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Drivers of decadal vegetation change in Northern Alaska Jacob Allen Harris

A Thesis Submitted to the Graduate Faculty of GRAND VALLEY STATE UNIVERSITY

In

Partial Fulfillment of the Requirements

For the Degree of

Master of Science

Biology

December 2020

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Abstract

The Arctic is experiencing rapid climate change. This research documents vegetation change near Atqasuk and Utqiagvik, Alaska. At each location, 30 plots distributed in a matrix across the landscape, were sampled annually from 2010 to 2019 using a point frame. For every encounter we recorded the height and classified it into eight broad functional groups (deciduous shrubs, evergreen shrubs, forbs, graminoids, bryophytes, lichens, litter and standing dead vegetation); for vascular plants we also identified the species. We found a consistent increase in plant stature and cover over time which was dramatic at Atqasuk. Graminoid cover and height increased at both sites. At Atqasuk shrub and forb cover and height increased. Species diversity decreased at both sites. Year was generally the strongest predictor of vegetation change suggesting a cumulative change over time; however, soil moisture and soil temperature were also predictors of vegetation change in many cases. We anticipate plants in the region will continue to grow taller as the region warms resulting in further increases in plant cover, especially graminoids. The accumulation of litter will likely result in a decline of bryophytes and lichens. These changes in community structure will impact energy balance and carbon cycling and habitat quality for wildlife and therefore have regional and global consequences.

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Chapter I

Introduction

Climate change is a well-documented phenomenon which is altering the world's ecosystems. Temperatures around the world may increase by as much as about 5°C over the next 100 years (IPCC 2013). High latitude regions may expect at least twice the rate of warming as lower latitude regions (AMAP 2019). The Arctic region will experience increases in annual soil thawing, increases in the growing season length, changing range distributions of plants and animals, and further declines in sea ice. It is expected that climate related changes in the Arctic will have global consequences. Warming temperatures, which may hasten decomposition rates and release large amounts of carbon dioxide and methane into the atmosphere, will amplify the greenhouse effect and elicit further warming (Chapin et al. 2000; Aerts 2006). Warming temperatures would also likely reduce the snow and ice cover of the Arctic, reducing the reflection of photosynthetic radiation reflected off the Earth's surface as albedo (Chapin et al. 2005). Because Arctic vegetation affects these processes it is important to understand what changes are occurring throughout Arctic plant communities. In addition, changes in the life cycle timing of plants including leaf, flower, and fruit growth will have implications for herbivores (Post and Forchhammer 2008).

Several organizations such as the International Tundra Experiment (ITEX) and the Arctic Observatory Network (AON) have formed research networks to study ecological change associated with a warming world. These organizations study environmental changes in Arctic and alpine regions such as carbon flux, snow level manipulation, and air temperature warming. A collaborative project known as the ITEX-AON was funded by the National Science Foundation (NSF) to monitor terrestrial ecosystem change in Arctic Alaska. The project monitors sites at

Atqasuk, Imnavait Creek, Toolik Lake, and Utqiaʻgvik, Alaska. Universities involved in this project include Grand Valley State University (GVSU), Florida International University (FIU), University of Texas at El Paso (UTEP), and University of Alaska Anchorage (UAA). The goals of the ITEX-AON project include understanding the drivers of long-term ecological change including especially the effects of warming over long timer periods.

This thesis is funded through the ITEX-AON project and aimed to document changes within plant communities at Atqasuk and Utqiagvik, Alaska. The thesis includes nine years of data from both sites. This research builds upon previous research performed in Utqiagvik (Botting 2015), which primarily found notable changes in standing dead plant material cover over time as well as strong relationships between soil temperature and the cover of cover of forbs, graminoids, litter, and standing dead. This thesis takes into consideration other documented trends in vegetation change occurring across the tundra biome (Elmendorf et al. 2015; and Hollister 2015).

Purpose

The purpose of this thesis is to increase our understanding of the environmental drivers of change on plant communities in Northern Alaska. This thesis quantifies changes in plant height, cover, and diversity over time and explores their relationships to environmental variables including time expressed as years. This thesis examines broad functional groups and abundant species at sites in both Atqasuk and Utqiagʻvik. The overall goal of this thesis is to better determine what the most important drivers of vegetative change are at either site.

Scope

This thesis focuses on tundra plant communities in both the Low Arctic and High Arctic in Atgasuk and Utqiagvik, respectively. Results from this study are applicable to other tundra

sites across the Arctic, even on other continents. The results from this study are also valuable to villages and other communities across the Arctic in so far as this study is documenting changes that are occurring and is intended to provide insights into how their environment may change in the near future.

Assumptions

It is assumed that between the two study regions there are differences in environmental variables and that they are the drivers of change in the plant community metrics of cover, height, and diversity. It is also assumed that the sample size of thirty plots over nine years of sampling is adequate and represents the sites. Lastly, it is assumed that the best predictive models from this study will indicate which abiotic factors are likely responsible for driving change at the community level.

Hypotheses

Chapter II examines the change of the plant community cover, height, and diversity at Atqasuk and Utqiagʻvik. The goals are to 1) determine whether or not change has occurred over the sampling period of nine years for the functional groups and the selected species at either Atqasuk or Utqiagʻvik, 2) determine which, if any, abiotic factors are driving changes at either site, and 3) examine if the abiotic factors driving change at either site are similar. One hypothesis is that all three metrics have changed over time at both sites for one or more functional groups and selected species, with similar findings to Botting 2015. Additionally, it may be likely to see different major driving abiotic factors between Atqasuk and Utqiagʻvik owing to differences in climate. Because Atqasuk is generally warmer, changes in Atqasuk are expected to be more pronounced.

Significance

Chapter II will contribute to existing knowledge of the drivers of plant community change in the Arctic. There is already an existing body of literature regarding some of this information, but this will provide stronger evidence for these claims and specifically contribute to the understanding of changes in the high Arctic via the study performed in Utqiagvik which may be prone to the most severe changes in the future. Additionally, this will contribute to public databases which catalogue data from long-term monitoring studies. Overall, it will contribute to the overall understanding of changing environmental conditions in the Arctic and how these may affect the plant community.

Definitions

<u>Functional group</u> – a broad grouping of plants or plant like organisms which are used as an aggregated unit for understanding community wide changes in an ecosystem.

<u>ITEX</u>– International Tundra Experiment, it is a network of researchers examining the impacts of warming on tundra ecosystems.

<u>AON</u>–Arctic Observatory Network, it is a network of projects funded by the National Science Foundation.

ARCSS—Arctic System Science, it is a program at the National Science Foundation begun in the 1990s.

Understanding the climate impacts on decadal vegetation change in northern Alaska

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Abstract

The Arctic is experiencing rapid climate change. This research documents vegetation

changes near Atqasuk and Utqiagvik, Alaska. At each location, 30 plots were sampled annually

from 2010 to 2019 using a point frame. For every plant encounter we recorded the height and

classified it into eight broad functional groups (deciduous shrubs, evergreen shrubs, forbs,

graminoids, bryophytes, lichens, litter and standing dead vegetation); for vascular plants we also

identified the species. We found a consistent increase in plant stature and cover over time which

was dramatic at Atqasuk. At both sites graminoids increased in cover and height over time; at

Atgasuk cover of shrubs and forbs also increased. At both sites, species diversity decreased. Year

was generally the strongest predictor of vegetation change suggesting a cumulative change over

time; however, soil moisture and soil temperature were also predictors of vegetation change in

many cases. We anticipate plants in the region will continue to grow taller as the region warms,

resulting in further increases in plant cover, especially graminoids. The accumulation of litter

will likely result in a decline of bryophytes and lichens. These changes in community structure

will impact energy balance and carbon cycling and therefore have regional and global

consequences.

Key words: tundra, vegetation change, plant height, climate change, abiotic

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Introduction

Anthropogenic climate change has been documented for over a century, though the intensity of change has increased within the past few decades; temperatures around the world may increase by as much as about 5°C over the next 100 years (IPCC 2018). High latitude regions may expect at least twice the rate of warming as lower latitude regions (AMAP 2019). The observed warming trend is of interest because the Arctic region is both particularly sensitive to climate change and in part responsible for balancing the global atmospheric carbon budget and regulating the energy balance of Earth (Chapin et al. 2000). Vegetation responses to climate change are a focal point of research because vegetative communities are determined at least partially by regional climate. Generally, Arctic plants are limited by the cold conditions in which they are found (cold and freezing temperatures, low nutrient availability) (Chapin 1983; Chapin et al. 1995). Therefore, plants respond to warming with enhanced growth and life cycle progression (Arft et al. 1999; Hollister and Flaherty 2010) and increased reproductive success (Myers-Smith et al. 2011), although there is evidence that this effect may wane with time (Kremers et al. 2015). An extension of the growing season, warmed air temperatures, and hastened rate of snowmelt are largely responsible for this enhanced growth and life cycle progression (Walther 2010; Oberbauer et al. 2013). Warming of the Arctic may cause increased rates of soil organic matter decomposition and enhanced greenhouse gas emissions leading to an increase and acceleration of warming and changes for the Earth's environments in a positive feedback loop (Rustad et al. 2001; Melillo et al. 2002; Davidson and Janssens 2006).

It is difficult to forecast vegetation response to warming because changes in environmental conditions in addition to air temperature may significantly alter Arctic vegetation. Soil moisture is a major controlling factor on the species composition for any given geographic

area; this is equally true in tundra vegetation (Chapin et al. 1996; Phoenix et al. 2001; Gamon et al. 2013). Soil moisture and soil temperature are limiting factors on decomposition rates of plant litter (Hobbie 1996; Shaver et al. 2006) which have consequent effects on carbon and nitrogen cycling within a community. Soil temperature is a known influencer of plant phenological progression (Oberbauer 1998), overall nutrient availability (Melillo et al. 2002), and net primary productivity (Natali et al. 2012). Growing season soil thaw depth is another important abiotic factor affecting plant communities, as it influences community growth rates and composition (Anisimov and Reneva 2006; Schuur et al. 2007)

Plants are a critical component of terrestrial ecological systems. As net primary producers, they provide bottom up controls for other trophic levels of entire ecosystems. Thus, the characteristics of a plant community influence herbivory patterns via variations in forage quality or quantity (Augustine and McNaughton 1998; Joly et al. 2009) and energetic exchanges within ecosystems (Post et al. 2008). This ultimately affects animal community composition (Orians and Wittenberger 1991; Rettie and Messier 2000). Additionally, plant species differ in their impacts on nutrient cycling, resource partitioning, and ultimately soil nutrient dynamics which has ecosystem-wide implications (Vinton and Burke 1995).

Long-term study of Arctic plant communities and their responses is needed to document and understand the drivers of tundra vegetation change, in light of extended growing seasons, prolonged exposure to summer temperatures, and fluctuations in soil moisture and soil thaw depth (Blok et al. 2011). Detailed information on plant cover and height provide the building blocks necessary to understand changes in the competitive interactions between species and functional groups, and enable better prediction of changes in canopy structure and its implications on energy balance and habitat for migratory birds or yearlong residential mammals

(Post and Forchhammer 2008; Gilg et al. 2009; Gauthier et al. 2013). This project documents a decade of vegetation change at two locations in northernmost Alaska in relation to regional warming and other environmental factors. The following specific questions were addressed:

- 1) How have plant cover, height, and diversity changed over time?
- 2) What are the drivers of vegetation change?
- 3) Are the drivers of vegetation change consistent across locations?

Materials and Methods

Study Sites

Two study sites in Northern Alaska were sampled during this study, one near the Arctic Ocean coast at Utqiaʻgvik (formerly Barrow), Alaska (71°19' N, 156°36'W), and the other approximately 100 km south at Atqasuk, Alaska (70°27' N, 157°24'W) (Figure II.1). There are long-term plots at both locations laid out in a 1-km² grid with 100 plots spaced 100 m apart; these plots were originally established to monitor long-term terrestrial ecosystem change by the Arctic System Science Program and are commonly referred to as the ARCSS grid. They are also used by the Circum-Arctic Active Layer Monitoring Program in other studies so they are sometimes referred to as the CALM grid. Both grids have a subset of 30 plots that are sampled annually, which is the focus of this study. Habitats within the grid range from dry, raised ridges to saturated meadows and ponds. These are the same plots sampled in Betway et al. (in review) and adjacent to but not part of the warming experiments at the International Tundra Experiment (ITEX) sites (Hollister et al. 2006; Hollister et al 2015).

Climate monitoring

Weather stations were installed within the ARCSS grids at both Atqasuk and Utqiaʻgvik in the 1990s as part of International Tundra Experiment sites. Air temperature (°C) was measured at a height of 2 m off the ground with a model 107-temperature probe (Campbell Scientific Inc., Logan, UT). Precipitation (cm) was measured with a 35-cm, TE525 tipping bucket rain gauge (Campbell Scientific Inc., Logan, UT). These data were logged every hour to a CR10X datalogger (Campbell Scientific Inc., Logan, UT). Further details regarding climate monitoring at the sites are available in Hollister et al. 2006. Thawing degree day values (temperature departures above 0°C) were calculated from the temperature data obtained from either weather station.

Other environmental variables examined in this study were collected throughout the summer by collaborators from the University of Texas at El Paso. On a biweekly basis the following abiotic variables were sampled at each plot: soil moisture as unitless volumetric water content measured by a FieldScout TDR 300, soil temperature (°C) obtained by a kitchen thermometer, and active layer soil thaw depth (cm) with a graduated steel probe. All values used in this analysis were collected between June 15 and July 15. Soil temperatures were not collected at Utqiagvik in 2010 and Atqasuk in 2015, and active layer soil thaw depth was not collected at Atqasuk in 2013.

Vegetation sampling

Plots were sampled annually from 2010 to 2019, excluding 2011. The method used for vegetation sampling was a non-destructive point frame as described in the ITEX manual (Molau and Mølgarrd 1997). A 75-cm² 100-point frame with point coordinates spaced 7.5 cm apart was raised on aluminum rods to just above the observed canopy height (Figure II.2). Each plot had

permanent markers affixed to the ground that were used to align the frame to ensure the same points were measured at each yearly sampling. Each point was measured with a graduated rod to assess plant identity, living status, and position in the canopy. All plants contacted by the rod were counted as occupying that coordinate, with no set maximum number of occupants per coordinate point; this is a modification of the method explained by Walker (1996) because it included all encounters (May and Hollister 2012). Vascular plants were identified to species. Non-vascular species were grouped by growth forms. Each individual plot was sampled within a 14-day range of sampling dates across years to minimize differences in phenological progression between years.

Species cover was calculated as the sum of encounters in a plot. Species height (cm) was calculated as the height of the encounter relative to the ground. For the height analysis the maximum height of each taxa (functional group or species) per plot was used. The following functional groups were used in this analysis: deciduous shrubs, evergreen shrubs, forbs, graminoids, bryophytes, lichens, leaf litter, and standing dead vegetation. Non-vascular species were not identified to species so they were further grouped into the following functional groups: acrocarpous mosses, pleurocarpous mosses, crustose lichens, foliolose lichens, and fruticose lichens.

Data Analysis

When calculating cover metrics for each plot, all thirty plots were used regardless of whether or not a functional group or species was encountered in the plot for a given year (in other words zeros were entered into the resulting database). Species visibly present in a plot but not encountered during point-framing were given a value of 0.1 for the year in which they were present. When calculating height metrics only plots in which a functional group or species

occurred for all nine sampling years were included in the analysis, thus a variable number of plots were used for each functional group or species (in other words the sample size varied between taxa based on frequency). Non-vascular plants were omitted from the height analysis. Only taxa which had over 200 encounters throughout all the sampling years were included for cover and height analyses. For a complete list of species represented by functional groups see Supplemental Table 2.S1. For calculating diversity metrics, only vascular species which occurred in five or more plots for a single year were used to mis-sampling issues of very rare species. *Alpha* diversity was calculated as the total number of vascular plant species that occurred in a given plot. *Gamma* diversity was calculated as the total number vascular plant species that occurred throughout the site (all 30 plots) in a given year. *Beta* diversity was calculated by dividing gamma diversity by alpha diversity. The following diversity indices were calculated using R Software for Statistical Computing v. 3.6.2 R Core Team (2019) and the R package "vegan" (Oksanen et al. 2019): Shannon's index, and Pielou's evenness.

The distribution of datasets was checked using the Shapiro-Wilk normality test. If a dataset did not approximate a normal distribution after data transformation attempts, then non-parametric tests were used. For cover analyses, a Bayesian Poisson regression was used to model the relationship between plant cover and abiotic factors including time, and model the relationships between the cover of functional groups used while accounting for the non-normality of the dataset due to presence of many zeros. The packages "rstan" (Stan Development Team 2020) and "brms" (Bürkner 2017) were used. A Poisson distribution was assumed due to the count-based nature of the dataset. Bayesian regression models were considered significant if the credible intervals for the model did not overlap zero. For Bayesian regression we chose Widely Applicable Information Criterion (WAIC) as a means of comparing models which share

the same regressed variable. WAIC allows for comparing various explanatory variables to a single explained variable. For height analyses, a general linear mixed model was used to model relationships between the height of functional groups and abiotic variables using the package "lme4" (Bates et al. 2015). Marginal r² was obtained from a function within the package "MuMIn" (Barton 2019). Diversity indices were also modeled with linear mixed models. Abiotic trends over time were measured using Spearman's rho test.

Results

Abiotic Factors

At Atqasuk all measured abiotic factors were correlated with year (Table 2.1). At Utqiagʻvik, the abiotic factors correlated with year were average air temperature, maximum air temperature, thawing degree day sums, maximum soil temperature, sum of precipitation, and average soil moisture (Table 2.1).

Vegetation Cover

The change in cover over time showed the following (Figure II.3, Table II.2). At Atqasuk the cover of woody deciduous shrubs, woody evergreen shrubs, forbs, graminoids, and leaf litter correlated with years. From 2010 to 2019 woody deciduous shrubs increased in cover from 11.5 to 26.1. Woody evergreen shrub cover increased from 12.2 to 29.6. Graminoid cover increased from 20.7 to 108.4 and leaf litter cover increased from 27.7 to 67.2. Bryophyte cover increased from 12.4 to 18.9. Vascular plant species which correlated with year were *Betula nana* (increased from 11.5 to 26.1), *Salix pulchra* (increased from 3.5 to 10.0), *Vaccinium vitis-idaea* (increased from 5.3 to 14.2), *Carex aquatilis* (increased from 6.7 to 38.6), *Carex bigelowii* (increased from 2.5 to 11.2), *Eriophorum angustifolium* (increased from 0.4 to 7.1), *Eriophorum*

russeolum (increased from 1.2 to 12.3), Eriophorum vaginatum (increased from 6.5 to 33.0, and Trisetum spicatum (increased from 0.9 to 4.6). At Utqiagvik the cover of graminoids (increased from 43.1 to 104.7) correlated with years. Vascular plant species which correlated with year were Petasites frigidus (increased from 1.7 to 9.5), Arctagrostis latifolia (increased from 2.0 to 3.7), E. russeolum (increased from 5.0 to 16.9), Eriophorum triste (increased from 2.6 to 14.1), Luzula arctica (decreased from 1.9 to 1.1) and acrocarpous mosses (decreased from 16.6 to 9.8).

The relationship between functional groups showed the following (Table 2.3). At Atqasuk woody deciduous shrubs covaried with evergreen shrubs, bryophytes, and leaf litter, with the best fit model indicating a closest fit with woody evergreens. Woody evergreen shrubs covaried with woody deciduous shrubs, graminoids, lichens, standing dead and leaf litter with the best fit model indicating a closest fit with woody deciduous shrubs. Forbs covaried with graminoids and leaf litter with the best fit model indicating a closest fit with leaf litter. Graminoids covaried with woody evergreen shrubs, forbs, lichens, standing dead, and leaf litter while the best fit model indicating a closest fit with lichens. Bryophytes covaried with forbs and lichens with the best fit model indicating a closest fit with forbs. Lichens covaried with woody evergreens, forbs, graminoids, standing dead plants and leaf litter with the best fit model indicating the closest fit with forbs. Standing dead plants covaried with woody deciduous shrubs, woody evergreen shrubs, graminoids, bryophytes, lichens, standing dead plants, and leaf litter, with the best fit being with woody deciduous shrubs. Leaf litter covaried with woody evergreen shrubs, graminoids, lichens, standing dead, and leaf litter, with the best fit model indicating the closest fit with graminoids. At Utqiagvik woody deciduous shrubs covaried with forbs, graminoids, standing dead, and leaf litter with the best fit model indicating a closest fit with forbs. Forbs covaried with woody deciduous shrubs, bryophytes, lichens, standing dead plants,

leaf litter with the best fit model indicating that lichens fit forbs the best. Graminoids covaried with woody deciduous shrubs, forbs, bryophytes, lichens, and leaf litter with best fit model indicating that forbs were the closest fit to graminoids. Bryophytes covaried with forbs, lichens, and leaf litter with lichens indicating the closest fit. Lichens covaried with graminoids and leaf litter with leaf litter the closest fit.

The relationship between cover and abiotic variables showed the following (Table 2.4). At Atqasuk woody deciduous shrubs covaried with years and average soil moisture, with the best fit model indicating a closest fit with years. Woody evergreens covaried with years, average soil temperature and average soil moisture, with the best fit model indicating a closest fit with years. Forbs covaried with both years and average soil temperature with the best fit model indicating a closest fit with years. Graminoids covaried with years, maximum air temperature, average soil temperature, average thaw depth, and average soil moisture with the best fit model indicating a closest fit with average years and average soil moisture. Bryophytes covaried with average soil temperature and the sum of precipitation, with the best fit model occurring with precipitation. Lichens covaried with average soil moisture. Standing dead plants covaried with maximum air temperature, average soil temperature, maximum soil temperature, average thaw depth and average soil moisture with the best fit model indicating a closest fit with average soil moisture. Leaf litter covaried with years, maximum soil temperature, average thaw depth, and average soil moisture with the best fit model indicating a closest fit with years. Betula nana and S. pulchra covaried with years. Vaccinium vitis-idaea and Rubus chamaemorus covaried with years and average soil moisture, with the best fit model indicating a closest fit with years. Carex aquatilis covaried with year, maximum air temperature, average soil temperature, average thaw depth, and average soil moisture with the best fit model indicating a closest fit with maximum air

temperature. Carex bigelowii covaried with year and average soil moisture, with a best fit model indicating a closest fit with average soil moisture. Eriophorum angustifolium covaried with years and maximum air temperature with the best fit model indicating a closest fit with years. Eriophorum russeolum covaried with years. Eriophorum vaginatum covaried with both year and average soil moisture with the best fit model indicating a closest fit with year. Trisetum spicatum covaried with years and maximum air temperature with the best fit model indicating a closest fit with Acrocarpous mosses covaried with average thaw depth and sum of precipitation with a best fit model indicating a closest fit with sum of precipitation. Pleurocarpous mosses covaried with maximum air temperature, average soil temperature, average thaw depth, and average soil moisture with the best fit model indicating a closest fit with average soil moisture. Foliose and fruticose lichens covaried with average soil moisture.

At Utqiagvik, woody deciduous shrubs covaried with average soil temperature. Forbs covaried with average soil temperature, maximum soil temperature, and average thaw depth with the best fit model occurred with average thaw depth. Graminoids covaried only with year. Bryophytes covaried with average soil temperature, maximum soil temperature, and average thaw depth with the best fit model indicating a closest fit with average thaw depth. Standing dead plants covaried with average thaw depth and average soil moisture with the best fit model indicating a closest fit with thaw depth. Leaf litter covaried with average soil temperature, maximum soil temperature, average thaw depth, and average soil moisture with the best fit model indicating a closest fit with average soil moisture. Salix pulchra covaried with average soil moisture. Petasites frigidus covaried with years, average air temperature, maximum air temperature, and sum of thawing degree days with the best fit model indicating a closest fit with average years and air temperature. Stellaria laeta covaried with average soil moisture. Carex

stans covaried with maximum air temperature. Dupontia fisheri covaried with average soil moisture. Eriophorum russeolum covaried with years and maximum air temperature with the best fit model indicating a closest fit with years. Eriophorum triste covaried with years. Luzula arctica covaried with years, average soil temperature and average soil moisture with the best fit model indicating a closest fit with years. Poa arctica covaried with average thaw depth and average soil moisture with the best fit model indicating a best fit model with average soil moisture. Acrocarpous mosses covaried with year, maximum air temperature, average soil temperature, and maximum soil temperature with the best fit model indicating a closest fit with maximum air temperature.

Diversity

At both Atqasuk and Utqiagʻvik, neither *alpha*, *beta*, nor *gamma* diversity were significantly related to years (Table 2.5). However, Shannon's index at Utqiagʻvik (1.4 to 1.3, $r^2 = 0.02$) and Pielou's evenness (0.8 to 0.7, $r^2 = 0.04$ at Atqasuk were significantly related to year and declined over time.

Vegetation Height

At Atqasuk the heights of all functional groups increased over years: woody deciduous shrubs (from 11.5 cm to 20.5 cm, $r^2 = 0.11$), woody evergreen shrubs (from 7.4 cm to 11.2 cm, $r^2 = 0.04$), forbs (from 3.6 cm to 10.4 cm, $r^2 = 0.19$) and graminoids (from 14.0 cm to 32.1 cm, $r^2 = 0.21$) (Figure II.4, Table II.6). Species in Atqasuk which increased over years were *S. pulchra* (from 9.3 cm to 22.0 cm, $r^2 = 0.31$), *Ledum palustre* (from 6.9 cm to 10.5 cm, $r^2 = 0.05$), *V. vitisidaea* (from 2.1 cm to 8.3 cm, $r^2 = 0.10$), *R. chamaemorus* (from 3.7 cm to 10.8 cm, $r^2 = 0.30$), *C. aquatilis* (from 15.6 cm to 35.8 cm, $r^2 = 0.31$), *C. bigelowii* (from 11.3 cm to 23.3 cm, $r^2 = 0.15$),

E. russeolum (from 9.6 cm to 28.8 cm, $r^2 = 0.44$), and E. vaginatum (from 9.5 cm to 25.5 cm, $r^2 = 0.18$).

At Utqiaġvik, graminoids were the only functional group that increased in height over time (from 10.00 to 23.10 cm, $r^2 = 0.21$) (Figure II.4, Table II.6). Species in Utqiaġvik which increased over years were *Saxifraga cernua* (from 0.90 cm to 4.20 cm, $r^2 = 0.16$), *C. stans* (from 10.2 to 22.8 cm, $r^2 = 0.20$), *D. fisheri* (from 8.60 to 20.20 cm, $r^2 = 0.26$), *E. russeolum* (from 6.90 to 17.60 cm, $r^2 = 0.39$), *E. triste* (from 5.70 to 17.90 cm, $r^2 = 0.34$), *Luzula confusa* (from 2.90 to 6.70 cm, $r^2 = 0.11$), *and P. arctica* (from 4.30 to 10.70 cm, $r^2 = 0.12$).

At Atqasuk the height of woody deciduous shrubs correlated with year ($r^2 = 0.11$) (Table 2.7). The height of woody evergreen shrubs correlated with year ($r^2 = 0.04$), maximum air temperature ($r^2 = 0.02$), average soil temperature ($r^2 = 0.04$), and maximum soil temperature ($r^2 = 0.04$) 0.03). Forb height correlated with year ($r^2 = 0.19$). Graminoid height correlated with year ($r^2 = 0.19$). 0.21), maximum air temperature ($r^2 = 0.09$), average soil temperature ($r^2 = 0.03$), maximum soil temperature ($r^2 = 0.02$), and average soil moisture ($r^2 = 0.01$). Regarding abiotic influences on the height of various taxa, B. nana ($r^2 = 0.07$), S. pulchra ($r^2 = 0.31$), and Cassiope tetragona ($r^2 = 0.07$) = 0.31) height correlated with year. Ledum palustre height correlated with year ($r^2 = 0.05$) and average soil temperature ($r^2 = 0.04$). Vaccinium vitis-idaea height correlated with year ($r^2 = 0.04$). 0.10). Rubus chamaemorus height correlated with year ($r^2 = 0.30$) and average thaw depth ($r^2 =$ 0.08). Carex aquatilis height correlated with year ($r^2 = 0.31$), average soil temperature ($r^2 = 0.08$). 0.04), maximum soil temperature ($r^2 = 0.03$), average thaw depth ($r^2 = 0.04$), and average soil moisture ($r^2 = 0.03$). Carex bigelowii height correlated with year ($r^2 = 0.15$). Eriophorum russeolum height correlated with year ($r^2 = 0.44$), average soil temperature ($r^2 = 0.10$) and maximum soil temperature ($r^2 = 0.12$). Eriophorum vaginatum height correlated with year ($r^2 = 0.12$).

0.18) and maximum air temperature ($r^2 = 0.13$). *Trisetum spicatum* height correlated with year ($r^2 = 0.30$).

At Utqiagvik forb height correlated with maximum air temperature ($r^2 = 0.05$) and thawing degree days ($r^2 = 0.03$) (Table 2.7). Graminoid height correlated with year ($r^2 = 0.21$), average air temperature ($r^2 = 0.14$), and maximum air temperature ($r^2 = 0.14$). Regarding abiotic influences on the height of various taxa, S. pulchra height correlated with maximum air temperature ($r^2 = 0.10$) and thawing degree days ($r^2 = 0.07$). Salix rotundifolia height correlated with year ($r^2 = 0.08$). Petasites frigidus height correlated with year ($r^2 = 0.05$) and maximum air temperature ($r^2 = 0.04$). Saxifraga cernua height correlated with year ($r^2 = 0.16$) and maximum air temperature ($r^2 = 0.18$). Stellaria laeta height correlated average air temperature ($r^2 = 0.15$), maximum air temperature ($r^2 = 0.12$), and thawing degree days ($r^2 = 0.10$). Arctagrostis latifolia height correlated with year ($r^2 = 0.20$). Carex stans height correlated with year ($r^2 = 0.20$), average air temperature ($r^2 = 0.11$), and maximum air temperature ($r^2 = 0.11$). Dupontia fisheri height correlated with year ($r^2 = 0.26$), average air temperature ($r^2 = 0.24$), maximum air temperature ($r^2 = 0.24$), and thawing degree days ($r^2 = 0.17$). Eriophorum triste height correlated with year ($r^2 = 0.34$), average air temperature ($r^2 = 0.21$), and maximum air temperature ($r^2 = 0.21$) 0.22). Eriophorum russeolum height correlated with year ($r^2 = 0.39$), average air temperature (r^2 = 0.18), and maximum air temperature ($r^2 = 0.22$). Luzula arctica height correlated with average soil moisture ($r^2 = 0.19$). Luzula confusa height correlated with year ($r^2 = 0.11$), average air temperature ($r^2 = 0.10$), maximum air temperature ($r^2 = 0.13$), thawing degree days ($r^2 = 0.10$), average soil temperature ($r^2 = 0.11$), maximum soil temperature ($r^2 = 0.14$), and average thaw depth ($r^2 = 0.17$). Poa arctica height correlated with year ($r^2 = 0.12$), average air temperature ($r^2 = 0.12$) = 0.14), maximum air temperature ($r^2 = 0.12$), and thawing degree days ($r^2 = 0.10$).

Discussion

At Atqasuk there were consistent increases in plant cover and height over time (Figure II.2, Figure II.3) that were large enough to be detected by satellite imagery (Huemmrich 2020, personal communication 23 February). Changes in plant cover and height were also detected at Utqiagvik, but the strength of the change was not as large. Overall, the best predictors for change in either cover or height were year, soil temperature, soil moisture, or air temperature. The strong relationship between plant cover and plant height with year implies a cumulative response to regional climate warming.

The correspondences between vegetation cover, soil moisture and temperature of the existing year suggests considerable plasticity in overall tundra vegetation growth between years (Walker et al. 1994). Biomass in tundra regions has been linked to soil temperature (Hill and Henry 2011; Natali et al. 2012). Soil moisture and precipitation are known constraints on arctic vegetation growth (Chapin et al. 1996; Blok et al. 2011). In our study, precipitation was not a modest predictor of cover change and did not successfully predict height change. Soil moisture was an important predictor in Atqasuk and a modest predictor of cover change in Utqiagvik as well as a modest predictor of height change at either site. This is reasonable given that past work indicates soil moisture is a limiting factor on vegetation growth (Chapin et al. 1995; Gamon et al. 2013; Botting 2015). Thaw depth was about a median predictor of cover change at either research site and was not as well represented as soil temperature for predicting plant height change at either site, though thaw depth is associated with community composition and growth (Schuur et al. 2007; Lantz et al. 2009). It would be beneficial for future studies to discern the best groups of predictors are for broad functional groups and the most numerous taxa via multivariate modeling on this dataset.

The larger documented change at the lower Arctic site, Atqasuk, relative to the higher Arctic site, Utqiagvik, is consistent with previous studies that found greater changes in the cover of shrubs at warmer locations (Walker et al. 2006; Elmendorf et al. 2012). While Utqiagvik is considered a high arctic site, it appears to be slowly transitioning to more resemble low arctic communities as erect shrubs become more dominant, which may explain inconsistencies with previous findings. Global monitoring networks across the tundra biome have shown a general increase in stature of most tundra plants and consistent increases in cover over time (particularly for shrubs), which is consistent with our own findings (Elmendorf et al. 2012; Bjorkman et al. 2018; Myers-Smith et al. 2019; Bjorkman et al. 2020). Our results were also consistent with experimental warming studies that have shown an increase in shrub and graminoid cover with temperature at other tundra locations, (Callaghan et al. 2011; Elmendorf et al. 2012; Bjorkman et al. 2020) and at adjacent sites at Atqasuk and Utqiagvik (Hollister et al. 2015). The one notable exception is warming experiments have generally shown a decline in bryophytes and lichens as vascular plants increase; here we show considerable variability in the cover of these taxa with the only significant change a decline in acrocarpous mosses at Utqiagvik. The lack of a consistent decrease in bryophyte and lichen cover is likely due to both considerable variability between years and that the average cover of vascular plants has only reached full cover (100%) in the past few years, leaving considerable amounts of open ground; therefore, vascular plants have not yet imposed considerable shading or other adverse impacts such as decreasing nutrient availability on non-vascular plants. Inconsistent trends in bryophyte cover could also be attributed to fluctuations in lemming populations, particularly at Utqiagvik, which have been shown to drastically reduce graminoid cover and promote bryophyte cover (Lara et al. 2017). Herbivory

coupled with sensitivity to even small fluctuations in temperature (Hollister et al. 2015) may explain much of the interannual variability in tundra vegetation cover.

The cover of standing dead plants and leaf litter were somewhat inverse to each other at both sites (Table 2.2). Other research has indicated that standing dead cover fluctuates between years as a function of leaf retention time (Knapp and Seastedt 1986) and herbivory, especially during high lemming years (Villarreal et al. 2012). Both processes may also account for increases in leaf litter. Standing dead and leaf litter cover are important to include in vegetation cover change studies because they largely influence not only the surrounding plant community composition, but the overall productivity of the ecosystem as well (Knapp and Seastedt 1986). Leaf litter accumulation coupled with increased temperatures over time also influences decomposition rates, which has the potential to alter the rate of carbon exchange, and therefore the overall carbon budget, in the tundra (McLaren et al. 2017; Parker et al. 2018).

Changes in vegetation cover over time in arctic communities are important to document because plant community composition can greatly influence the overall energy balance of tundra ecosystems. The energy balance of tundra ecosystems is crucial for ecosystem processes such as carbon and nutrient cycling, plant growth and productivity, and microbial activity (Lund et al. 2014). Woody species (i.e., deciduous and evergreen shrubs) have been shown to greatly alter belowground carbon exchange rates (Parker et al. 2020), thus dramatic increases in cover of woody species have the potential to greatly alter ecosystem structure and function. Additionally, encroachment of tall-statured shrubs shades neighboring plants, which has been shown to restrict plant growth (Graglia et al. 1997).

Increases in shrub and graminoid cover affect more than plant-plant interactions, however. Shading imposed from neighboring shrubs has been shown to delay flowering, which

could reduce (or eliminate) pollinator visitation and/or berry production (Holloway et al. 2002; Høye et al. 2013). Reduced berry production could affect populations of mammalian and avian species that rely on berries as a food source. Graminoids and deciduous shrubs are the primary food source for most arctic herbivores. Long-term herbivore exclusion experiments have shown that absence of herbivory (i.e., lemmings) greatly alters several ecosystem properties, including thaw depth, water-table, and CH₄ exchange (Lara et al. 2016). Presence of herbivores also caused a shift in community composition in wet meadow communities from predominately graminoids to mosses (Lara et al. 2016). More research is needed to understand the various trophic cascades associated with shifts in vegetation community composition, but documenting vegetation change over time and in response to warming is the first step to understanding how the Arctic is responding to a warming climate.

Species diversity (both Shannon's index and Pielou's evenness), declined at both sites over time due to a disproportionate increase in the abundant species. Measures of species richness (*alpha*, *beta*, and *gamma* diversity) did not change. Declines in species diversity contradict previous studies showing increased species diversity over time (Villarreal et al. 2012; Løkken et al. 2020) and the general pattern of increased diversity at warmer locations (Walker 1995). Because species diversity is a function of species evenness, increases in cover for the dominant species without the addition of newly introduced species would cause an overall decrease in diversity. Because the study sites span a wide range of community types, it is likely that a 30-plot sample is sufficient in capturing all species present in the surrounding area. Previous studies, which focus on one or two community types, may show increased species richness (*gamma* diversity) over time as the abiotic conditions (e.g., soil moisture, soil

temperature, etc.) change and new species migrate into the site. Over longer time scales, it is likely new species will invade both regions and increase species richness.

Conclusions

Results here show that the two research sites distinguished by climatic factors and geographic distance increased in plant cover and plant height from 2010 to 2019. While plant cover and height were associated with many abiotic factors such as soil moisture and soil temperature, most of the changes in vegetation were best predicted by year. At both sites, significant cover change was driven by shifts in species within the genera *Carex* and *Eriophorum*. In Atqasuk, there was more cover change in shrubs than in Utqiagvik. Diversity indices at both sites indicates that species evenness decreased over the monitoring period. It is likely that the similarities in cover change between both sites is the result of regional climate warming.

Documenting and understanding vegetative and environmental changes is important for many reasons. Successfully being able to predict changes as natural communities experience climate change will allow researchers and natural resource managers to better maintain ecosystem services and natural resources. In order to understand the bottom up effects, within ecosystems, it is necessary to understand the plant community. Plant community metrics such as cover and height are useful for understanding the influence of competition, albedo, and habitat suitability. In spite of numerous studies occurring across the Arctic, there is still much to be known. An ever-evolving awareness of how environmental abiotic factors influence the characteristics of the plant communities across the Arctic is necessary in order to develop more useful models for predicting change. Additionally, it would be useful to develop a multivariate

set of models to predict changes which may integrate phenological and plant trait observations with vegetation cover.

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Table II.1. Abiotic factors at Atqasuk and Utqiagʻvik during the summer between 2010 and 2019. Values for a given year represent the average and the standard deviation (in parentheses) for measurements made at each plot (n=30) or as a single value for measures of regional climate (missing values are noted with --). Spearman's rho (p) are based on the average per year (n=9) and are bolded when significant.

	2010	2012	2013	2014	2015	2016	2017	2018	2019	р
Atqasuk Grid										
Air temp (avg)	6.6	10.8	10.5	8.3	11.9	11.1	10.8	6.1	11.3	0.38
Air temp (max)	21.2	22.9	25.4	21.2	24.4	23.7	22.7	22.0	25.9	0.45
Degree Day (sum)	236.0	383.0	421.0	289.0	492.0	445.0	360.0	198.0	385.0	0.18
Soil temp (avg)	2.7 (1.5)	4.0 (1.5)	8.1 (2.6)	4.8 (1.5)		6.2 (2.1)	4.6 (1.8)	2.6 (2.1)	5.9 (1.4)	0.26
Soil temp (max)	2.7 (1.5)	5.3 (2.2)	8.8 (2.6)	7.6 (2.5)		7.2 (2.0)	6.3 (2.0)	2.6 (2.1)	7.4 (1.3)	0.29
Thaw depth (avg)	28.2 (13.7)	23.7 (11.7)		23.8 (10.8)	39.0 (18.3)	27.9 (12.3)	29.6 (13.6)	17.3 (9.6)	37.6 (16.6)	0.15
Precip (sum)	0.4	0.5	7.7	9.9	3.8	3.9	4.0	1.8	5.3	0.41
Soil moist (avg)	52.4 (23.1)	36.1 (19.2)	45.2 (20.5)	42.8 (7.1)	66.8 (16.5)	52.1 (13.0)	45.9 (14.4)	53.1 (20.2)	58.4 (14.8)	0.25
Utqiaġvik Grid										
Air temp (avg)	2.4	4.7	4.1	2.8	7.3	5.0	5.6	2.8	6.8	0.49
Air temp (max)	12.7	17.6	16.0	13.0	21.9	18.8	17.2	16.2	19.9	0.61
Degree Day (sum)	84.0	166.0	177.0	102.0	274.0	205.0	178.0	98.0	220.0	0.49
Soil temp (avg)		2.4 (0.8)	2.4 (1.1)	3.8 (2.4)	4.2 (2.1)	3.8 (1.4)	2.7 (1.6)	1.8 (1.0)	3.5 (1.1)	0.10
Soil temp (max)		3.1 (1.1)	3.5 (1.3)	5.0 (2.9)	4.2 (2.1)	5.4 (1.4)	4.0 (1.6)	1.8 (1.0)	4.9 (1.3)	0.13
Thaw depth (avg)	17.9 (4.9)	21.0 (4.6)	27.2 (5.6)	6.3 (2.9)	25.3 (5.4)	20.3 (3.9)	16.2 (4.6)	10.2 (7.0)	27.8 (8.1)	-0.04
Precip (sum)	0.4	0.5	4.3	8.7	1.8	3.3	3.8	1.9	4.8	0.31
Soil moist (avg)	53.9 (32.9)	41.6 (22.1)	52.6 (19.9)	43.2 (10.4)	34.6 (5.7)	56.9 (17.1)	37.0 (12.2)	61.2 (13.9)	61.0 (12.3)	0.19

Table II.2. Cover of functional groups and the most abundant vascular plant species at Atqasuk and Utqiagvik between 2010 and 2019. Values for a given year represent the average and the standard deviation (in parenthesis) for each plot (=30) in that year. Significant change over time (Ch) was determined by Widely Applicable Information Criterion (WAIC) from Bayesian Poisson regression between cover values and year and noted with an arrow for the direction ($\uparrow \downarrow$) or no change if it was not significant (-). A complete listing of all species is available in Supplemental Table II.S1.

<u> </u>	2010		2012		2012		2014		2015		2016		2015		2010		2010		GI
	2010		2012		2013		2014		2015		2016		2017		2018		2019		Ch
Atqasuk Grid																			
Woody deciduous	11.5	(17.5)	17.1	(23.3)	20.1	(28.6)	18.7	(27.0)	19.2	(26.4)	19.8	(28.6)	24.9	(34.4)	23.3	(33.6)	26.1	(38.0)	个
Betula nana	8.0	(15.8)	12.8	(22.4)	15.0	(26.8)	14.1	(25.4)	13.0	(22.9)	14.2	(27.0)	16.6	(30.2)	14.8	(25.9)	16.1	(27.9)	个
Salix pulchra	3.5	(10.0)	4.3	(11.6)	5.1	(13.8)	4.6	(13.0)	6.2	(17.0)	5.7	(14.2)	8.3	(22.0)	8.5	(26.4)	10.0	(30.5)	个
Woody evergreen	12.2	(11.2)	22.0	(19.8)	21.6	(19.3)	26.4	(24.2)	21.5	(19.9)	20.7	(19.2)	22.5	(20.9)	24.5	(23.5)	29.6	(30.5)	个
Cassiope tetragona	3.0	(6.5)	3.9	(9.5)	4.3	(10.8)	4.0	(9.2)	4.0	(8.9)	3.6	(8.1)	3.0	(7.0)	3.9	(9.9)	4.7	(11.9)	-
Ledum palustre	3.9	(4.4)	9.3	(9.9)	8.2	(8.5)	9.2	(10.3)	7.5	(7.9)	7.9	(8.8)	8.4	(8.8)	8.1	(9.1)	10.7	(12.7)	-
V. vitis-idaea	5.3	(6.2)	8.8	(9.1)	9.1	(9.7)	13.3	(13.2)	10.0	(10.9)	9.1	(10.0)	11.0	(12.4)	12.4	(13.0)	14.2	(16.0)	个
Forb	3.2	(4.2)	3.4	(5.0)	3.7	(4.9)	4.6	(6.2)	3.8	(5.5)	3.2	(5.1)	4.3	(6.4)	5.1	(7.5)	6.4	(9.4)	1
R. chamaemorus	1.9	(3.6)	2.3	(4.6)	2.0	(4.0)	2.5	(4.4)	2.8	(5.3)	2.5	(4.8)	2.9	(5.6)	3.4	(6.0)	4.6	(8.4)	\uparrow
Graminoid	20.7	(11.5)	48.1	(28.2)	52.4	(27.8)	63.3	(28.1)	72.6	(35.4)	58.1	(35.9)	83.4	(39.5)	86.1	(45.0)	108.4	(46.0)	1
Carex aquatilis	6.7	(8.2)	12.0	(13.2)	16.7	(18.6)	18.4	(20.7)	22.4	(25.5)	20.7	(26.4)	29.0	(32.6)	28.5	(33.5)	38.6	(44.5)	\uparrow
Carex bigelowii	2.5	(4.6)	4.7	(9.3)	6.3	(12.1)	7.0	(14.1)	7.7	(14.9)	5.0	(9.9)	10.1	(18.8)	8.5	(15.8)	11.2	(21.7)	1
E. angustifolium	0.4	(1.5)	1.6	(5.0)	1.7	(4.6)	2.0	(5.5)	3.4	(8.7)	2.1	(6.4)	4.8	(11.3)	5.0	(13.5)	7.1	(17.3)	1
E. russeolum	1.2	(2.7)	4.3	(8.6)	6.5	(13.6)	9.5	(17.8)	9.5	(17.3)	6.4	(11.8)	8.4	(14.8)	6.9	(13.4)	12.3	(24.5)	\uparrow
E. vaginatum	6.5	(9.6)	21.2	(29.7)	18.0	(25.1)	22.1	(29.8)	23.5	(33.2)	21.6	(32.8)	27.5	(38.4)	32.8	(44.3)	33.0	(42.2)	1
Trisetum spicatum	0.9	(2.4)	2.5	(7.1)	1.6	(4.6)	2.3	(5.5)	2.7	(6.2)	1.2	(4.3)	2.2	(5.2)	3.3	(8.5)	4.6	(12.3)	\uparrow
Bryophyte	12.4	(11.3)	12.2	(12.3)	29.7	(22.6)	31.4	(21.0)	22.4	(18.0)	18.1	(16.8)	20.2	(17.7)	17.9	(18.1)	18.9	(18.4)	-
Acrocarpous moss	7.7	(9.7)	8.2	(7.8)	15.5	(15.5)	16.3	(13.0)	9.4	(9.2)	6.5	(7.5)	9.5	(10.6)	7.4	(9.1)	8.0	(9.7)	-
Pleurocarpous moss	1.8	(4.4)	2.8	(7.4)	2.4	(6.6)	4.4	(9.6)	3.9	(7.9)	4.8	(11.7)	1.9	(5.7)	2.7	(6.9)	3.2	(6.8)	-
Lichen	9.3	(10.5)	12.5	(12.1)	17.4	(17.4)	22.3	(21.9)	10.1	(12.8)	6.4	(7.8)	7.9	(9.7)	8.6	(9.7)	8.9	(11.0)	-
Crustose	0.0	(0.0)	0.1	(0.5)	3.2	(6.4)	1.2	(2.8)	1.0	(2.8)	0.6	(2.0)	0.3	(1.3)	0.4	(1.7)	0.5	(1.4)	-
Foliose	3.9	(4.9)	4.1	(4.4)	5.0	(5.0)	6.2	(6.8)	3.1	(3.7)	1.6	(2.0)	2.9	(3.8)	3.2	(3.5)	3.1	(3.8)	-
Fruticose	5.4	(6.5)	8.3	(8.5)	9.3	(9.5)	14.9	(14.4)	6.1	(7.3)	4.3	(5.0)	4.7	(5.5)	5.0	(5.7)	5.2	(6.9)	-
Standing dead plants	59.7	(36.3)	100.1	(45.3)	67.4	(34.0)	64.2	(28.0)	32.4	(18.0)	48.5	(29.2)	62.1	(37.9)	87.6	(41.3)	35.8	(17.3)	-
Leaf litter	27.7	(12.0)	35.5	(15.1)	30.2	(14.9)	37.9	(18.4)	56.2	(19.8)	56.0	(23.1)	40.4	(17.6)	37.2	(13.9)	67.2	(34.4)	1
Bare ground	0.0	0.0	0.6	1.6	0.1	0.4	0.1	0.3	2.0	4.5	0.0	0.2	0.1	0.4	0.6	1.6	0.6	0.4	-

Table II.2. Continued.

-	2010		2012		2012		2014		2015		2016		2017		2019		2010		Ch
Th : : 1 C :1	2010		2012		2013		2014		2013		2010		2017		2018		2019		Ch
Utqiagvik Grid		(4.5.0)	0 =								0 =			(10.0)	0.5				
Woody deciduous	7.2	(12.9)	8.7	(16.3)	9.6	(16.8)	7.5	(13.7)	7.6	(14.4)	8.5	(16.7)	9.8	(18.2)	8.3	(15.1)	7.3	(14.0)	-
Salix pulchra	1.5	(6.9)	2.6	(11.4)	2.0	(8.5)	1.2	(5.0)	2.1	(9.1)	2.1	(9.3)	2.3	(10.2)	1.6	(7.1)	1.7	(7.9)	-
Salix rotundifolia	5.6	(10.6)	6.2	(10.9)	7.6	(13.4)	6.4	(12.1)	5.5	(11.0)	6.4	(12.4)	7.4	(14.3)	6.7	(13.3)	5.6	(12.0)	-
Forb	6.5	(7.2)	10.6	(17.9)	13.6	(17.0)	6.5	(9.1)	9.9	(19.9)	8.4	(17.2)	10.3	(20.8)	7.9	(17.4)	13.1	(30.8)	-
Petasites frigidus	1.7	(3.6)	5.6	(16.2)	4.1	(11.4)	2.3	(6.2)	6.5	(19.0)	5.1	(15.0)	6.1	(17.5)	5.0	(14.7)	9.5	(29.0)	1
Stellaria laeta	1.6	(3.3)	1.3	(2.3)	2.3	(4.1)	1.4	(2.6)	0.9	(2.0)	0.8	(1.5)	1.6	(3.9)	0.8	(2.5)	0.9	(2.0)	-
Graminoid	43.1	(21.2)	67.5	(40.5)	89.3	(40.1)	48.6	(24.6)	78.9	(38.1)	75.0	(35.7)	97.1	(40.4)	91.0	(44.8)	104.7	(42.3)	↑
A. latifolia	2.0	(4.2)	2.5	(5.0)	3.1	(5.8)	1.7	(4.4)	3.1	(6.4)	2.8	(6.6)	4.9	(11.1)	3.6	(10.0)	3.7	(8.7)	↑
Carex stans	17.0	(15.4)	26.8	(24.1)	38.8	(32.6)	16.6	(14.2)	36.0	(30.9)	29.9	(27.8)	39.7	(33.3)	37.4	(37.7)	41.7	(31.1)	-
Dupontia fisheri	6.6	(9.1)	9.6	(13.5)	9.9	(14.9)	6.0	(9.2)	8.2	(10.3)	10.4	(17.6)	16.6	(19.1)	10.5	(12.3)	12.9	(14.0)	-
E. russeolum	5.0	(5.2)	7.8	(14.6)	10.7	(15.5)	7.6	(11.3)	11.8	(14.6)	12.6	(18.9)	9.9	(15.0)	13.2	(16.6)	16.9	(20.3)	1
E. triste	2.6	(4.9)	8.7	(16.0)	7.9	(14.8)	6.5	(12.3)	10.2	(16.6)	9.9	(15.6)	12.5	(19.5)	14.8	(25.1)	14.1	(23.1)	1
Luzula arctica	1.9	(4.9)	3.1	(6.5)	4.2	(10.2)	1.7	(5.3)	1.8	(4.6)	1.4	(3.6)	1.6	(5.6)	1.0	(3.4)	1.1	(3.0)	\downarrow
Luzula confusa	1.7	(2.5)	1.6	(2.5)	2.4	(4.1)	1.0	(2.0)	2.3	(3.8)	2.2	(3.5)	1.9	(3.4)	2.0	(4.8)	1.7	(4.5)	-
Poa arctica	4.6	(7.5)	6.0	(15.5)	9.9	(20.2)	5.6	(10.3)	4.4	(9.6)	5.0	(9.2)	8.0	(15.4)	6.8	(14.1)	10.8	(20.5)	-
Bryophyte	32.6	(16.9)	40.5	(25.4)	40.5	(19.1)	34.2	(16.4)	20.6	(12.1)	24.7	(16.7)	27.3	(19.6)	27.0	(20.4)	26.6	(16.9)	-
Acrocarpous moss	16.6	(15.6)	13.6	(14.2)	18.5	(13.1)	13.2	(11.7)	9.6	(9.2)	11.3	(14.1)	11.8	(12.8)	11.7	(16.7)	9.8	(13.1)	\downarrow
Pleurocarpous moss	3.8	(7.2)	20.8	(23.3)	16.9	(19.0)	14.6	(18.2)	9.6	(12.8)	12.0	(15.7)	13.2	(17.3)	12.2	(16.6)	15.1	(16.5)	-
Lichen	10.0	(13.2)	14.1	(16.8)	18.7	(22.5)	14.9	(17.8)	9.2	(12.4)	10.9	(15.2)	11.9	(15.4)	12.9	(19.3)	12.6	(17.3)	-
Foliose	3.2	(4.7)	4.9	(7.3)	6.3	(9.2)	4.5	(6.9)	3.0	(5.0)	4.0	(9.0)	4.2	(7.4)	4.1	(7.6)	4.6	(7.9)	-
Fruticose	6.8	(9.8)	9.1	(12.4)	11.9	(16.2)	10.0	(12.9)	6.0	(9.2)	6.7	(10.2)	7.6	(11.1)	8.8	(14.6)	7.9	(13.0)	-
Standing dead plants	45.2	(21.1)	100.4	(40.7)	27.2	(18.8)	49.8	(23.6)	28.2	(11.6)	33.4	(15.5)	50.7	(26.8)	38.7	(23.0)	32.8	(17.3)	-
Leaf litter	47.6	(20.9)	28.4	(20.7)	26.7	(19.5)	38.0	(17.2)	51.5	(23.0)	45.9	(27.2)	34.4	(22.8)	59.9	(25.4)	55.7	(28.0)	-
Bare ground	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.8	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.2	-

Table II.3. The relationship between functional groups at Atqasuk and Utqiagvik. Values represent the Widely Applicable Information Criterion (WAIC) from Bayesian log linked regression models between cover values of each functional group. Values can be compared horizontally with lower numbers indicating a better fit. A Poisson distribution was assumed. Plot location (n=30) was considered a source of random error. Column and row headers indicate functional groups. WAIC values from significant models are indicated in bold.

	Woody Deciduous	Woody Evergreen	Forb	Graminoid	Bryophyte	Lichen	Standing dead	Leaf litter
Atqasuk Grid					<u> </u>			
Woody Deciduous	1116	1289	1291	1296	1290	1292	1280	1284
Woody Evergreen	1423	1177	1428	1400	1431	1426	1401	1413
Forb	816	819	641	809	803	800	817	813
Graminoid	3446	2751	2767	2100	2784	2784	2703	2782
Bryophyte	2335	2336	2344	2339	1560	2339	2341	2203
Lichen	1253	1246	1257	1236	1227	1102	1213	1184
Standing dead	2646	2585	2640	2428	2641	2608	1768	2530
Leaf litter	2766	2742	2778	2777	2659	2716	2647	1710
Utqiagvik Grid								
Woody Deciduous	587	-	707	701	713	712	705	699
Woody Evergreen	-	-	-	-	-	-	-	-
Forb	1560	-	1303	1534	1560	1565	1548	1556
Graminoid	2682	-	2722	1956	2719	2719	2720	2674
Bryophyte	2981	-	2980	2987	1764	2984	2984	2428
Lichen	1208	-	1202	1192	1190	994	1198	1161
Standing dead	2588	-	2582	2561	2600	2596	1640	2536
Leaf litter	3029	-	3047	3041	2558	3016	3006	1749

Table II.4. The relationship between vegetation cover and abiotic factors at Atqasuk and Utqiaʻgvik. Values represent the Widely Applicable Information Criterion (WAIC) from Bayesian regression models between cover groups. WAIC values were determined after regressing a single log linked cover group variable to every other functional group sequentially. Values can be compared horizontally with lower numbers indicating a better fit. A Poisson distribution was assumed. Plot location (n=30) was considered a source of random error. Column and row headers indicate abiotic factors and growth form respectively. WAIC values from significant models are indicated in bold.

		Air	Air	Degree	Soil	Soil	Thaw		Soil
		temp	temp	Day	temp	temp	depth	Precip	moist
	Year	(avg)	(max)	(sum)	(avg)	(max)	(avg)	(sum)	(avg)
Atqasuk Grid									
Woody deciduous	1289	1291	1185	1290	1185	1290	1153	1290	1288
Betula nana	846	847	772	846	771	847	749	847	848
Salix pulchra	582	585	536	584	537	584	542	585	586
Woody evergreen	1428	1427	1258	1427	1255	1427	1287	1428	1410
Cassiope tetragona	618	619	562	619	562	615	559	618	620
Ledum palustre	1055	1055	926	1055	926	1054	945	1054	1040
Vaccinium vitis-idaea	1047	1047	944	8575	944	1046	930	1047	1043
Forb	813	815	733	815	729	813	733	814	816
Rubus chamaemorus	518	522	471	522	466	522	477	522	521
Graminoid	2781	2779	2477	2782	2461	2782	2457	2781	2781
Carex aquatilis	1446	1447	1251	1449	1247	1448	1238	1448	1445
Carex bigelowii	277	597	543	792	543	596	540	596	592
Eriophorum angustifolium	478	480	438	480	440	480	439	480	484
Eriophorum russeolum	636	636	585	636	585	635	567	635	637
Eriophorum vaginatum	1177	1176	1059	1177	1059	1175	1078	1175	1169
Trisetum spicatum	577	578	465	578	471	578	541	577	579
Bryophyte	2336	2334	2127	2339	2123	2337	2092	2336	2337
Acrocarpous moss	1553	1551	1358	1551	1358	1550	1369	1550	1554
Pleurocarpous moss	983	985	834	984	817	985	894	983	974
Lichen	1254	1255	1092	1254	1093	1254	1133	1254	1241
Crustose	327	327	287	327	289	327	235	327	329
Foliose	839	839	745	840	747	839	731	839	837
Fruticose	1081	1081	959	1187	959	1081	965	1080	1069
Standing dead	3646	3649	3249	3761	3248	3647	3217	3647	3654
Leaf litter	2942	2944	2697	2940	2695	2940	2552	2942	2911

Table II.4. Continued.

	V 7	Air temp	Air temp	Degree Day	Soil temp	Soil temp	Thaw depth	Precip	Soil moist
Th. 1. 1. C. 1.	Year	(avg)	(max)	(sum)	(avg)	(max)	(avg)	(sum)	(avg)
Utqiagvik Grid									
Woody deciduous	713	713	713	713	633	635	711	713	712
Salix pulchra	183	183	183	183	173	172	183	182	183
Salix rotundifolia	689	689	688	689	614	614	689	689	690
Forb	1562	1563	1561	1560	1339	1328	1535	1562	1566
Petasites frigidus	623	622	623	622	551	550	625	622	622
Stellaria laeta	562	562	563	563	498	497	557	562	561
Graminoid	2715	2714	2713	2716	2445	2449	2721	2716	2721
Arctagrostis latifolia	567	569	568	569	514	516	571	569	570
Carex stans	1820	1820	1818	1819	1656	1653	1825	1819	1822
Dupontia fisheri	1516	1514	1514	1513	1341	1341	1520	1515	1515
Eriophorum russeolum	1561	1560	1558	1560	1356	1355	1565	1561	1566
Eriophorum triste	1408	1406	1409	1408	1259	1256	1421	1411	1414
Luzula arctica	480	481	481	481	428	431	480	481	476
Luzula confusa	703	703	702	702	640	634	706	702	706
Poa arctica	1191	1188	1189	1189	1044	1046	1183	1189	1186
Bryophyte	2978	2976	2980	2979	2620	2614	2971	2976	2985
Acrocarpous moss	2261	2268	2263	2266	1800	1800	2268	2264	2276
Pleurocarpous moss	2068	2067	2067	2068	1818	1811	2071	2065	2075
Lichen	1203	1203	1204	1203	1081	1080	1204	1203	1204
Foliose	863	865	863	864	767	763	866	863	868
Fruticose	949	948	949	949	860	860	948	950	950
Standing dead	3788	3792	3791	3790	3358	3358	3801	3789	3794
Leaf litter	3047	3047	3049	3047	2778	2771	3031	3049	3048

Table II.5. Change in vascular plant diversity at Atqasuk and Utqiagʻvik between 2010 and 2019. *Alpha*, *beta*, Shannon and Evenness diversity indices were calculated for each plot (n=30); the average index value and the standard deviation (in parentheses) are presented. *Gamma* diversity represents the species richness for the site and is therefore a single value for each year. Linear mixed models were used to generate marginal r² for the relationship between diversity metrics and years; significant relationships are noted in bold. A listing of each species sampled each year is available in Supplemental Table II.S2.

	2010	2012	2013	2014	2015	2016	2017	2018	2019	r ²
Atqasuk Grid										
Alpha	5.77 (2.14)	5.53 (2.08)	5.63 (2.03)	5.83 (2.02)	6.30 (1.84)	5.13 (1.74)	6.00 (2.20)	6.07 (2.30)	5.70 (1.84)	0
Beta	0.22 (0.08)	0.22 (0.08)	0.23 (0.08)	0.23 (0.08)	0.25 (0.07)	0.21 (0.07)	0.23 (0.08)	0.23 (0.09)	0.26 (0.08)	0.01
Gamma	26	25	25	25	25	24	26	26	22	0.88
Shannon	1.34 (0.45)	1.27 (0.41)	1.27 (0.41)	1.29 (0.44)	1.29 (0.38)	1.20 (0.41)	1.27 (0.39)	1.21 (0.44)	1.23 (0.39)	0.01
Evenness	0.81 (0.12)	0.79 (0.11)	0.79 (0.12)	0.76 (0.17)	0.72 (0.15)	0.77 (0.12)	0.75 (0.13)	0.70 (019)	0.72 (0.13)	0.04
Utqiagvik Gri	1									
Alpha	7.30 (2.51)	6.77 (2.31)	8.13 (2.62)	7.23 (2.67)	7.60 (2.59)	6.63 (2.63)	7.93 (3.02)	6.43 (2.34)	7.33 (2.51)	0
Beta	0.25 (0.09)	0.27 (0.09)	0.27 (0.09)	0.27 (0.10)	0.24 (0.08)	0.24 (0.09)	0.26 (0.10)	0.25 (0.09)	0.25 (0.09)	0
Gamma	29	25	30	27	32	28	30	26	29	0.32
Shannon	1.42 (0.45)	1.30 (0.37)	1.41 (0.39)	1.36 (0.39)	1.30 (0.35)	1.24 (0.36)	1.30 (0.33)	1.23 (0.34)	1.28 (0.32)	0.02
Evenness	0.72 (0.15)	0.70 (0.13)	0.68 (0.11)	0.71 (0.11)	0.66 (0.14)	0.68 (0.13)	0.65 (0.10)	0.68 (0.12)	0.67 (0.12)	0.01

Table II.6. Change in maximum height within a plot of each functional group at Atqasuk and Utqiagvik between 2010 and 2019. Not all functional groups were present in each plot. Values represent the number of plots present, the average height (cm) and the standard deviation (in parenthesis). Bold values represent significant marginal r² values based on a linear mixed model.

	n	2010	2012	2013	2014	2015	2016	2017	2018	2019	\mathbf{r}^2
Atqasuk Grid											
Woody deciduous	28	11.5 (6.0)	13.5 (6.0)	14.5 (7.8)	14.4 (7.3)	17.6 (8.1)	16.2 (6.6)	18.4 (7.2)	18.2 (8.1)	20.5 (9.7)	0.11
Betula nana	12	12.5 (6.6)	15.6 (6.0)	16.6 (8.3)	16.0 (8.0)	18.5 (8.2)	17.0 (7.3)	19.1 (7.9)	18.9 (8.3)	20.3 (8.9)	0.07
Salix pulchra	7	9.3 (3.3)	9.0 (2.2)	11.3 (4.2)	11.3 (3.5)	14.8 (6.7)	14.8 (3.9)	17.0 (4.8)	16.3 (6.6)	22.0 (10.5)	0.31
Woody evergreen	19	7.4 (5.0)	9.6 (4.2)	9.8 (6.0)	8.2 (5.6)	10.4 (7.0)	10.2 (5.0)	10.8 (4.3)	10.9 (5.8)	11.2 (4.5)	0.04
Cassiope tetragona	8	7.0 (4.8)	7.7 (3.7)	8.6 (5.9)	8.1 (7.7)	8.6 (5.2)	8.8 (4.1)	9.2 (3.5)	9.2 (5.7)	10.5 (7.3)	0.03
Ledum palustre	17	6.9 (4.6)	8.6 (4.6)	9.7 (6.3)	6.7 (4.3)	8.5 (4.8)	9.9 (5.2)	10.2 (4.6)	11.4 (6.0)	10.5 (3.2)	0.05
V. vitis-idaea	19	2.1 (3.5)	5.9 (3.4)	5.1 (3.6)	5.1 (3.0)	6.9 (7.1)	5.7 (3.7)	6.5 (3.9)	6.5 (4.4)	8.3 (3.0)	0.10
Forb	21	3.6 (1.4)	5.2 (3.1)	6.6 (5.5)	7.2 (4.1)	7.8 (4.8)	6.0 (3.5)	9.7 (3.8)	8.9 (3.9)	10.4 (3.7)	0.19
Rubus chamaemorus	8	3.7 (1.6)	5.0 (3.2)	5.1 (3.6)	5.5 (1.8)	8.0 (4.2)	6.1 (3.5)	8.9 (1.8)	8.8 (3.8)	10.8 (3.6)	0.30
Graminoid	15	14.0 (5.2)	19.6 (7.3)	21.6 (8.6)	18.5 (6.8)	23.5 (8.7)	20.9 (8.3)	26.4 (9.1)	25.9 (9.8)	32.1 (10.8)	0.21
Carex aquatilis	17	15.6 (4.5)	22.1 (7.3)	23.1 (8.0)	21.0 (6.1)	25.6 (7.8)	25.3 (7.8)	30.3 (8.6)	30.0 (9.3)	35.8 (10.4)	0.31
Carex bigelowii	9	11.3 (6.0)	13.8 (7.6)	15.2 (6.9)	13.1 (6.1)	16.5 (8.5)	14.6 (3.2)	19.9 (7.9)	18.3 (6.8)	23.3 (10.9)	0.15
E. russeolum	6	9.6 (3.7)	13.6 (5.9)	20.1 (3.7)	19.4 (6.4)	22.5 (6.3)	18.6 (5.4)	26.0 (4.5)	24.8 (7.0)	28.8 (7.6)	0.44
E. vaginatum	14	9.5 (3.7)	14.4 (7.1)	17.7 (9.3)	13.7 (5.8)	19.1 (7.5)	14.5 (6.0)	18.4 (7.8)	19.6 (6.7)	25.5 (10.0)	0.18
Trisetum spicatum	4	9.3 (3.0)	14.2 (3.8)	14.6 (4.7)	13.2 (3.1)	13.8 (5.3)	14.1 (4.2)	19.1 (2.3)	17.8 (3.9)	21.6 (9.1)	0.30

Table II.6. Continued.

	n	2010	2012	2013	2014	2015	2016	2017	2018	2019	\mathbf{r}^2
Utqiagvik Grid											
Woody deciduous	28	2.0 (1.2)	2.4 (1.2)	2.3 (1.1)	2.3 (1.4)	2.9 (2.4)	2.9 (1.3)	3.9 (2.7)	2.9 (1.4)	3.0 (1.9)	0.06
Salix pulchra	2	3.5 (1.1)	3.9 (1.3)	3.5 (0.9)	2.6 (0.8)	5.0 (3.6)	4.7 (0.5)	3.8 (2.4)	4.2 (1.4)	3.9 (1.5)	0.02
Salix rotundifolia	7	1.6 (0.7)	2.0 (0.6)	2.0 (0.9)	2.2 (1.5)	2.2 (1.7)	2.5 (0.8)	3.6 (2.8)	2.5 (1.0)	2.7 (1.9)	0.08
Forb	10	4.5 (3.4)	5.7 (4.8)	4.6 (3.5)	3.6 (2.8)	5.9 (3.9)	5.6 (3.9)	6.4 (4.3)	5.4 (3.7)	8.3 (5.4)	0.04
Petasites frigidus	7	3.8 (2.6)	7.3 (6.1)	5.4 (3.8)	5.4 (3.5)	6.6 (4.6)	5.2 (4.2)	6.3 (4.5)	6.8 (4.1)	9.7 (6.5)	0.05
Saxifraga cernua	4	0.9 (0.5)	4.7 (4.4)	1.5 (1.2)	1.0 (1.3)	2.8 (1.2)	3.8 (2.5)	2.8 (0.7)	4.0 (0.4)	4.2 (1.4)	0.16
Stellaria laeta	4	2.8 (0.8)	4.9 (2.3)	3.7 (1.8)	3.7 (1.6)	5.4 (1.1)	3.5 (1.3)	5.1 (2.4)	3.7 (1.9)	5.6 (3.4)	0.05
Graminoid	22	10.0 (4.1)	13.8 (5.4)	12.7 (4.9)	11.9 (5.3)	17.4 (6.2)	15.1 (4.9)	18.8 (7.4)	17.1 (8.0)	23.1 (8.3)	0.21
Arctagrostis latifolia	4	7.2 (0.9)	7.3 (1.8)	7.5 (2.8)	7.1 (1.7)	8.4 (1.7)	9.8 (4.1)	12.5 (4.9)	11.5 (5.3)	13.8 (10.4)	0.20
Carex stans	23	10.2 (4.4)	14.2 (5.1)	12.8 (4.5)	12.0 (5.8)	16.2 (5.4)	15.1 (5.3)	19.1 (8.1)	17.3 (9.1)	22.8 (7.7)	0.20
Dupontia fisheri	16	8.6 (3.2)	11.5 (5.2)	11.2 (3.7)	9.3 (3.9)	17.8 (5.9)	12.8 (4.2)	16.7 (5.3)	15.2 (4.0)	20.2 (7.0)	0.26
E. russeolum	14	6.9 (2.0)	11.2 (3.5)	10.6 (3.5)	9.2 (2.7)	13.2 (3.0)	12.3 (2.2)	14.6 (3.3)	14.9 (4.5)	17.6 (4.5)	0.39
E. triste	9	5.7 (2.9)	10.4 (4.2)	9.6 (4.9)	9.5 (1.5)	14.3 (5.0)	10.5 (2.8)	14.3 (3.8)	14.0 (4.7)	17.9 (5.0)	0.34
Luzula arctica	3	4.1 (1.2)	9.7 (4.2)	6.4 (2.7)	4.4 (0.4)	5.5 (5.1)	8.3 (2.2)	9.3 (3.2)	3.8 (3.4)	5.8 (2.9)	0.00
Luzula confusa	8	2.9 (1.2)	5.6 (2.1)	5.2 (2.6)	3.8 (1.6)	5.7 (3.6)	7.8 (3.1)	6.6 (3.7)	5.6 (2.8)	6.7 (3.3)	0.11
Poa arctica	13	4.3 (1.8)	6.7 (4.1)	5.8 (3.3)	3.6 (2.2)	6.8 (2.9)	7.2 (4.4)	8.2 (3.5)	5.7 (3.0)	10.7 (6.4)	0.12

Table II.7. The relationship between plant height (by growth from and species) and abiotic factors at Utqiagvik and Atqasuk. Values represent marginal r^2 values from general linear mixed models regressing functional group average max height with abiotic factors including time. Plot location and year were considered sources of random error (n varies by functional group and site, see Table II.5). Column headers indicate abiotic variables and row headers indicate broad functional groups. Bold values represent significant effects.

	Year	Air temp (avg)	Air temp (max)	Degree Day (sum)	Soil temp (avg)	Soil temp (max)	Thaw Depth (avg)	Precipitation (sum)	Soil moisture (avg)
Vegetation Height									
Atqasuk Grid									
Woody deciduous	0.11	0.02	0.03	0.01	0.00	0.00	0.02	0.00	0.00
Betula nana	0.07	0.01	0.02	0.01	0.00	0.00	0.00	0.00	0.00
Salix pulchra	0.31	0.03	0.08	0.01	0.02	0.01	0.10	0.00	0.00
Woody evergreen	0.04	0.01	0.02	0.01	0.04	0.03	0.00	0.00	0.00
Cassiope tetragona	0.03	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Ledum palustre	0.05	0.00	0.02	0.00	0.04	0.02	0.00	0.00	0.00
Vaccinium vitis-idaea	0.10	0.04	0.05	0.02	0.00	0.00	0.01	0.00	0.00
Forb	0.19	0.02	0.03	0.00	0.02	0.01	0.02	0.02	0.00
Rubus chamaemorus	0.30	0.03	0.06	0.00	0.02	0.02	0.08	0.00	0.00
Graminoid	0.21	0.04	0.09	0.01	0.03	0.02	0.02	0.00	0.01
Carex aquatilus	0.31	0.04	0.09	0.01	0.04	0.03	0.04	0.00	0.03
Carex bigelowii	0.15	0.02	0.06	0.00	0.00	0.00	0.00	0.00	0.00
Eriophorum russeolum	0.44	0.05	0.11	0.02	0.10	0.12	0.04	0.06	0.00
E. vaginatum	0.18	0.05	0.13	0.02	0.00	0.00	0.01	0.01	0.00
Trisetum spicatum	0.30	0.03	0.08	0.00	0.02	0.00	0.17	0.01	0.00

Table II.7. Continued.

	Year	Air temp (avg)	Air temp (max)	Degree Day (sum)	Soil temp (avg)	Soil temp (max)	Thaw Depth (avg)	Precipitation (sum)	Soil moisture (avg)
Vegetation Height									
Utqiagvik Grid									
Woody deciduous	0.06	0.04	0.03	0.02	0.01	0.01	0.00	0.00	0.00
Salix pulchra	0.02	0.06	0.10	0.07	0.02	0.01	0.00	0.05	0.00
Salix rotundifolia	0.08	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.00
Woody evergreen	-	-	-	-	-	-	-	-	-
Forb	0.04	0.05	0.05	0.03	0.00	0.00	0.02	0.00	0.01
Petasites frigidus	0.05	0.04	0.04	0.02	0.00	0.00	0.02	0.00	0.05
Saxifraga cernua	0.16	0.09	0.18	0.07	0.08	0.06	0.00	0.04	0.00
Stellaria laeta	0.05	0.15	0.12	0.10	0.00	0.00	0.05	0.00	0.03
Graminoid	0.21	0.14	0.14	0.09	0.00	0.00	0.00	0.00	0.01
Arctagrostis latifolia	0.20	0.05	0.05	0.02	0.00	0.02	0.08	0.00	0.01
Carex stans	0.20	0.11	0.11	0.06	0.00	0.00	0.00	0.00	0.01
Dupontia fisheri	0.26	0.24	0.24	0.17	0.00	0.00	0.00	0.00	0.00
Eriophorum triste	0.34	0.21	0.22	0.13	0.00	0.00	0.01	0.01	0.00
Eriophorum russeolum	0.39	0.18	0.22	0.12	0.01	0.01	0.01	0.00	0.00
Luzula arctica	0.00	0.07	0.06	0.06	0.03	0.09	0.12	0.01	0.19
Luzula confusa	0.11	0.10	0.13	0.10	0.11	0.14	0.17	0.00	0.00
Poa arctica	0.12	0.14	0.12	0.10	0.01	0.03	0.00	0.00	0.00



Figure II.1. Locations of Atqasuk (red) and Utqiagʻvik (blue) on the North Slope of Alaska (Google Earth, 2020).

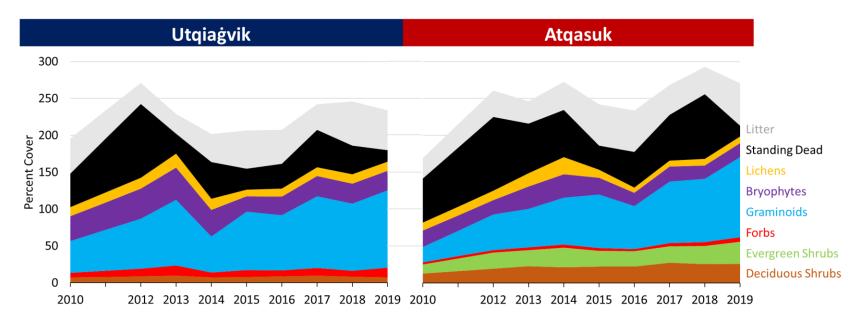


Figure II.2. Cover change over years at both Atqasuk and Utqiagvik.

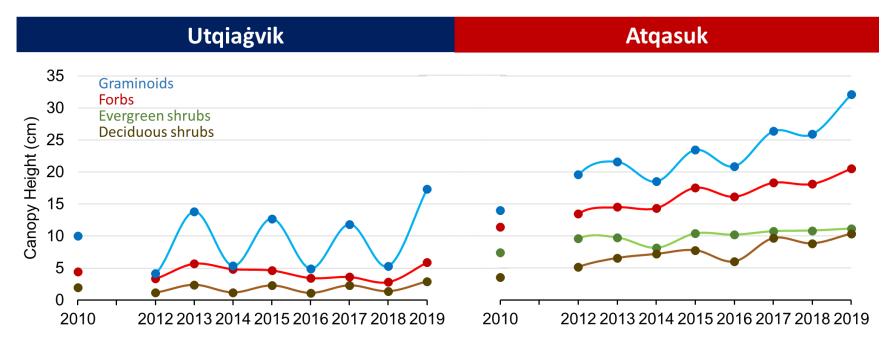


Figure II.3. Height change of functional groups over years in Atqasuk and Utqiaġvik.

Supplementary Table II.S1. Cover of functional groups and the most abundant vascular plant species at Atqasuk and Utqiagvik between 2010 and 2019. Values for a given year represent the average and the standard deviation (in parenthesis) for each plot (=30) in that year. Significant change over time (Ch) was determined by Widely Applicable Information Criterion (WAIC) from Bayesian Poisson regression between cover values and year and noted with an arrow for the direction ($\uparrow \downarrow$), values which varied significantly between years based on a Kruskal-Wallis H test are noted with an *, and the remaining are noted with a --.

-	2010)	2012	2	2013		2014		2015	i	2016	·)	2017	1	2018	3	2019)	Ch
Atqasuk Grid																			
Woody deciduous	11.5	(17.5)	17.1	(23.3)	20.1	(28.6)	18.7	(27.0)	19.2	(26.4)	19.8	(28.6)	24.9	(34.4)	23.3	(33.6)	26.1	(38.0)	1
Betula nana	8.0	(15.8)	12.8	(22.4)	15.0	(26.8)	14.1	(25.4)	13.0	(22.9)	14.2	(27.0)	16.6	(30.2)	14.8	(25.9)	16.1	(27.9)	-
Salix pulchra	3.5	(10.0)	4.3	(11.6)	5.1	(13.8)	4.6	(13.0)	6.2	(17.0)	5.7	(14.2)	8.3	(22.0)	8.5	(26.4)	10.0	(30.5)	↑
Woody evergreen	12.2	(11.2)	22.0	(19.8)	21.6	(19.3)	26.4	(24.2)	21.5	(19.9)	20.7	(19.2)	22.5	(20.9)	24.5	(23.5)	29.6	(30.5)	↑
C. tetragona	3.0	(6.5)	3.9	(9.5)	4.3	(10.8)	4.0	(9.2)	4.0	(8.9)	3.6	(8.1)	3.0	(7.0)	3.9	(9.9)	4.7	(11.9)	-
Empetrum nigrum	0.4	(2.0)	0.3	(1.5)	0.2	(0.9)	0.2	(1.3)	0.2	(1.1)	0.2	(0.9)	0.2	(0.9)	0.4	(2.0)	0.4	(2.0)	-
Ledum palustre	3.9	(4.4)	9.3	(9.9)	8.2	(8.5)	9.2	(10.3)	7.5	(7.9)	7.9	(8.8)	8.4	(8.8)	8.1	(9.1)	10.7	(12.7)	-
V. vitis-idaea	5.3	(6.2)	8.8	(9.1)	9.1	(9.7)	13.3	(13.2)	10.0	(10.9)	9.1	(10.0)	11.0	(12.4)	12.4	(13.0)	14.2	(16.0)	↑
Forb	3.2	(4.2)	3.4	(5.0)	3.7	(4.9)	4.6	(6.2)	3.8	(5.5)	3.2	(5.1)	4.3	(6.4)	5.1	(7.5)	6.4	(9.4)	1
A. polifolia	0.0	(0.2)	0.0	(0.2)	0.5	(2.6)	0.7	(3.1)	0.0	(0.0)	0.0	(0.0)	0.5	(2.7)	0.6	(2.6)	0.7	(3.8)	-
Oxyria digyna	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)	0.1	(0.5)	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)	-
P. lapponica	0.1	(0.4)	0.3	(1.1)	0.2	(0.7)	0.3	(1.5)	0.2	(0.9)	0.0	(0.2)	0.1	(0.4)	0.1	(0.6)	0.0	(0.0)	\downarrow
P. sudetica	0.1	(0.4)	0.1	(0.4)	0.2	(0.7)	0.2	(0.5)	0.1	(0.3)	0.0	(0.2)	0.1	(0.4)	0.2	(1.1)	0.0	(0.2)	-
Petasites frigidus	0.0	(0.0)	0.0	(0.0)	0.0	(0.2)	0.1	(0.4)	0.1	(0.4)	0.1	(0.7)	0.1	(0.4)	0.1	(0.4)	0.1	(0.7)	-
P. bistorta	0.3	(1.0)	0.2	(1.1)	0.4	(1.7)	0.4	(1.7)	0.2	(0.9)	0.2	(1.1)	0.3	(1.5)	0.1	(0.5)	0.5	(1.9)	-
P. grandiflora	0.1	(0.4)	0.1	(0.5)	0.1	(0.5)	0.1	(0.7)	0.0	(0.0)	0.1	(0.5)	0.1	(0.4)	0.2	(0.9)	0.0	(0.0)	-
R. pallasii	0.0	(0.0)	0.1	(0.5)	0.1	(0.4)	0.1	(0.5)	0.1	(0.5)	0.0	(0.2)	0.0	(0.0)	0.1	(0.5)	0.1	(0.5)	-
R. chamaemorus	1.9	(3.6)	2.3	(4.6)	2.0	(4.0)	2.5	(4.4)	2.8	(5.3)	2.5	(4.8)	2.9	(5.6)	3.4	(6.0)	4.6	(8.4)	1
Graminoid	20.7	(11.5)	48.1	(28.2)	52.4	(27.8)	63.3	(28.1)	72.6	(35.4)	58.1	(35.9)	83.4	(39.5)	86.1	(45.0)	108.4	(46.0)	1
C. aquatilis	6.7	(8.2)	12.0	(13.2)	16.7	(18.6)	18.4	(20.7)	22.4	(25.5)	20.7	(26.4)	29.0	(32.6)	28.5	(33.5)	38.6	(44.5)	1
C. bigelowii	2.5	(4.6)	4.7	(9.3)	6.3	(12.1)	7.0	(14.1)	7.7	(14.9)	5.0	(9.9)	10.1	(18.8)	8.5	(15.8)	11.2	(21.7)	↑
C. rotundata	0.4	(1.7)	0.6	(3.5)	0.4	(2.2)	0.8	(3.7)	0.6	(2.3)	0.4	(1.4)	0.2	(1.1)	0.1	(0.4)	0.4	(1.7)	-
D. psilosantha	0.1	(0.5)	0.1	(0.3)	0.0	(0.0)	0.0	(0.0)	1.5	(3.1)	0.1	(0.4)	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)	-
E. angustifolium	0.4	(1.5)	1.6	(5.0)	1.7	(4.6)	2.0	(5.5)	3.4	(8.7)	2.1	(6.4)	4.8	(11.3)	5.0	(13.5)	7.1	(17.3)	↑
E. russeolum	1.2	(2.7)	4.3	(8.6)	6.5	(13.6)	9.5	(17.8)	9.5	(17.3)	6.4	(11.8)	8.4	(14.8)	6.9	(13.4)	12.3	(24.5)	-
E. vaginatum	6.5	(9.6)	21.2	(29.7)	18.0	(25.1)	22.1	(29.8)	23.5	(33.2)	21.6	(32.8)	27.5	(38.4)	32.8	(44.3)	33.0	(42.2)	1
Hierochloe alpina	0.2	(0.7)	0.0	(0.0)	0.0	(0.0)	0.2	(1.1)	0.0	(0.0)	0.1	(0.7)	0.4	(1.5)	0.2	(0.7)	0.1	(0.6)	-
Luzula arctica	0.1	(0.4)	0.1	(0.3)	0.0	(0.2)	0.1	(0.4)	0.0	(0.2)	0.1	(0.4)	0.2	(0.5)	0.1	(0.3)	0.2	(0.7)	-
Luzula confusa	1.6	(6.1)	0.9	(4.6)	1.1	(5.7)	0.8	(4.4)	0.9	(3.8)	0.4	(1.8)	0.5	(2.6)	0.6	(3.3)	0.9	(4.4)	\downarrow
T. spicatum	0.9	(2.4)	2.5	(7.1)	1.6	(4.6)	2.3	(5.5)	2.7	(6.2)	1.2	(4.3)	2.2	(5.2)	3.3	(8.5)	4.6	(12.3)	-

Table II.S1 continued.

	2010)	2012	2	2013	1	2014		2015	i	2016	í	2017		2018	3	2019)	Ch
Atqasuk Grid																			
continued																			
Bryophyte	12.4	(11.3)	12.2	(12.3)	29.7	(22.6)	31.4	(21.0)	22.4	(18.0)	18.1	(16.8)	20.2	(17.7)	17.9	(18.1)	18.9	(18.4)	-
A. moss	7.7	(9.7)	8.2	(7.8)	15.5	(15.5)	16.3	(13.0)	9.4	(9.2)	6.5	(7.5)	9.5	(10.6)	7.4	(9.1)	8.0	(9.7)	-
P. moss		(4.4)	2.8	(7.4)	2.4	(6.6)	4.4	(9.6)	3.9	(7.9)	4.8	(11.7)	1.9	(5.7)	2.7	(6.9)	3.2	(6.8)	-
Lichen	9.3	(10.5)	12.5	(12.1)	17.4	(17.4)	22.3	(21.9)	10.1	(12.8)	6.4	(7.8)	7.9	(9.7)	8.6	(9.7)	8.9	(11.0)	-
Crustose	0.0	(0.0)	0.1	(0.5)	3.2	(6.4)	1.2	(2.8)	1.0	(2.8)	0.6	(2.0)	0.3	(1.3)	0.4	(1.7)	0.5	(1.4)	-
Foliose	3.9	(4.9)	4.1	(4.4)	5.0	(5.0)	6.2	(6.8)	3.1	(3.7)	1.6	(2.0)	2.9	(3.8)	3.2	(3.5)	3.1	(3.8)	-
Fruticose	5.4	(6.5)	8.3	(8.5)	9.3	(9.5)	14.9	(14.4)	6.1	(7.3)	4.3	(5.0)	4.7	(5.5)	5.0	(5.7)	5.2	(6.9)	-
Standing dead plants	59.7	(36.3)	100.1	(45.3)	67.4	(34.0)	64.2	(28.0)	32.4	(18.0)	48.5	(29.2)	62.1	(37.9)	87.6	(41.3)	35.8	(17.3)	-
Leaf litter	27.7	(12.0)	35.5	(15.1)	30.2	(14.9)	37.9	(18.4)	56.2	(19.8)	56.0	(23.1)	40.4	(17.6)	37.2	(13.9)	67.2	(34.4)	1
Bare ground	0.0	0.0	0.6	1.6	0.1	0.4	0.1	0.3	2.0	4.5	0.0	0.2	0.1	0.4	0.6	1.6	0.6	0.4	
Utqiagvik Grid																			
Woody deciduous	7.2	(12.9)	8.7	(16.3)	9.6	(16.8)	7.5	(13.7)	7.6	(14.4)	8.5	(16.7)	9.8	(18.2)	8.3	(15.1)	7.3	(14.0)	-
Salix pulchra	1.5	(6.9)	2.6	(11.4)	2.0	(8.5)	1.2	(5.0)	2.1	(9.1)	2.1	(9.3)	2.3	(10.2)	1.6	(7.1)	1.7	(7.9)	-
Salix rotundifolia	5.6	(10.6)	6.2	(10.9)	7.6	(13.4)	6.4	(12.1)	5.5	(11.0)	6.4	(12.4)	7.4	(14.3)	6.7	(13.3)	5.6	(12.0)	-
Forb	6.5	(7.2)	10.6	(17.9)	13.6	(17.0)	6.5	(9.1)	9.9	(19.9)	8.4	(17.2)	10.3	(20.8)	7.9	(17.4)	13.1	(30.8)	-
C. pratensis	0.2	(0.7)	0.3	(0.9)	1.1	(2.9)	0.4	(0.9)	0.2	(0.5)	0.2	(0.7)	0.3	(0.8)	0.2	(0.6)	0.2	(0.9)	-
C. beeringianum	0.3	(1.0)	0.8	(2.8)	1.2	(4.2)	0.5	(1.7)	0.0	(0.0)	0.1	(0.4)	0.0	(0.0)	0.0	(0.2)	0.5	(1.5)	$\mathbf{\downarrow}$
C. officinalis	0.0	(0.2)	0.2	(0.8)	0.3	(0.8)	0.2	(0.6)	0.2	(0.5)	0.2	(0.9)	0.0	(0.2)	0.2	(0.7)	0.0	(0.2)	-
P. frigidus	1.7	(3.6)	5.6	(16.2)	4.1	(11.4)	2.3	(6.2)	6.5	(19.0)	5.1	(15.0)	6.1	(17.5)	5.0	(14.7)	9.5	(29.0)	-
P. hyparctica	0.0	(0.0)	0.0	(0.0)	0.0	(0.2)	0.0	(0.0)	0.0	(0.2)	0.0	(0.2)	0.1	(0.4)	0.0	(0.2)	0.1	(0.3)	-
R. nivalis	0.0	(0.0)	0.0	(0.0)	0.1	(0.3)	0.0	(0.2)	0.1	(0.3)	0.1	(0.4)	0.0	(0.0)	0.0	(0.2)	0.1	(0.3)	-
Saxifraga cernua	1.3	(2.4)	1.0	(1.9)	2.2	(3.4)	0.7	(1.2)	0.7	(1.1)	1.0	(1.6)	1.1	(1.8)	0.9	(1.5)	1.0	(1.5)	-
S. foliolosa	0.3	(0.9)	0.5	(1.4)	0.9	(1.5)	0.5	(1.3)	0.0	(0.2)	0.2	(0.6)	0.2	(0.6)	0.1	(0.4)	0.1	(0.4)	-
S. hieracifolia	0.1	(0.4)	0.1	(0.4)	0.2	(0.7)	0.0	(0.2)	0.1	(0.4)	0.1	(0.4)	0.0	(0.2)	0.1	(0.4)	0.1	(0.4)	-
S. punctata	0.4	(0.9)	0.3	(0.7)	0.4	(1.4)	0.2	(0.7)	0.6	(1.4)	0.4	(1.5)	0.5	(1.4)	0.4	(1.3)	0.5	(1.5)	-
S. atropurpureus	0.2	(0.5)	0.2	(0.7)	0.2	(0.6)	0.2	(0.6)	0.1	(0.3)	0.0	(0.0)	0.1	(0.4)	0.0	(0.0)	0.0	(0.2)	-
S. humifusa	0.2	(0.9)	0.2	(1.1)	0.3	(1.5)	0.0	(0.2)	0.2	(0.5)	0.2	(0.6)	0.0	(0.0)	0.0	(0.0)	0.0	(0.0)	$\mathbf{\downarrow}$
Stellaria laeta	1.6	(3.3)	1.3	(2.3)	2.3	(4.1)	1.4	(2.6)	0.9	(2.0)	0.8	(1.5)	1.6	(3.9)	0.8	(2.5)	0.9	(2.0)	-

Table II.S1 continued.

	2010)	2012	,	2013		2014	ļ	2015	i	2016		2017	,	2018	3	2019)	Ch
Utqiagvik Grid continued																			
Graminoid	43.1	(21.2)	67.5	(40.5)	89.3	(40.1)	48.6	(24.6)	78.9	(38.1)	75.0	(35.7)	97.1	(40.4)	91.0	(44.8)	104.7	(42.3)	1
A. alpinus	1.4	(4.3)	0.9	(3.9)	1.4	(4.3)	1.4	(3.3)	0.6	(1.9)	0.4	(1.0)	0.3	(1.0)	1.2	(3.6)	1.0	(2.7)	$\mathbf{\downarrow}$
Arctophila fulva	0.2	(0.9)	0.3	(1.8)	0.2	(1.1)	0.1	(0.7)	0.2	(0.7)	0.1	(0.5)	0.0	(0.2)	0.1	(0.4)	0.0	(0.2)	-
A. latifolia	2.0	(4.2)	2.5	(5.0)	3.1	(5.8)	1.7	(4.4)	3.1	(6.4)	2.8	(6.6)	4.9	(11.1)	3.6	(10.0)	3.7	(8.7)	-
Carex stans	17.0	(15.4)	26.8	(24.1)	38.8	(32.6)	16.6	(14.2)	36.0	(30.9)	29.9	(27.8)	39.7	(33.3)	37.4	(37.7)	41.7	(31.1)	-
Dupontia fisheri	6.6	(9.1)	9.6	(13.5)	9.9	(14.9)	6.0	(9.2)	8.2	(10.3)	10.4	(17.6)	16.6	(19.1)	10.5	(12.3)	12.9	(14.0)	-
E. russeolum	5.0	(5.2)	7.8	(14.6)	10.7	(15.5)	7.6	(11.3)	11.8	(14.6)	12.6	(18.9)	9.9	(15.0)	13.2	(16.6)	16.9	(20.3)	-
E. triste	2.6	(4.9)	8.7	(16.0)	7.9	(14.8)	6.5	(12.3)	10.2	(16.6)	9.9	(15.6)	12.5	(19.5)	14.8	(25.1)	14.1	(23.1)	1
H. pauciflora	0.0	(0.0)	0.1	(0.5)	1.0	(2.8)	0.4	(1.0)	0.1	(0.4)	0.3	(1.5)	0.8	(3.1)	0.5	(1.4)	0.2	(0.8)	-
Luzula arctica	1.9	(4.9)	3.1	(6.5)	4.2	(10.2)	1.7	(5.3)	1.8	(4.6)	1.4	(3.6)	1.6	(5.6)	1.0	(3.4)	1.1	(3.0)	-
Luzula confusa	1.7	(2.5)	1.6	(2.5)	2.4	(4.1)	1.0	(2.0)	2.3	(3.8)	2.2	(3.5)	1.9	(3.4)	2.0	(4.8)	1.7	(4.5)	-
Poa arctica	4.6	(7.5)	6.0	(15.5)	9.9	(20.2)	5.6	(10.3)	4.4	(9.6)	5.0	(9.2)	8.0	(15.4)	6.8	(14.1)	10.8	(20.5)	-
Bryophyte	32.6	(16.9)	40.5	(25.4)	40.5	(19.1)	34.2	(16.4)	20.6	(12.1)	24.7	(16.7)	27.3	(19.6)	27.0	(20.4)	26.6	(16.9)	-
A. moss	16.6	(15.6)	13.6	(14.2)	18.5	(13.1)	13.2	(11.7)	9.6	(9.2)	11.3	(14.1)	11.8	(12.8)	11.7	(16.7)	9.8	(13.1)	$\mathbf{\downarrow}$
P. moss	3.8	(7.2)	20.8	(23.3)	16.9	(19.0)	14.6	(18.2)	9.6	(12.8)	12.0	(15.7)	13.2	(17.3)	12.2	(16.6)	15.1	(16.5)	-
Lichen	10.0	(13.2)	14.1	(16.8)	18.7	(22.5)	14.9	(17.8)	9.2	(12.4)	10.9	(15.2)	11.9	(15.4)	12.9	(19.3)	12.6	(17.3)	-
Crustose	0.0	(0.0)	0.1	(0.4)	0.5	(1.1)	0.4	(1.1)	0.2	(0.5)	0.2	(0.5)	0.1	(0.3)	0.0	(0.2)	0.1	(0.4)	-
Foliose	3.2	(4.7)	4.9	(7.3)	6.3	(9.2)	4.5	(6.9)	3.0	(5.0)	4.0	(9.0)	4.2	(7.4)	4.1	(7.6)	4.6	(7.9)	-
Fruticose	6.8	(9.8)	9.1	(12.4)	11.9	(16.2)	10.0	(12.9)	6.0	(9.2)	6.7	(10.2)	7.6	(11.1)	8.8	(14.6)	7.9	(13.0)	-
Standing dead plants	45.2	(21.1)	100.4	(40.7)	27.2	(18.8)	49.8	(23.6)	28.2	(11.6)	33.4	(15.5)	50.7	(26.8)	38.7	(23.0)	32.8	(17.3)	-
Leaf litter	47.6	(20.9)	28.4	(20.7)	26.7	(19.5)	38.0	(17.2)	51.5	(23.0)	45.9	(27.2)	34.4	(22.8)	59.9	(25.4)	55.7	(28.0)	-
Bare ground	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.8	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.2	-

Supplementary Table II.S2. Presence or absence of taxa (1 = present; - = absent) at Atqasuk and Utqiagʻvik between 2010 and 2019. The sum of all the years the species occurred is provided as the frequency (Freq) and the *gamma* diversity is provided for each year as the sum of the vascular plants that were encountered each year.

Atqasuk Grid	2010	2012	2013	2014	2015	2016	2017	2018	2019	Freq
Andromeda polifolia	1	1	1	1	-	-	1	1	1	7
Betula nana	1	1	1	1	1	1	1	1	1	9
Carex aquatilis	1	1	1	1	1	1	1	1	1	9
Carex bigelowii	1	1	1	1	1	1	1	1	1	9
Carex rariflora	-	-	-	-	-	-	1	1	-	2
Carex rotundata	1	1	1	1	1	1	1	1	1	9
Cassiope tetragona	1	1	1	1	1	1	1	1	1	9
Diapensia lapponica	-	_	-	-	-	-	1	-	-	1
Dupontia psilosantha	1	1	-	-	1	1	-	-	-	4
Empetrum nigrum	1	1	1	1	1	1	1	1	1	9
Eriophorum angustifolium	1	1	1	1	1	1	1	1	1	9
Eriophorum russeolum	1	1	1	1	1	1	1	1	1	9
Eriophorum vaginatum	1	1	1	1	1	1	1	1	1	9
Hierochloe alpine	1	-	-	1	-	1	1	1	1	6
Juncus biglumis	1	-	-	-	-	-	-	-	-	1
Ledum palustre	1	1	1	1	1	1	1	1	1	9
Lloydia serotine	1	_	-	-	-	-	-	-	-	1
Luzula arctica	1	1	1	1	1	1	1	1	1	9
Luzula confusa	1	1	1	1	1	1	1	1	1	9
Luzula wahlenbergii	-	1	1	1	1	-	-	-	-	4
Oxyria digyna	-	-	-	-	1	-	-	-	-	1
Pedicularis lapponica	1	1	1	1	1	1	1	1	-	8
Pedicularis sudetica	1	1	1	1	1	1	1	1	1	9
Petasites frigidus	-	-	1	1	1	1	1	1	1	7
Poa arctica	_	_	-	-	1	-	_	-	-	1
Polygonum bistorta	1	1	1	1	1	1	1	1	1	9
Polygonum viviparum	1	-	1	-	-	-	-	1	-	3
Potentilla hyparctica	_	1	-	-	-	-	_	-	-	1
Pyrola grandiflora	1	1	1	1	_	1	1	1	-	7
Ranunculus pallasii	_	1	1	1	1	1	1	1	1	8
Rubus chamaemorus	1	1	1	1	1	1	1	1	1	9
Salix pulchra	1	1	1	1	1	1	1	1	1	9
Trisetum spicatum	1	1	1	1	1	1	1	1	1	9
Vaccinium vitis-idaea	1	1	1	1	1	1	1	1	1	9
gamma diversity	26	25	25	25	25	24	26	26	22	7

Supplementary Table II.S2. Continued.

Utqiagvik Grid	2010	2012	2013	2014	2015	2016	2017	2018	2019	Freq
Alopecurus alpinus	1	1	1	1	1	1	1	1	1	9
Arctophila fulva	1	1	1	1	1	1	1	1	1	9
Arctagrostis latifolia	1	1	1	1	1	1	1	1	1	9
Calamagrostis holmii	1	-	-	-	1	-	-	-	-	2
Cardamine pratensis	1	1	1	1	1	1	1	1	1	9
Carex stans	1	1	1	1	1	1	1	1	1	9
Carex subspathacea	1	-	-	-	-	-	_	-	-	1
Cerastium beeringianum	1	1	1	1	-	1	1	1	1	8
Chrysosplenium tetrandrum	1	-	1	-	-	1	_	-	-	3
Cochlearia officinalis	1	1	1	1	1	1	1	1	1	9
Draba lacteal	1	_	_	-	1	-	1	_	_	3
Draba micropetala	-	_	1	-	1	1	_	_	-	3
Dupontia fisheri	1	1	1	1	1	1	1	1	1	9
Eriophorum russeolum	1	1	1	1	1	1	1	1	1	9
Eriophorum triste	1	1	1	1	1	1	1	1	1	9
Eriophorum vaginatum	_	_	_	_	_	-	1	_	1	2
Festuca brachyphylla	1	1	_	_	1	_	_	_	_	3
Hierochloe pauciflora	_	1	1	1	1	1	1	1	1	8
Juncus biglumis	_	_	_	_	_	_	_	_	1	1
Luzula arctica	1	1	1	1	1	1	1	1	1	9
Luzula confusa	1	1	1	1	1	1	1	1	1	9
Oxyria digyna	1	_	_	_	_	_	_	_	-	1
Pedicularis kanei	_	_	_	1	1	1	1	_	1	5
Pedicularis sudetica	_	_	_	_	1	_	1	1	-	3
Petasites frigidus	1	1	1	1	1	1	1	1	1	9
Poa arctica	1	1	1	1	1	1	1	1	1	9
Potentilla hyparctica	-	_	1	-	1	1	1	1	1	6
Ranunculus nivalis	_	_	1	1	1	1	1	1	1	7
Ranunculus pallasii	_	_	1	1	1	_	1	1	1	6
Ranunculus pygmaeus	_	_	1	_	_	-	_	_	_	1
Salix pulchra	1	1	1	1	1	1	1	1	1	9
Salix rotundifolia	1	1	1	1	1	1	1	1	1	9
Saxifraga cernua	1	1	1	1	1	1	1	1	1	9
Saxifraga foliolose	1	1	1	1	1	1	1	1	1	9
Saxifraga hieracifolia	1	1	1	1	1	1	1	1	1	9
Saxifraga punctate	1	1	1	1	1	1	1	1	1	9
Senecio atropurpureus	1	1	1	1	1	-	1	_	1	7
Stellaria humifusa	1	1	1	1	1	1	-	_	-	6
Stellaria laeta	1	1	1	1	1	1	1	1	1	9
Gamma diversity	29	25	30	27	32	28	30	26	29	

Chapter III

Extended Review of Literature

Arctic relevance

The Arctic is expected to change in the near future due to climate change (IPCC 2018). The Arctic is warming at twice the rate of the rest of the world (AMAP 2019). The primary effects of climate change include the melting of glaciers, and the thawing of permafrost. The Arctic is therefore at the forefront of climate change research.

The Arctic is of interest to ecologists and climate scientists because it is a region responsible for helping to balance the Earth's carbon and energy balances, largely as a carbon sink (Billings 1987; Chapin et al. 2005). 97% or more of the carbon in the Arctic is locked in permafrost soils relatively free from decomposition and as temperatures warm this carbon may decompose and become a net source of carbon dioxide instead of a regional sink (Oechel et al. 1993). Additionally, there is evidence that ecosystem net primary productivity and carbon loss increases with warming (Oechel et al. 1993; Oberbauer 2007). The region is considered especially vulnerable to the average global temperature increases as the temperature swings are much higher and the effects on the landscape more noticeable (IPCC 2018). Climate change is already affecting the species distribution of some organisms. Animal species are migrating northward or increase in altitude (if alpine) at a median rate of 16.9 km per decade (Chen et al. 2011). Estimations for plant species migrations are at a much lower pace, averaging 29 meters per decade (Lenoir et al. 2008). Terrestrial isotherms (determinant of possible vegetation communities, i.e. the "tree line") are progressing northward at a median velocity of 27.3 km per

decade over the last 50 years (Burrows et al. 2011). This may outpace the northward progression of many plant species; estimates predict that plants will not be able to keep up with changing isotherms or animal communities and that habitat and trophic mismatches will occur as entire species shift their natural ranges (Corlett & Westcott 2013). Species are generally dependent on both the capacity to migrate and the capacity to undergo adaptive physiological changes to meet the demands of regional climate changes (Pauls et al. 2013).

Arctic Vegetation Communities

The Arctic may be described as a series of environments which have short growing seasons and low average temperatures for most of the year which limit growth and soil microbial activity (Bliss 1962; Billings and Mooney 1968). The vegetative communities in the Arctic are adapted to cold summers, freezing winters, and low nutrient availability (Chapin 1983; Chapin et al. 1995a). The typical cold and windy conditions restrict plants to slow growth and reproductive rates and put them at risk of desiccation when overly exposed (Bliss 1962; Billings and Mooney 1968; Bell and Bliss 1980). Vegetation is thus adapted to the extreme climatic conditions of the area (Bliss 1962; Billings and Mooney 1968; Savile 1972).

Arctic plant species are essentially all perennial. This includes graminoids (grasses, sedges, and rushes), forbs, mosses, lichens, and prostrate shrubs. Species are typically long lived; *Betula* and *Salix* (birch and willow) may live for around 200-400 years, *Luzula* (woodrushes) may live for 90-130 years, and *Eriophorum* (cotton grass) may live for 120-190 years (Quinn 2008). Asexual reproduction is especially common, although plants also practice sexual reproduction as well (Quinn 2008). Arctic soils are typically considered to be rich in their soil seed banks and may persist for years. (Chapin 1995b).

Since the last glacial maximum (LGM) approximately 23,000-18,000 years ago the Arctic has been open to colonization (Hewitt 1996). This recolonization sequence has likely occurred during each glacial recession period (Hewitt 1996). Recolonization of the Arctic has thus always followed in the wake of receding glaciers (Stewart et al. 2016). For plant species, recolonization of the Arctic has relied on unglaciated areas which acted as refuge for plants during the ice age (Eidesen et al. 2013).

Recent efforts utilizing landscape genetics has allowed scientists to track the probable migration routes and determine probable refuge sites of the ancestors of today's modern Arctic plants, in addition to accounting for likely landscape barriers impeding plant migration ((Hewitt 1996, Eidesen 2013). Understanding these patterns may eventually allow for useful modeling of climate change related species range shifts in the Arctic.

The Arctic is an environment determined largely by glaciation patterns. The last glaciation occurred from approximately 23,000 to 18,000 years ago, in some cases preserving vegetation from the era (Hewitt 1996). The ancestors of today's North American and Eurasian vegetation were situated far south enough of the glaciers to find habitable areas (Hewitt 1996) or were residing in suitable mountain habitats which served as refugia for cold adapted vegetation (Eidesen et al. 2013). Potential areas of refuge include the Pyrenees mountains, the Carpathian mountains, the Balkan mountains, the Urals, the Alps range, the Caucasus range, Florida, Mexico, Fennoscandia (Finland and Scandinavia), and Beringia (peninsulas on either side of the Bering Strait) (Hewitt 1996, Eidesen 2013).

Not all refugia maintained the same level of genetic diversity. Amplified fragment length polymorphism analysis of circumpolar plant species shows that Beringia was probably the biggest refuge for plant diversity during the last glaciation. Species and genetic diversity are

highest in Beringia, with more species richness found in Eastern Siberia (Eidesen et al. 2013; Stewart et al. 2016). Fennoscandia retained an unglaciated environment large enough to maintain some plant species from before the last glaciation (Eidesen et al. 2013). The Urals and the Alps appear to have contributed more to current Arctic plant species genetics than other European mountain ranges (Skrede et al. 2016).

It is apparent that glaciation was a major barrier to the movement of plants across the Arctic landscape, and colonization became possible as the glaciers receded (Stewart et al 2016). The Greenland ice cap is a geographically large physical barrier to plant dispersal (Eidesen et al. 2013). Large bodies of water also appear to be significant barriers to migration. Specifically, travel across the Atlantic and the Arctic ocean is difficult for vascular plants; moss spores appear to be an exception (Kyrkjeeide et al. 2016). Large rivers are also a barrier to vascular plant species. Specific examples include Siberia's largest rivers the Lena and the Kolyma (Eidesen et al. 2013). Mountain ranges appear to be barriers between populations. Mountain ranges in Europe divide their surrounding areas into distinct genetic groups (Eidesen et al. 2013). However, it is important to note that mountains host alpine species which are closely related to contemporary Arctic species (an example is *Dryas octopetala*, or mountain avens). The fact that many tundra plants are descended from alpine populations is an example of a population bridge becoming a barrier with geological time (Slatkin 1987). There is no genetic exchange across the North Pole (Eidesen et al. 2013; Hoffman 2012).

Regional diversity in the Arctic tends to correlate strongly with landscape age, accounting for a trend of deglaciation (Stewart et al. 2016). Species and genetic diversity decrease both west and east of Beringia indicating that it was a refuge source for many species common throughout the Eurasian and North American Arctic (Eidesen et al. 2013; Stewart et al.

2016). The regions with the highest gene flow exist between central Canada and Beringia, between Fennoscandia, Iceland, and the British Isles, and within Siberia between the Lena river, the Ural mountain range, and central northern Russia (Eidesen et al. 2013). This effectively accounts for gene flow east and west of Beringia and from out of Fennoscandia. Areas with very little genetic exchange (borders to migration) include the Arctic and Atlantic oceans, the area across the Greenland ice cap, and between the Ural Mountains and southern European mountain ranges (Eidesen et al. 2013). Areas with more limited dispersal include Beringia southward from the Hudson Bay area into Eastern North America, and the areas surrounding the Lena and the Kolyma rivers (Eidesen et al. 2013).

As species move in response to shifting climates, changes in the plants of migrating populations is likely to occur. This may occur gradually or suddenly. In a gradual case, genetic changes may occur as a population migrates into habitats with different abiotic conditions. The expanding edges of populations will tend to have less diversity than centralized portions of populations, due in part to natural selection and lesser quantities of individuals at the periphery (less representative of possible alleles than the central population) (Slatkin 1987, Rolland et al. 2015). This may result in a failure to colonize a habitat. In other cases, this may result in patchy colonization distribution. In a sudden migration scenario, a population may experience a founder effect where the colonizing plants represent only a fraction of the genes found within the total population. Examples of this sudden migration scenario include long distance dispersal (LDD), where individuals from a given population are dispersed over a relatively long distance. Founder events resulting from successful LDD can effectively reduce the number of alleles found in the newly colonized area (Alsos et al. 2015). Vectors for LDD include wind, driftwood, sea ice, ocean currents, and birds (Nathan et al. 2006). However, successful LDD is a rare event and

ultimately not necessary for colonizing most mainland areas of the Arctic; what is necessary for colonizing new areas is the number of dispersal events, number of migration routes available, the distance of migration and the number of available vectors, including birds, wind, sea ice, and driftwood (Alsos et al. 2015; Hoffman 2012).

There is a decrease in genetic diversity with migration distance in the Arctic. Diversity decreases not only east and west of Beringia, but also as populations move northward.

Hybridizations may occur between related colonizing species and introgressions back into the population may reduce genetic distinctness between species (Nichols & Hewitt 1994). This produces immature plant communities in the northern extremes of habitable land including small islands in the Arctic Ocean (Alsos et al. 2015). Long-distance dispersal is not necessary for the colonization of the most extreme reaches of habitable land, nor is adaptation. What is necessary for colonizing new areas is the number of dispersal events, number of migration routes available, the distance of migration and the number of available vectors, including birds, wind, sea ice, and driftwood (Alsos et al. 2015; Hoffman 2012).

Arctic vegetation has well documented responses to changes in environmental conditions. Plants found in Arctic regions are typically limited by cold temperatures, low nutrient availability, and a short growing season (Chapin 1983; Chapin et al. 1995). Plants respond to warming with accelerated life cycle progression (Arft et al. 1999; Hollister and Flaherty 2010), and reproductive success with a dampening effect over time (Kremers et al. 2015). The primary causes of enhanced plant growth are a prolonged growing season, warmer air and soil temperatures, earlier snowmelt, and soil moisture (Walther 2010; Oberbauer et al. 2013; Gamon et al. 2013).

Due to the fact that plant physiology and morphology are constrained by their temperatures, it is almost certain that Arctic plants and their community composition will be impacted by climate change. Research shows that in general, responses to warming vary between species, location, and also from year to year (Hollister et al. 2005; Dunne et al. 2003). The effects of warming are examined by observing vegetation response to both natural and artificial warming (Thorhallsdottir 1998; Arft et al. 1999; Hollister et al. 2005a).

Changes in vegetation composition vary. There has been a northward expansion of shrubs and trees, altering community composition (Tape et al. 2006; Elmendorf et al. 2012). In general, lichens and bryophytes are on the decline globally (Elmendorf et al. 2012a). Among the most consistent responses to warming are increases in inflorescence heights (Hollister et al. 2005a; Hollister et al. 2005b), reproductive biomass (Klady et al. 2011; Campioli et al. 2013), and overall plant height (Hudson et al. 2011).

Extended Methodology

Relevance of the measurements collected

Plant cover and height are two important characteristics of plant communities which may be measured. Cover and height influence albedo via scattering radiation and emitting short-wave radiation, shifting the timing of snow melt or reducing overall snow cover, each of which has implications for modifying ecosystem energy exchanges (Betts 2000; Loranty et al. 2011). Vegetation structure has implications for animals such as birds or small mammals. Variations in plant height or cover determine how much nesting or hiding space is available (Cody 1981; Batzli and Pitelka 1983). Additionally, species may compete with each other for light and may shade each other out (Cornelissen et al. 2001; Zona et al. 2011).

Plants may be divided into functional groups to approximate their roles in ecosystems. While functional groups do not necessarily reflect each specie's life strategy accurately (Chapin and Shaver 1985; Hollister et al. 2015) they allow for large and coarse resolution analysis of a wide manner of vegetation patterns within an efficient time frame (Ustin and Gamon 2010). Functional groups have been commonly used in climate change studies to model alterations in plant community structure and function as well as forecast larger scale ecosystem changes in past research (Lavorel and Garnier 2002; Walker et al. 2006; Dorrepaal 2007).

Vegetation diversity is an important component of ecosystems. The number of species present at a site is linked to the overall productivity of that ecosystem in terms of biomass (Cadotte et al. 2008, Marquard et al. 2009). The number of species present at a site is also linked to the stability of the ecosystem, as the ecosystem can retain functions even if a few species are lost over time (Hector et al. 2010). If accumulated species lost is great enough over time, ecosystems will change often with attendant bottom up trophic cascades (Cardinale et al. 2011; Reich et al. 2012; Scherber et al. 2010). Measuring diversity can help to predict the future plant and animal communities of an ecosystem which is necessary for proper natural resource management (Kessler et al. 2009; Cingolani et al. 2010).

How this Thesis Fits in the Larger ITEX-AON Project

This thesis was completed as a component of several ongoing initiatives which are consistently documenting ecosystem wide climate related fluctuations in the region. The research aimed to document changes within plant communities and was conducted on two Arctic System Science Grids located in Atqasuk and Utqiaʻgvik, Alaska. The thesis was part of a collaborative project known colloquially as the International Tundra Experiment Arctic Observing Network (ITEX-AON) (Figure III.1).

Arctic System Science (ARCSS) Grids

In the early 1990s the National Science Foundation (NSF) established the Arctic System Science (ARCSS) program. The mission of the program is to investigate environmental changes in the Arctic and the resultant physical, chemical, biological, and sociocultural changes in the region. Spatial grids were established in order to conduct research in natural Arctic landscapes. Numerous interdisciplinary regional and landscape scale research projects have been established (National Science Foundation). Plots were sampled using a point frame (Figure III.2) following ITEX protocols.

International Tundra Experiment (ITEX)

In 1990 the International Tundra Experiment (ITEX) was established to investigate environmental changes and the response from plant communities and their ecosystems. The project primarily looks at vegetative responses across a range of habitat extremes. Each site maintained an artificial warming experiment, the most common of which is the utilization of hexagonal open-top chambers (OTCs) to passively warm plants by roughly 1-3°C (Henry and Molau 1997; Hollister et al. 2006). Other protocols have been developed to maintain the consistency of measurements between research sites (Molau and Molgaard 1996). Because research between sites is conducted in a consistent manner syntheses projects examining change over time, space, and optionally artificial warming have been produced (Elmendorf 2012). Research sites are present in both northern tundra and alpine environments with over 30 sites spread throughout the world and within the circumpolar Arctic. Each Arctic nation is represented in ITEX. Common areas of research interests are plant growth rates, phenological development, reproductive efforts, and abundance measurements amongst others.

Arctic Observatory Network (AON)

In 2006 the Arctic Observatory Network (AON) was established as a funding initiative by the NSF to encourage research related to environmental monitoring. The goals of the AON are to better understand current changes occurring in the Arctic, to better predict future changes which may occur in the Arctic, and to develop responses to future changes which may occur in the Arctic. The NSF funds over fifty projects through the AON, including research into the atmosphere, ocean and sea ice, the cryosphere, hydrology, terrestrial ecosystems and sociocultural interactions.

Research on the North Slope

Many historical and contemporary research projects have been conducted in the vicinity of Utqiagʻvik, Alaska located in the high Arctic tundra of the Alaskan North Slope. From 1882 to 1893, during the first International Polar Year (IPY), a weather station was established by explorers to facilitate the documentation of changes within the area. In 1947 the Naval Arctic Research Laboratory was established to facilitate research in the area (Shelesnyak 1948). In 1973, the National Oceanic and Atmospheric Administration began the Barrow, Alaska observatory to monitor the weather patterns and the carbon cycle of the area (Earth System Research Laboratory). In 1992 the Barrow Environmental Observatory was established by the Ukpeagʻvik Iñupiat Corporation for research, which was then rezoned as the Scientific Research District in 2003 by the North Slope Borough. Approximately forty research projects are hosted in Utqiagʻvik every year and the town is well known for its relationship with the scientific community https://eu-interact.org/field-sites/barrow-arctic-research-centerenvironmental-observatory/ (Interact).

Atqasuk, Alaska is roughly 100 km south of Utqiagʻvik and is characterized as low Arctic tundra. The town was formerly a host to a coal mine operated by the Alaska Native Service with a nearby airstrip and Naval Arctic Research Laboratory (Komárková and Webber 1980).

Research in Atqasuk has a shorter history but was studied extensively in the 1980 (Komárková and Webber 1980) and has hosted several research projects since the ITEX sites were established in 1996 (Eisner and Peterson 1998; Streletskiy et al. 2012 Polar Geography; Oechel et al. 2014 Journal Of Geophysical Research: Biogeosciences, 119(3), 323-339 DOI: 10.1002/2013JG002431).

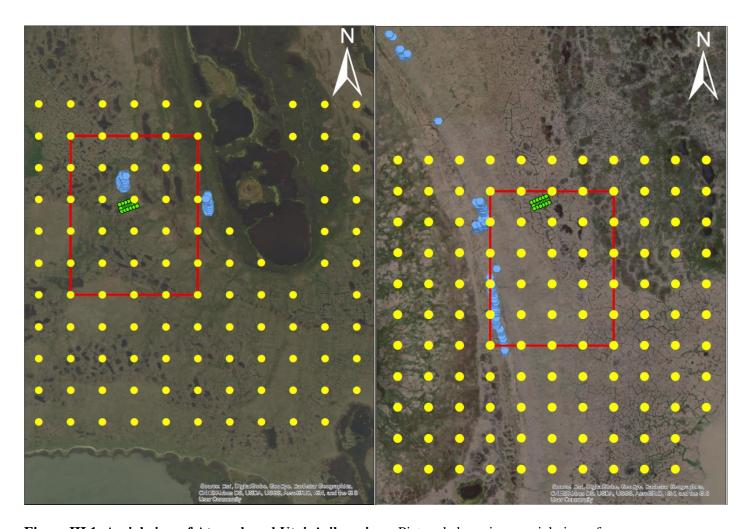


Figure III.1. Aerial view of Atqasuk and Utqiagvik regions. Pictured above is an aerial view of Atqasuk (bottom) and Utqiagvik (top). Yellow dots in each image show the ARCSS grid in either region. Yellow dots connected by a red line represent a subset of 30 plots which are sampled annually and are the focus of this thesis. Blue dots represent ITEX experimentally warmed plots (Hollister et al. 2015) and green dots represent plots from the MISP (spell out and cite). Figure credit goes to Sergio Vargas with the Systems Ecology Lab (SEL) at the University of Texas at El Paso (UTEP).



Figure III.2. Top-down view of a plot with point frame affixed to a plot at Utqiagvik.

Annotated R Code

All analyses were performed using the R statistical software version 3.6.2 (R Core Team 2018). Annotated samples of R code are included for each statistical test. Variables in all caps, bold, and orange font are the variables being tested. Variables in blue and bold font are the categorical variables used for grouping. Datasets used for each test are in green and underlined and defined beneath each section of code. Variables are defined as follows:

COVER: Years of sampling (2010, 2012, 2013, 2014, 2015, 2016, 2017, 2018, 2019) for the average cover of each functional group or species at each site

HEIGHT: Years of sampling (2010, 2012, 2013, 2014, 2015, 2016, 2017, 2018, 2019) for the average max height of functional group or species at each species at each site

ABIOTIC: Years of sampling (2010, 2012, 2013, 2014, 2015, 2016, 2017, 2018, 2019) for average or max of various abiotic factors at each site

YEAR: Years of sampling treated as an integer variable

Year: Years of sampling treated as a factor

PlotID: Plots are coded by letters and numbers

Species: Each species present in a dataset

Spearman's rank correlation coefficient

This test was used to (1) determine the directionality of change for abiotic factors over time (Table II.1) and (2) determine the directionality of functional groups or species cover change over time (Table II.2, Table II.S1), All tests used the "cor.test" function in from the stats package in R.

(1) cor.test(YEAR , ABIOTIC, data=dataset1)

<u>dataset1</u>: each abiotic factor had 30 observations per year. These observations were averaged to one value per year so that the spearman correlation was working with one value per year for each abiotic variable.

(2) cor.test(YEAR, COVER, data=dataset2)

dataset2: observations consisted of cover values for each species for 30 plots at each site and for every year of sampling (2010, 2012:2019); n=270 for each species entry) with each species' cover used for a separate test. The dataset has zeros for all instances in which a species did not occur in a plot. Values were averaged.

Bayesian regression model

This test was used to (1) determine the fit of various functional groups and species cover values to various abiotic factors including time (Table II.2, Table II.4) and (2) determine the fit of various functional group cover values to other functional group cover values (Table II.3). All tests used the "brm" function in the brms package in R.

<u>dataset2</u>: observations consisted of cover values for each species for 30 plots at each site and for every year of sampling (2010, 2012:2019); *n*=270 for each species entry) with each species' cover used for a separate test. The dataset has zeros for all instances in which a species did not occur in a plot. Values were averaged.

Kruskal-Wallis test

This test was used to detect significant differences between years for the cover values of functional groups or species (Table II.2, Table II.S1) using the "kruskal.test" function in R.

(1) <u>kruskal.test(COVER ~ YEAR, data = dataset2)</u>

<u>dataset2</u>: observations consisted of cover values for each species for 30 plots at each site and for every year of sampling (2010, 2012:2019); *n*=270 for each species entry) with each species' cover used for a separate test. The dataset has zeros for all instances in which a species did not occur in a plot. Values were averaged.

Diversity analysis

This test was used for determining various diversity indices (Table II.5). All tests used the "diversity" function in the Vegan package.

- (1) diversity(dataset3\$species, index = "index")
- (2) diversity(dataset3)\$species,
 index="shannon")/log(specnumber(dataset3))

<u>dataset3</u>: observations consisted of presence or absence values for vascular species which occurred in five or more plots for a single year for 30 plots at each site and for every year of

sampling (2010, 2012:2019); *n*=270 for each species entry. Zeros indicate the absence of species in a plot for any given year while non-zero numbers indicate the presence of species.

Linear Mixed Models

This test uses linear mixed models to estimate models and marginal r squared values for height values for either time (1) or other abiotic factors (2) (Table II.6, Table II.7). All tests use the "lmer" function from the lme4 package.

```
(1) lmer(HEIGHT ~ YEAR + (1|PlotID), data = dataset4)
(2) lmer(HEIGHT ~ ABIOTIC + (1|PlotID) + (1|Year), data
= dataset4)
```

<u>dataset4</u>: observations consisted of height values for each species which was present for all nine years of sampling. Only the plots in which the species occurred were used for that species; thus *n* varies by species.

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