narrower LDMC range in 2021 than 2008, and the SLA and leaf area of both *Empetrum hermaphroditum* and *Phyllodoce caerulea* is significantly lower in 2021 than 2008.

Leaf area of the evergreen shrub species are very low and narrow compared to species from the two other functional groups. Especially *Salix glauca, Pyrola grandiflora* and *Bistorta vivipara* have a wider range of leaf size within the individuals, and *Bistorta vivipara* does also have significantly larger leaves in 2021. The range of plant height is widest within deciduous shrubs, and especially within individuals of *Salix glauca*. There is a significant variation between plant height of *Betula nana* in the two years, where the species shows a trend of being taller in 2021 (but Tukey HSD is not significant).

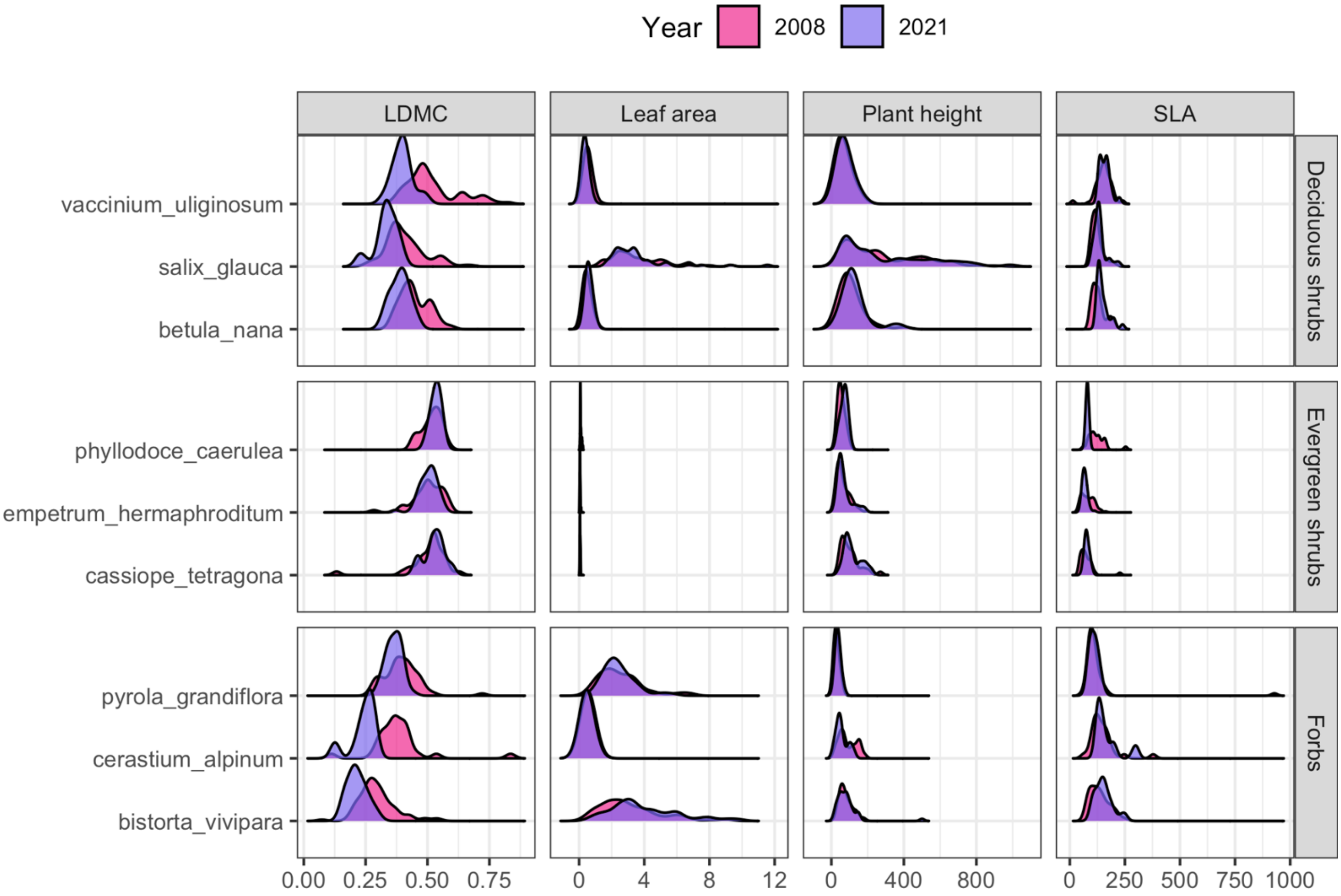

Figure 10: Twelve density plots visualising species trait distribution.
Trait distribution of plant height (mm), leaf area (cm^2), SLA (cm^2/g), and LDMC between 2008 (pink) and 2021 (light purple). The species are divided between deciduous shrubs, evergreen shrubs, and forbs, and traits were sampled in 2008 and 2021 from plant communities at Disko Island, Greenland.

There is also significant variation between the different traits and the vegetation types, where individuals within willow shrubs often have higher or lower trait values than individuals within dwarf shrubs and meadows. Species across the functional groups have the tallest individuals within willow shrubs (table 4 and appendix x). *Bistorta vivipara have significantly highest leaf area within willow* *shrubs (Tukey HDS p < 0.001), and Empetrum hermaphroditum* have significantly lower LDMC within willow shrubs, than in dwarf shrubs and meadows (Tukey HDS p < 0.001).

Table 4: F-values from a linear model explaining variation of trait values.
Trait values are listed for nine different species, and four different traits (plant height (mm), leaf area (cm^2), SLA (cm^2/g), and LDMC) across three different vegetation types (dwarf shrubs, meadow vegetation, and willow shrubs), and two years (2008 and 2021). The nine species are divided by three functional groups which are deciduous shrubs, evergreen shrubs, and forbs. P values < 0.05 are considered significant and are highlighted in bold.

			Height (mm)	**Leaf area (cm^2)**	**SLA (cm2/g)**	**LDMC**
DECIDUOUS SHRUBS						
	Vaccinium uliginosum					
		Year	$F_{1,119} = 3.37$	**$F_{1,119} = 7.78$**	$F_{1,112} = 0.003$	**$F_{1,113} = 67.15$**
		Vegetation type	**$F_{2,7} = 5.38$**	$F_{2,8} = 1.65$	$F_{2,5} = 1.5$	$F_{2,4} = 1.50.31$
		Year:Vegetation type	$F_{2,119} = 1.29$	$F_{2,118} = 1.73$	$F_{2,112} = 2.45$	**$F_{2,113} = 5.34$**
	Salix glauca					
		Year	$F_{1,154} = 1.29$	$F_{1,153} = 0.41$	**$F_{1,152} = 14.89$**	**$F_{1,150} = 110.08$**
		Vegetation type	**$F_{2,9} = 8.9$**	$F_{2,9} = 1.48$	$F_{2,6} = 0.93$	$F_{2,6} = 1.23$
		Year:Vegetation type	$F_{2,154} = 2.57$	$F_{2,153} = 1.18$	$F_{2,152} = 1.6$	$F_{2,150} = 0.98$
	Betula nana					
		Year	**$F_{1,64} = 5.54$**	$F_{1,66} = 2.44$	**$F_{1,65} = 7.06$**	**$F_{1,65} = 19.17$**
		Vegetation type	$F_{2,4} = 5.57$	$F_{2,4} = 5.85$	$F_{2,4} = 0.66$	$F_{2,4} = 0.26$
		Year:Vegetation type	**$F_{2,64} = 10.63$**	**$F_{2,65} = 4.36$**	$F_{2,64} = 0.88$	**$F_{2,65} = 3.37$**
EVERGREEN SHRUBS						
	Phyllodoce caerulea					
		Year	$F_{1,34} = 3.84$	**$F_{1,30} = 10.74$**	**$F_{1,30} = 15.87$**	$F_{1,30} = 1.18$
		Vegetation type	$F_{2,34} = 3.73$	$F_{1,0} = 0.008$	$F_{1,1} = 0.42$	$F_{1,0.04} = 0.87$
		Year:Vegetation type	$F_{2,34} = 0.78$	$F_{1,30} = 2.04$	$F_{1,30} = 2.01$	$F_{1,30} = 0.32$
	Empetrum hermaphroditum					
		Year	$F_{1,122} = 1.78$	**$F_{1,109} = 18.67$**	**$F_{1,101} = 21.9$**	$F_{1,76} = 0.63$
		Vegetation type	**$F_{2,8} = 6.92$**	$F_{2,4} = 1.14$	$F_{2,4} = 4.47$	**$F_{2,86} = 14.75$**
		Year:Vegetation type	$F_{2,121} = 1.32$	**$F_{2,106} = 11.29$**	**$F_{2,100} = 4.66$**	$F_{2,86} = 0.77$
	Cassiope tetragona					
		Year	$F_{1,45} = 3.83$	$F_{1,47} = 3.45$	$F_{1,43} = 0.35$	$F_{1,43} = 0.06$
		Vegetation type	$F_{2,2} = 12.26$	$F_{2,47} = 1.62$	$F_{2,5} = 0.66$	$F_{2,6} = 2.02$
		Year:Vegetation type	$F_{2,45} = 1.0$	$F_{1,47} = 0.005$	$F_{1,43} = 0.03$	$F_{1,43} = 2.02$
FORBS						
	Pyrola grandiflora					
		Year	$F_{1,84} = 1.34$	$F_{1,78} = 2.74$	$F_{1,74} = 0.12$	**$F_{1,71} = 6.5$**
		Vegetation type	**$F_{2,6} = 11.31$**	$F_{2,6} = 1.87$	$F_{2,6} = 0.09$	$F_{2,2} = 1.09$
		Year:Vegetation type	$F_{2,73} = 2.38$	$F_{2,78} = 0.53$	$F_{2,65} = 0.55$	**$F_{2,57} = 5.95$**
	Cerastium alpinum					
		Year	$F_{1,46} = 2.11$	$F_{1,44} = 0.01$	$F_{1,45} = 0.05$	**$F_{1,47} = 25.71$**
		Vegetation type	**$F_{2,44} = 24.7$**	$F_{2,2} = 1.08$	$F_{2,2} = 0.91$	$F_{2,47} = 2.91$
		Year:Vegetation type	$F_{2,46} = 1.75$	**$F_{2,45} = 6.71$**	$F_{2,45} = 0.2$	$F_{2,47} = 0.1$
	Bistorta vivipara					
		Year	$F_{1,136} = 0.73$	**$F_{1,132} = 14.06$**	**$F_{1,126} = 11.65$**	**$F_{1,129} = 84.43$**
		Vegetation type	$F_{2,10} = 3.36$	**$F_{2,9} = 5.8$**	$F_{2,7} = 1.38$	$F_{2,9} = 1.57$
		Year:Vegetation type	**$F_{2,136} = 7.36$**	$F_{2,132} = 2.78$	**$F_{2,126} = 5.29$**	$F_{2,129} = 0.83$

DISCUSSION

Here I demonstrate that rapid warming in low-Arctic environments is changing species composition and plant functionality of tundra plant communities. Increasing temperatures were shown to especially affect dynamics within important functional groups, and cause a shift in functional diversity across communities. Plant communities shifted strategies towards less conservative, and more productive strategies, although there were some differences between forbs and deciduous shrubs, and evergreen shrubs (Perez-Harguindeguy et al., 2016). Trait variability were shown to decrease within species over thirteen years, suggesting that species turnover increases as the Arctic is warming, or that trait variation within species decreases.

Species composition - variation between communities and change through time

Species composition varied clearly across vegetation types. Species richness and diversity tended to be largest within dwarf shrub communities, and lowest in willow shrub communities. Species richness of forbs were highest in meadows, and evergreen shrubs were richest in dwarf shrub vegetation. In contrast, there was yet no significant evidence of deciduous shrubs being richest in willow shrubs. Nevertheless, this might be explained due to several of deciduous shrub species, like *Salix glauca, Betula nana,* and *Vaccinium uliginosum,* being quite common and abundant within all vegetation types.

Changes in composition dynamics through time were only significant within evergreen shrubs, with evidence of species richness increasing in tundra communities due to ambient warming. Shrubs are found to increase in abundance in the Arctic, and it has been suggested that warmer summer months are especially driving this increase (Bjorkman et al., 2020; Elmendorf et al., 2012; Myers-Smith et al., 2011). Still, evergreen shrubs did also become less even and less diverse as response to warming, suggesting that some species within this functional group has become more dominating than others.

Changes in plant functionality

As expected, due to the dominance of *Salix glauca* within the willow shrubs, these were the significantly tallest plant communities between the three vegetation types. The dwarf shrub vegetations were the shortest vegetation type, which can be explained by one of the meadow vegetation plots having very tall vegetation compared to the other three.

Warming caused a shift in the distribution of traits towards communities with taller plants and less conservative individuals with lower LDMC. Although not significant, the communities did also get higher SLA. These are similar trends that has been predicted in temperature-trait relationships in other studies, indicating that the plants invest more in production and less in protective strategies, as they experience a higher access to resources and are less exposed to harsh conditions in a warmer environment (Bjorkman et al., 2018; Perez-Harguindeguy et al., 2016).

I found that there also were significant trends of change in plant functionality within functional groups as response to warming. Forbs and deciduous shrubs had similar trends as measured on the community level, where LDMC decreased. Deciduous shrubs had in addition a significant increase in SLA. The evergreen shrubs had opposite patterns, with a trend of increasing LDMC, and decreasing SLA. As evergreens were the richest functional group within the dwarf shrub vegetations, this explain why LDMC-values were highest within dwarf shrub communities.

It has been suggested that functional groups better explain differences in resource-economic traits, such as LDMC and SLA, than size-related traits, such as plant height and leaf area (Thomas et al., 2019). These allegations are somewhat in line with findings from this study, but still, this study also reveals trends of decreasing leaf area within evergreen shrubs, as well as significant variation in both plant height and leaf area across vegetation types.

Trait variability within and across species

The intraspecific variability decreased over the thirteen years, in which can be explained by two reasons; (1) warming in an arctic ecosystem has increased changes in species composition (species turnover), and/or; (2) warming of the Arctic results in a larger abundance of individuals with narrower trait ranges (decrease in genotypic plasticity). Intensification of shrub expansion due to increasing temperatures is expected to amplify species turnover, and both species turnover and decreasing plasticity increases the risk of local extinction in a changing environment (Mod & Luoto, 2016).

Plant height and leaf dry matter content were the two traits from 2021 with highest proportion of intraspecific variability. The range of plant height variation within species suggest that especially evergreen shrubs have a narrow trait range, and the fact that they have increased in species richness, suggests that trait variability might be due to species turnover. The deciduous shrubs, and especially *Salix glauca*, has a much wider trait range, where willow shrubs, highly dominated by this species, has over 50% of the trait variation within species. This study therefore suggests that deciduous shrubs are more tolerant to ambient warming, and has an advantage of having a wide plant height range in the competition for light between individuals (Mekonnen et al., 2021; Perez-Harguindeguy et al., 2016).

Consequences of shifts in community composition and trait distribution in an Arctic environment

Shifts in community composition and functionality in Arctic vegetation, like increasing abundance of shrubs and increasing community plant height, will contribute to a change of tundra ecosystem dynamics (Callaghan et al., 2004; Myers-Smith & Hik, 2013). Taller shrubs for example, can trap snow, and thereby insulate and heat local soils (Callaghan et al., 2004). Studies have found that the most expanding shrub species through the Arctic are tall deciduous shrubs, like *Salix glauca* and *Betula nana*, and observations from my study found that deciduous shrub were quite abundant in all communities (Elmendorf et al., 2012; Mekonnen et al., 2021). There is evidence that increasing shrub biomass in the Arctic leads to slow decomposition of litter, as much of carbon is allocated to woody stems in shrubs (DeMarco, Mack, & Bret-Harte, 2014; Hobbie, 1996). This study also found that evergreens became more species rich, at least in dwarf shrub vegetation, and abundance of evergreen shrubs are also assumed to increase with temperature (Vowles & Björk, 2019). As LDMC of evergreen shrubs tended to increase, this would also support slow litter decomposition rates

(Perez-Harguindeguy et al., 2016). Yet, LDMC at the community level, as well as within forbs and deciduous shrubs, decreased through time, with significance. Low LDMC are often related to high decomposition rates and growth rates, and deciduous shrubs has higher quantity of litter than evergreen shrubs (Perez-Harguindeguy et al., 2016). These findings therefore emphasise the complexity of predicted vegetation responses, like future carbon and nutrient flows of changing ecosystems.

Study limitations

This study has some limitations that should be accounted for. The methods in 2008 was conducted a bit differently than in 2021, like the species composition analysis. This has perhaps resulted in small sources of errors when calculating species abundances between the two years. Also, as graminoids were not included in the vegetation and trait analysis in 2008, it was not possible to include this highly important functional group in the study. Still, both graminoids and pteridophytes were included in the analysis of 2021, giving future research a possibility to investigate these groups as well.

Climate data from this study had a larger gap of missing observations, making the regression slope less reliable. Although temperature showed an expected trend, precipitation and humidity did not (Box et al., 2019). Still, local conditions do occur, which may not be similar to expected observations. Also, the years from 2011-2021 were colder than the years from 1998-2008 on average, and it is important to keep in mind that the overall temperatures in the Arctic are increasing, and that there is a delay in plant reaction time to environmental change.

Lastly, this study did not account for other abiotic conditions than background climate change. An increasing number of studies has for instance documented the importance of local soil water availabilities and the responses in species richness, species diversity and shrub encroachments in tundra plant communities to climate change (Bjorkman et al., 2018; Myers-Smith et al., 2011; Nabe-Nielsen et al., 2017). This suggests that future investigations of vegetational response to climate change should also account for local soil water conditions.

Concluding remarks

Observations from this study provides additional reasons for assuming that climate warming are likely to shape and alter ecosystem functions in tundra plant communities in the Arctic. Plant communities in low Arctic environments has experienced climate warming through the past six decades. This study suggests that background warming has been driving changes in the species composition, as well as shifts in trait distribution in low-Arctic plant communities, with profound effects within important functional groups (deciduous shrubs, evergreen shrubs, and forbs). Species community composition did only change significantly within evergreen shrubs through time, with increasing species richness, and decreasing species diversity and evenness as response to warming. Plant functionality was observed to respond to warming at both the community level as well as within different functional groups, where communities has shifted towards more productive strategies. Trait variability within species has shown to decrease with warming, where plant height within willow shrubs had highest variability within species.

This study has found that low-arctic tundra communities are experiencing changes due to climate warming, and emphasises the importance of investigating plant functional groups in the study of plant ecosystem responses to climate change.

Future studies should consider to include soil moisture conditions to better explain the driving factors of plant responses, and also investigate other functional groups, like graminoids, pteridophytes, mosses and lichens to get a broader picture of species interactions in the communities.

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APPENDIX

APPENDIX 1

Table I: Overview of plot coordinates at Disko Island, Greenland.

Plot		Coordinates			
Site	Vegetation type	N°	N	W°	W
Apostelfjeld	Willow	69	15.912	53	33.892
Apostelfjeld	Dwarfshrub	69	15.903	53	33.872
Apostelfjeld	Meadow	69	15.915	53	34.075
Lyngmarksfjeld	Willow	69	15.629	53	32.508
Lyngmarksfjeld	Dwarfshrub	69	15.616	53	32.288
Lyngmarksfjeld	Meadow	69	15.405	53	31.478
Østerlien	Willow	69	15.307	53	30.939
Østerlien	Dwarfshrub	69	15.328	53	30.947
Østerlien	Meadow	69	15.199	53	30.874
Morenesø	Willow	69	16.104	53	27.809
Morenesø	Dwarfshrub	69	16.049	53	27.589
Morenesø	Meadow	69	15.166	53	30.764

APPENDIX 2

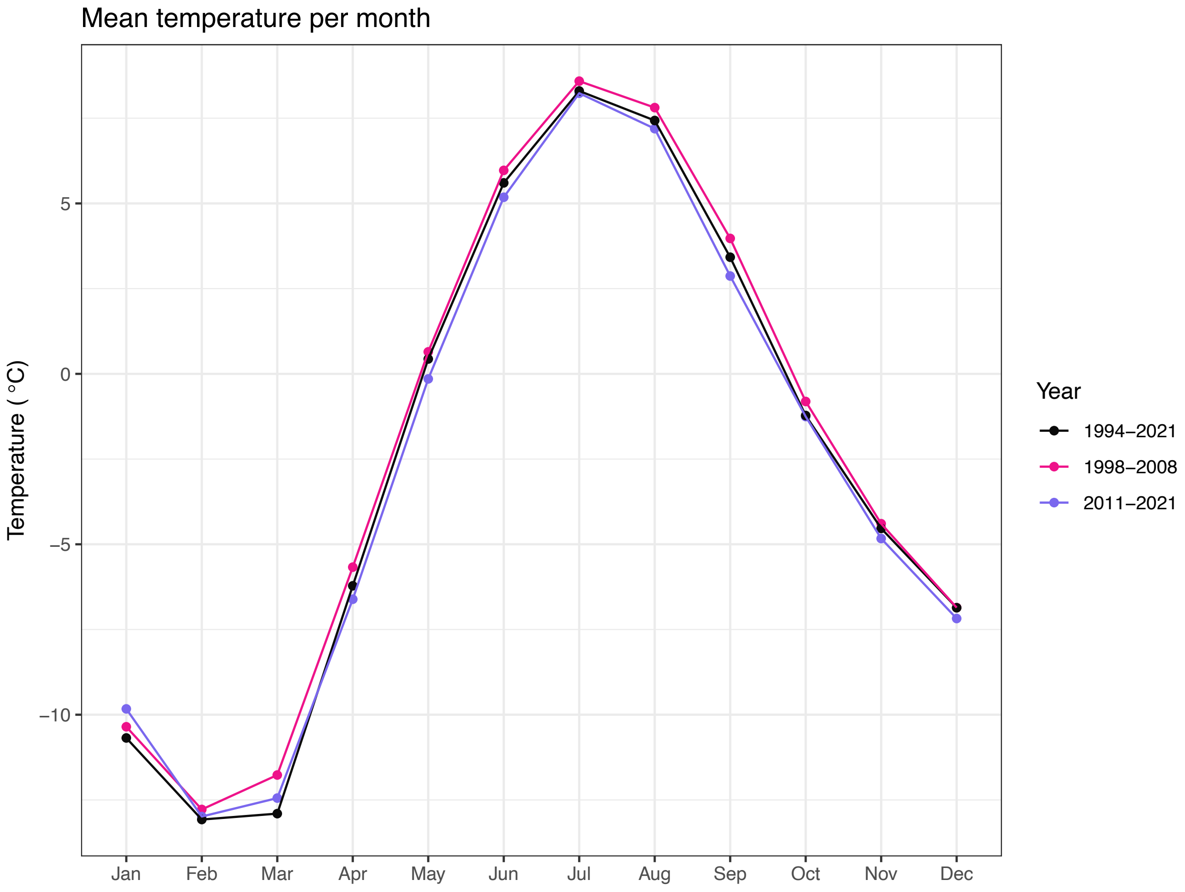

Figure I: Monthly average temperatures (°C) measured from Arctic station, from 1994 – 2021. *Black line = climate normal from 1994 – 2021, pink line = climate normal from 1998 – 2008, and light purple line = climate normal from 2011 – 2021.*

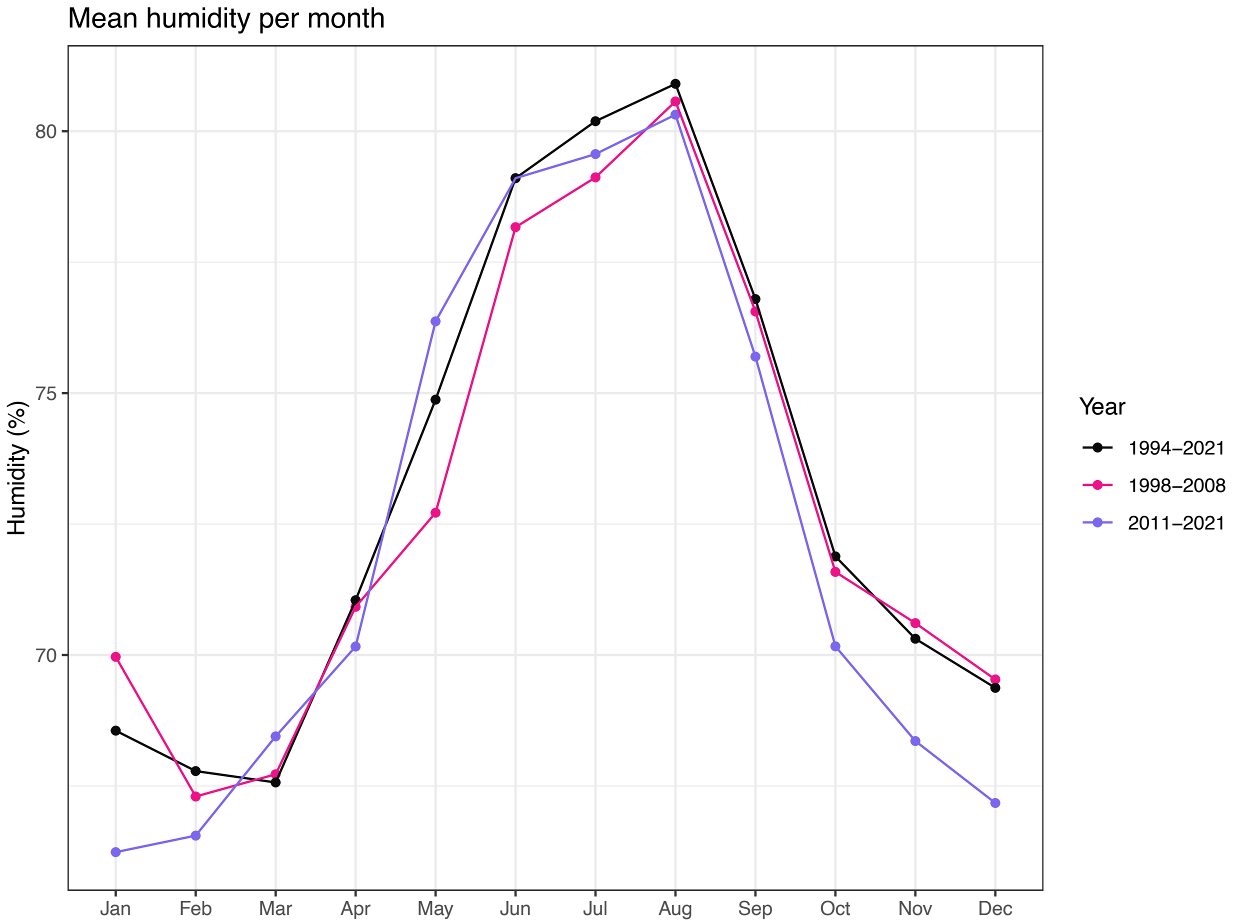

Figure II: Monthly average relative humidity (%) measured from Arctic station, from 1994 – 2021. *Black line = climate normal from 1994 – 2021, pink line = climate normal from 1998 – 2008, and light purple line = climate normal from 2011 – 2021.*

APPENDIX 3

Table II: Species table from 2008

Table explaining the number of individuals per species that were collected and measured from each plot in 2008. Blanc cells means that the species was not present inside the plot.
(Codes are explaning the plots:
Sites: apo = Apostelfjeld, lyn = Lyngmarksfjeld, mor = Morenesø, ost = Østerlien,
Vegetation types: dverg = dwarf shrub, pil = willow shrub, eng = meadow)

species_name	apo_dverg	apo_eng	apo_pil	lyn_dverg	lyn_eng	lyn_pil	mor_dverg	mor_eng	mor_pil	ost_dverg	ost_eng	ost_pil
alchemilla_glomerulans					10						10	
angelica_archangelica		10										
arnica_angustifolia											10	
bartsia_alpina										10		
betula_nana				10			10	10	4	10		
bistorta_vivipara	10		7	10	10	10	10	10	10	10	10	8
cassiope_tetragona	7						10		10	6		
cerastium_alpinum	10		10					5				4
chamaenerion_angustifolium											10	
diapensia_lapponica										3		
dryas_integrifolia			9							10		
empetrum_nigrum_hermaphroditum	10		10	10	10	8	10		10	10		10
epilobium_sp.		10										
erigeron_humilis					3							
gnaphalium_norvegicum											10	
pedicularis_flammea	2				10			10				4
pedicularis_hirsuta	10					10	3	10				3
pedicularis_lapponica				4			5					
phyllodoce_caerulea				10	10					6		
pyrola_grandiflora	10			10			10	10		9		10
pyrola_minor			10						10			
rhododendron_tomentosum							3					
salix_glauca	10	10	10	10	10	10	10	10	10	10	10	10
salix_herbacea					10							
saxifraga_tricuspidata			10							7		
sibbaldia_procumbens		10			10						10	
silene_acaulis										4		
stellaria_longipes			10									10
taraxacum_sp.		1	1		10						10	
thalictrum_alpinum					10							
tofeldia_pusilla					5					10		
vaccinium_uliginosum	10		10	10	10	6	10	5	10	10		11

Table III: Species table from 2021 (Next page)

Table explaining the number of individuals per species that were collected and measured from each plot in 2021. Blanc cells means that the species was not present inside the plot.

(Codes are explaning the plots:
Sites: apo = Apostelfjeld, lyn = Lyngmarksfjeld, mor = Morenesø, ost = Østerlien,
Vegetation types: dverg = dwarf shrub, pil = willow shrub, eng = meadow)

Species	**LYN_MEA**	**LYN_DWA**	**LYN_WIL**	**APO_DWA**	**APO_WIL**	**APO_MEA**	**OST_DWA**	**OST_WIL**	**OST_MEA**	**MOR_DWA**	**MOR_WIL**	**MOR_MEA**
alchemilla_glomerulans	4					4			4			
angelica_archangelica						4						
arnica_angustifolium									1			
arnica_sp.									3			
bartsia_alpina							2	4				
betula_nana	4	4					4	4		4	4	4
bistorta_vivipara	4	4	4	4	3	1	4	4	4	4	4	4
campanula_giesckiana					1							
campanula_uniflora										3		
carex_bicolor										4		
carex_bigelowii	4	4						4	4			4
carex_nigra											4	
cassiope_tetragona	4			4			4			4	4	NA
cerastium_alpinum				4	3	1		4	4	4		4
diapensia_lapponica										4		
diphasiastrum_alpinum	4											
draba_sp.				4								
dryas_integrifolia							4			3		
empetrum_hermaphroditum	4	4	4	4	4		4	4		4	4	8
epilobium_angustifolium									8			
epilobium_hornemannii						4						
equisetum_arvense	4		4	4	4	4	4	4	4	4	4	4
erigeron_humilis	4											
euphrasia_alpina								2				
euphrasia_frigida								2				
fern									3			
gnaphalium_norvegicum									5			
gnaphalium_supina	4											
harimanella_hypnoides	4	4										
huperzia_selago	4						2			1		
juncus_trifidus							4					
luzula_confusa				3								
luzula_multiflora		4		4			4	1		4		
luzula_parviflora					4						4	
lycopodium_annotinum		4			4			4				
pedicularis_flammea	4			2				2				4
pedicularis_groenlandica										4		
pedicularis_hirsuta	1			2				1				3
pedicularis_lanata				3								
pedicularis_lapponica		4		3						4		
phyllodoce_caerulea	4	4					4					
poa_alpina					4		4	4	4			
poa_arctica	4				5				4	3		
poa_nemoralis						4						
poa_pratensis				4				4				4
potentilla_sp.									4			
pyrola_grandiflora		4	4	4	4		4	4		4	4	4
pyrola_minor			4								4	
rhododendron_lapponicum										4		
sagina_sp.										1		
salix_glauca	4	4	4	4	4	4	4	4	6	4	5	4
salix_herbacea	4	4		4				4	4			
saxifraga_tricuspidata							4					
sibbaldia_procumbens	4								4			
silene_acaulis										1		
stellaria_longipes				4	1			3		2	4	4
taraxacum_sp.	4					4			4			
thalictrum_alpinum											4	
tofeldia_pusilla	4						4					
trisetum_spicatum	5				4		3	3				
vaccinium_uliginosum	4	4	4	4	4		4	4		4	4	4
veronica_alpina	5					4			1			

APPENDIX 4

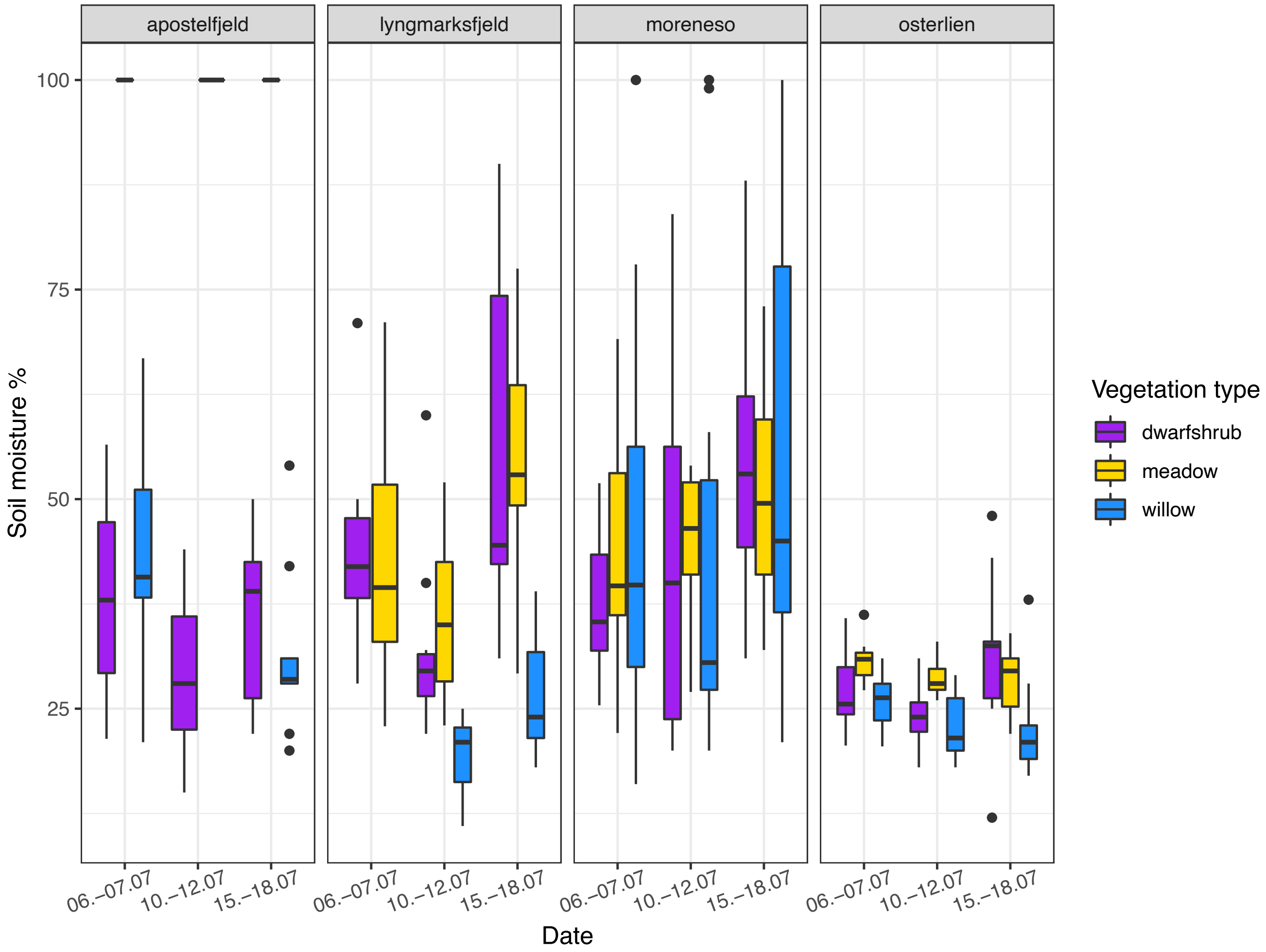

Figure III: Soil moisture measurements from study plots at Disko Island, Greenland.
Visualisation of soil moisture values (%) across vegetation types (purple = dwarf shrub vegetation, yellow = meadow vegetation, and blue = willow vegetation) and sites (Apostelfjeld, Lyngmarksfjeld, Morenesø, and Østerlien) during the study period in July 2021. Each vegetation type within each site is measured once per measuring period (06/07 – 07.07, 10/07 – 12/07, and 15/07-18/07), and each box represents the 10 observations distributed in the plot.

APPENDIX 5

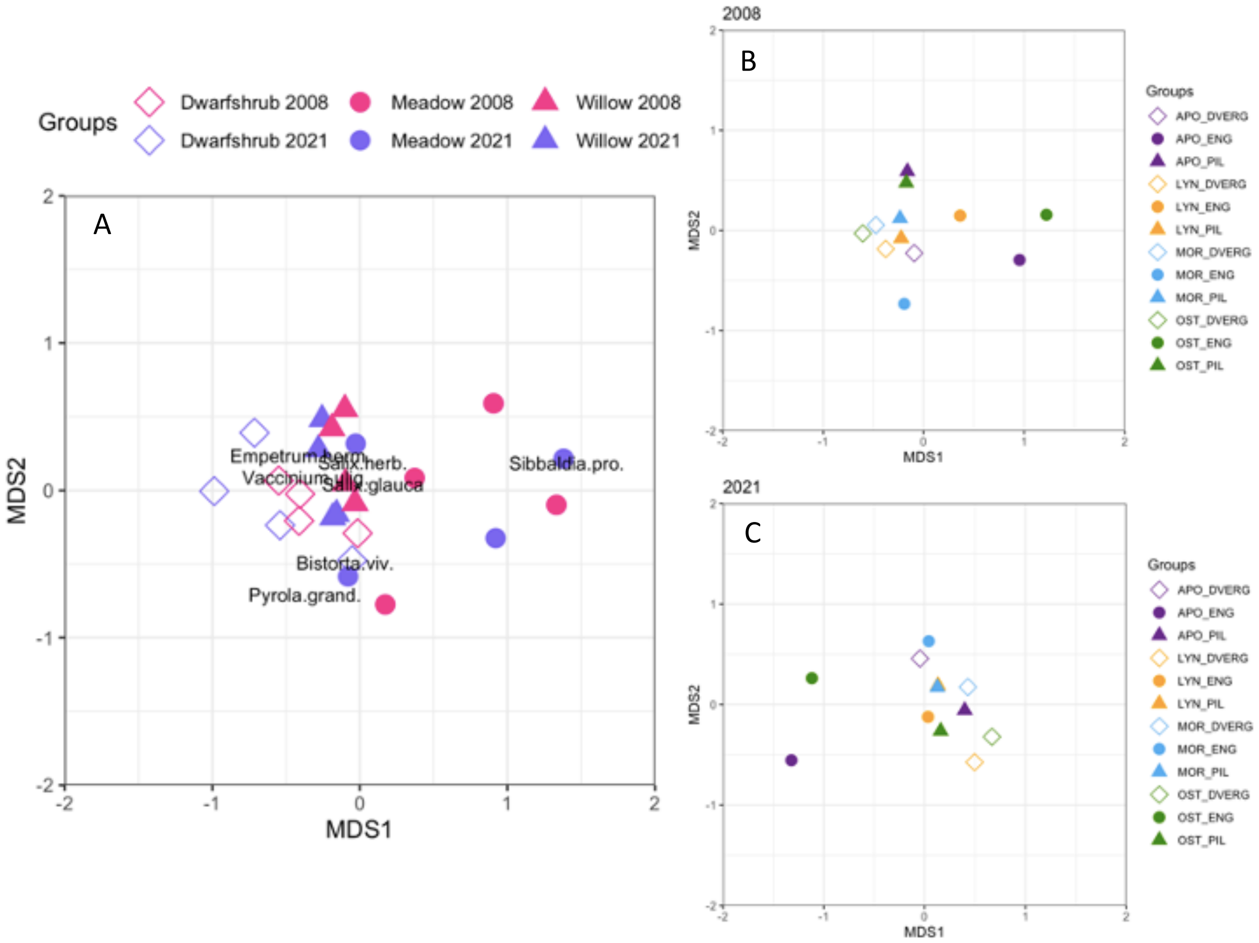

Figure IV: MDS-ordinations visualising presence of species.

The species were sampled from species proportions in the vegetation analysis conducted in three vegetation types at Disko Island, in 2008 and 2021 respectively. The Bray-Curtis dissimilarity index is used to calculate the distance for the community composition. Vegetation types are illustrated as different shapes (diamonds = dwarf shrubs, dots = meadow vegetation, and triangles = willow shrubs). Plot (A) is visualizing ordination across the three vegetation types, and between the two years (2008 = pink, and 2021 = light purple), and has a stress value = 0.13. Plot (B) and (C) visualize ordination from the vegetation analysis conducted in 2008 (B) and 2021 (C), where shapes illustrate the vegetation types, and colours illustrates the four sites (purple = Apostelfjeld, yellow = Lyngmarksfjeld, blue = Morenesø, and green = Østerlien). The stress value of plot B = 0.11, and stress value for plot C =0.08.

APPENDIX 6

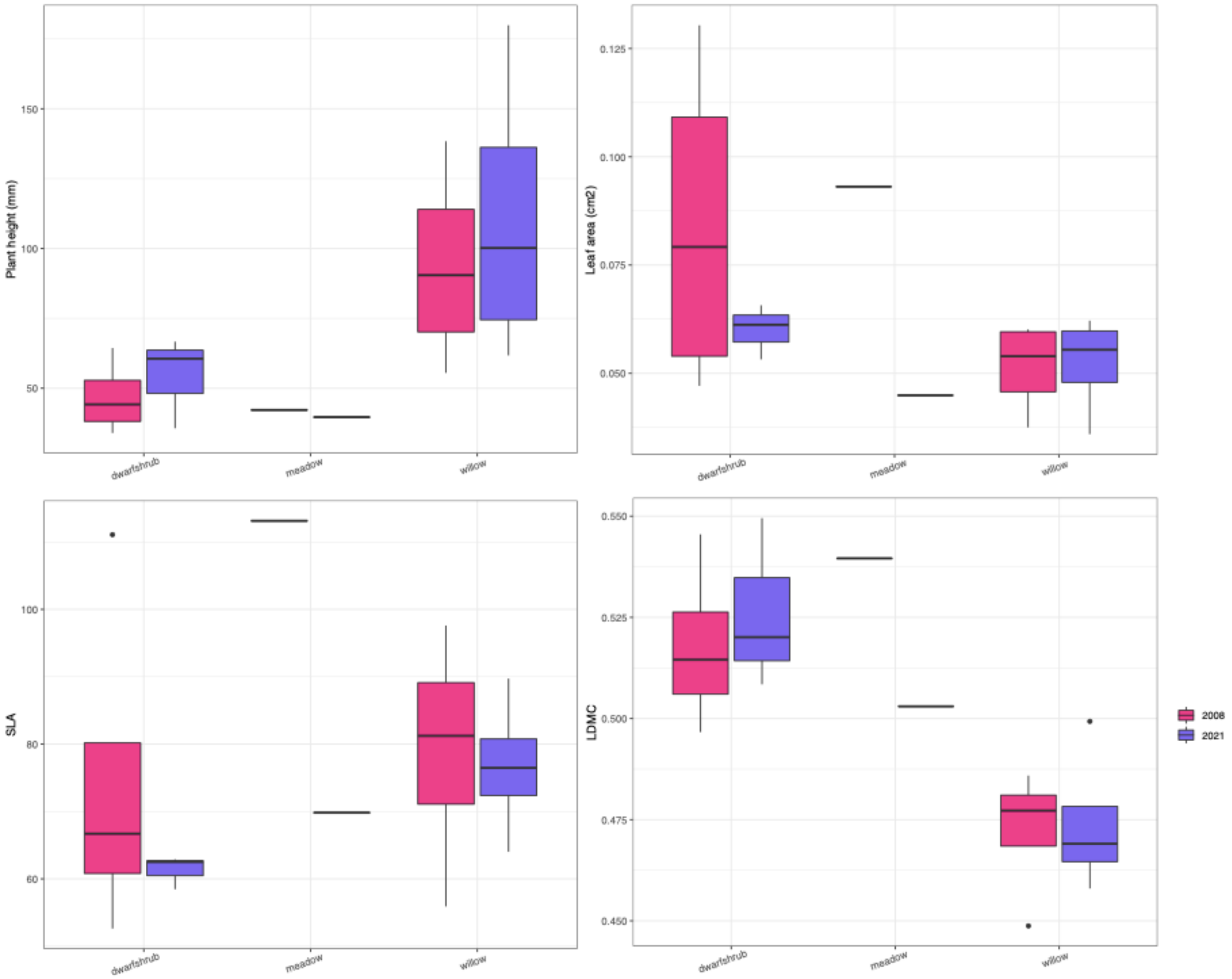

Figure V: Community weighted trait means within evergreen shrubs.

Four boxplots visualising the community weighted trait means (CWM) (y-axis) for four different traits (plant height - mm, leaf area – cm^2, SLA – cm^2/g, and LDMC), and how they change across vegetation types (x-axis) and between years (pink = 2008, light purple = 2021). Each box represents CWM for four different plots in the vegetation type, divided by four sites (Apostelfjeld, Morenesø, Østerlien, and Lyngmarksfjeld). The replicate for leaf area from the meadow vegetation at Apostelfjeld is removed from the dataset as this plot contained a species, Angelica archangelica, with much larger leaves than the othes species within the same plot. Traits were sampled from vegetation plots in Disko Island, Greenland, in 2008 and 2021.

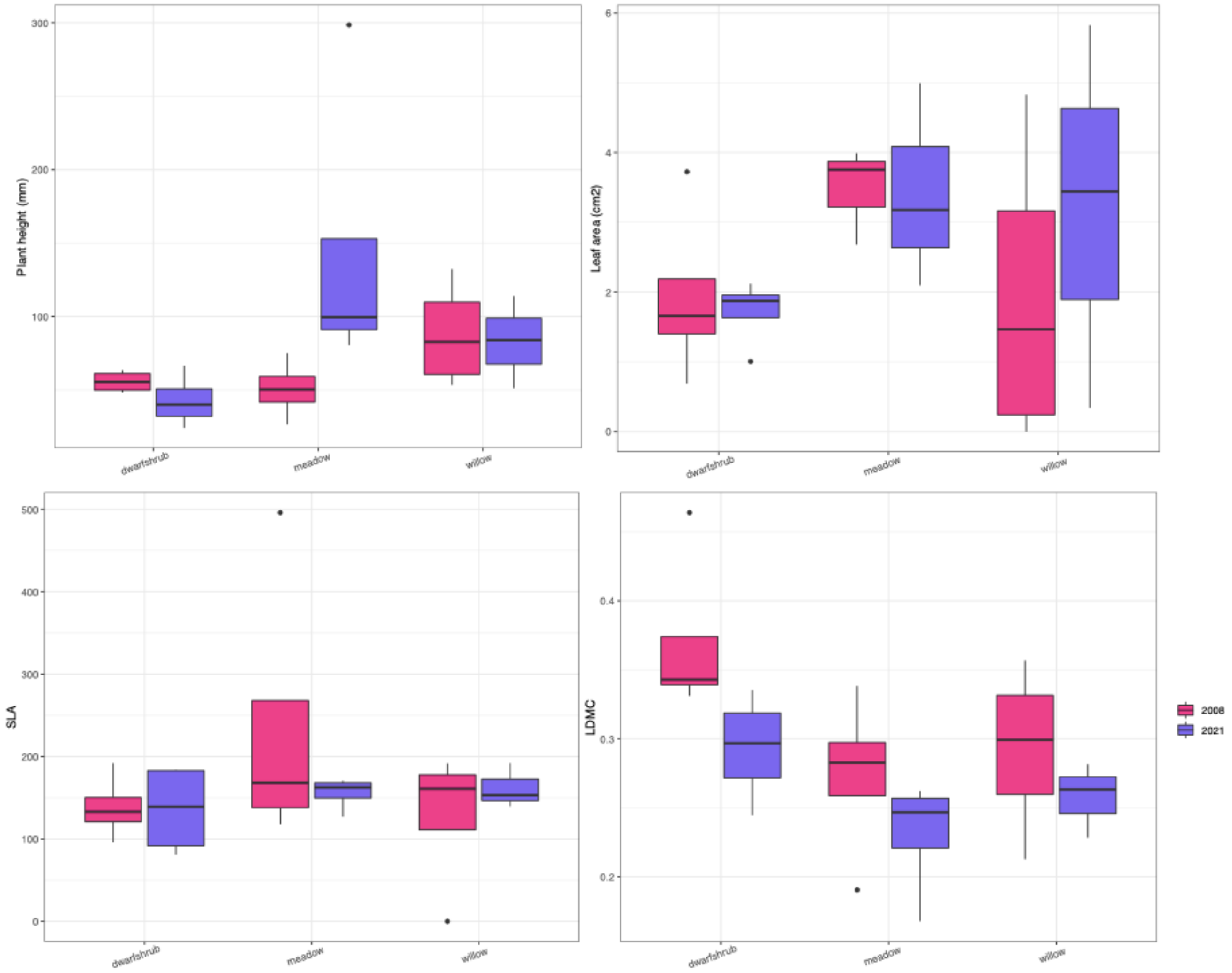

Figure VI: Community weighted trait means within forbs.

Four boxplots visualising the community weighted trait means (CWM) (y-axis) for four different traits (plant height - mm, leaf area – cm^2, SLA – cm^2/g, and LDMC), and how they change across vegetation types (x-axis) and between years (pink = 2008, light purple = 2021). Each box represents CWM for four different plots in the vegetation type, divided by four sites (Apostelfjeld, Morenesø, Østerlien, and Lyngmarksfjeld). The replicate for leaf area from the meadow vegetation at Apostelfjeld is removed from the dataset as this plot contained a species, Angelica archangelica, with much larger leaves than the othes species within the same plot. Traits were sampled from vegetation plots in Disko Island, Greenland, in 2008 and 2021.

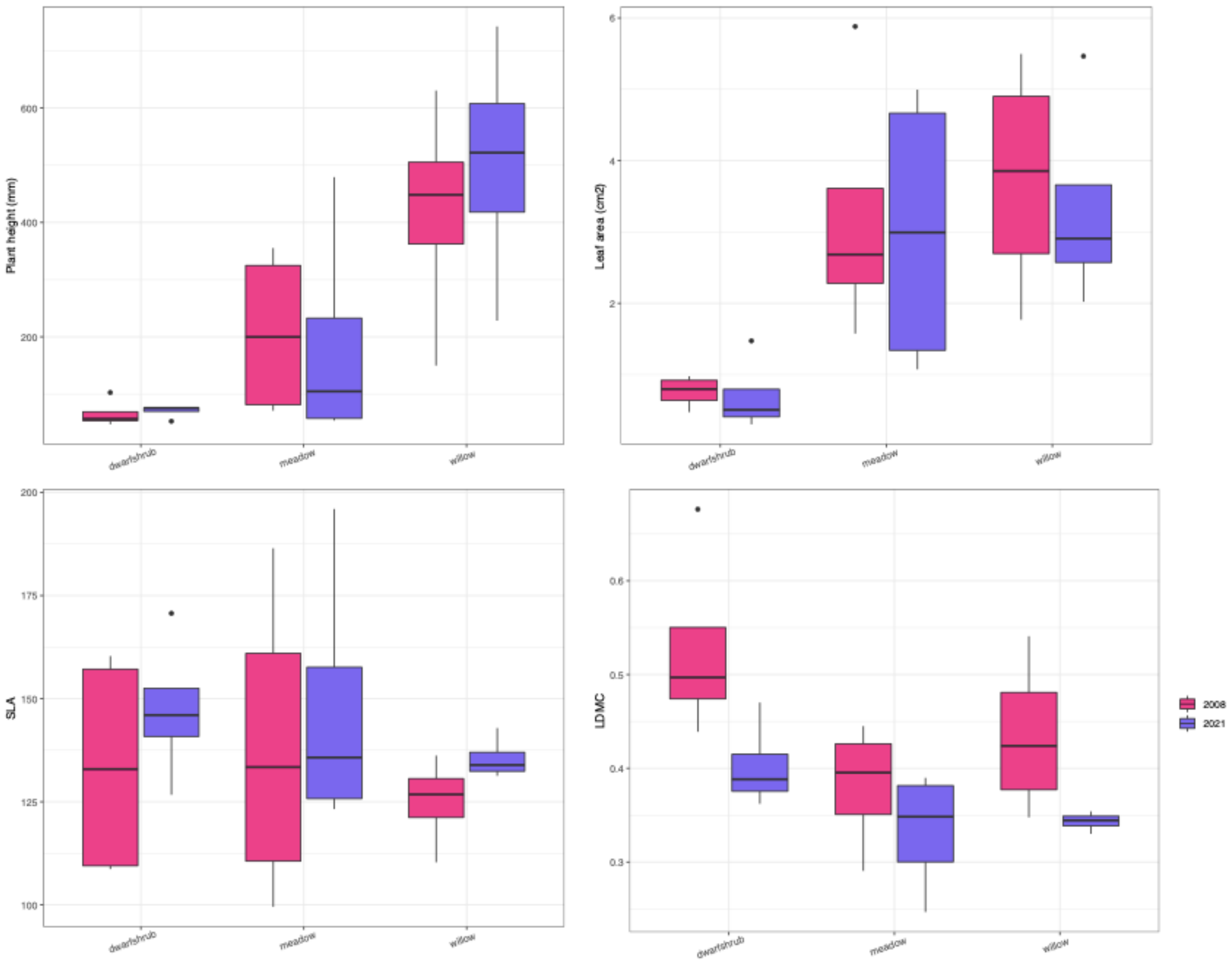

Figure VII: Community weighted trait means within deciduous shrubs.

Four boxplots visualising the community weighted trait means (CWM) (y-axis) for four different traits (plant height - mm, leaf area – cm^2, SLA – cm^2/g, and LDMC), and how they change across vegetation types (x-axis) and between years (pink = 2008, light purple = 2021). Each box represents CWM for four different plots in the vegetation type, divided by four sites (Apostelfjeld, Morenesø, Østerlien, and Lyngmarksfjeld). The replicate for leaf area from the meadow vegetation at Apostelfjeld is removed from the dataset as this plot contained a species, Angelica archangelica, with much larger leaves than the othes species within the same plot. Traits were sampled from vegetation plots in Disko Island, Greenland, in 2008 and 2021.