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Variation in Tundra Plant Traits Across a Latitudinal Gradient

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Variation in Tundra Plant Traits Across a Latitudinal Gradient

Katlyn Rose Betway

A Thesis Submitted to the Graduate Faculty of

GRAND VALLEY STATE UNIVERSITY

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Abstract

High latitude regions are warming faster than most regions. Studies documenting change in plant cover due to warming have reported that graminoids, deciduous shrubs, and evergreen shrubs are increasing in some regions of the Arctic, but not at others. Mixed responses to warming have caused researchers to shift towards an emphasis on functional traits of individual species rather than their growth forms. This thesis focuses on ten measured plant functional traits for twelve arctic species at three regions spanning a latitudinal gradient in northern Alaska (Utqiagvik, Atqasuk, and Toolik Lake). We compare mean trait values across the three regions for each species and find considerable variability within a growth form. Quantification of intraspecific variation (ITV) in the three populations showed high amounts of variation for some traits (>50% for normalized difference vegetation index (NDVI) and photosynthetic capacity (A_{max})) but not for other traits (<15% for plant height, leaf area, specific leaf area (SLA), leaf thickness, and leaf dry matter content (LDMC)). Amount of ITV also varied across regions. To better understand why trends in plant cover and functional traits vary across regions, change in cover (measured three times from 2008 to 2018) was also compared with observed trait values (measured in 2018) for twelve dominant species. Canonical correspondence analysis (CCA) suggested a relationship between change in species cover and functional traits. Species increasing in cover were associated with photosynthetic capacity (A_{max}) and species decreasing in cover were associated with LDMC. Investigation of community-weighted trait means (CWM) showed that whole community rather than species-specific trait values may be more indicative of future change. CWM changed significantly over time for all traits at Utqiagvik and Atqasuk, but not Toolik Lake. Non-

significant results in direct cover-trait relationships also suggest that multiple traits rather than a single trait may be responsible for shifts in plant cover, supporting a multidimensional approach to future trait-based studies. Additionally, studies investigating the impact of warming on vegetation that incorporate ITV will be able to provide more accurate predictions for future change.

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Chapter I

Introduction

Global climate change has been well documented over the last several decades with increases in atmospheric and oceanic temperatures being the most cited effects (IPCC 2018; AMAP 2019). High latitude regions are experiencing temperature increases more than twice the rate of the global average as well as rapid thawing of the permafrost and declines in sea ice extent (ACIA 2004; AMAP 2019). The Arctic is generally considered an indicator of future environmental change for other regions, and has been intensively studied in an effort to understand how effects from climate change will influence ecosystem dynamics.

Many aspects of ecosystem dynamics are currently being studied, but plant community change has been continuously studied for decades (Chapin et al. 1995; Walker et al. 2006; Callaghan et al. 2011; Elmendorf et al. 2012; Hollister et al. 2015; Bjorkman et al. 2020). Plant community change with increased temperature has been examined through long-term warming experiments set up and maintained by the International Tundra Experiment (ITEX) in arctic and alpine regions. Though monitoring community change is one of the primary objectives of ITEX, many projects exploring ecosystem functioning (e.g., carbon flux measurements, snow manipulation experiments, etc.) have since become incorporated into the network.

The United States constituents of the larger ITEX network formed the ITEX-AON (International Tundra Experiment-Arctic Observing Network). A collaborative project funded by the National Science Foundation (NSF), ITEX-AON includes Grand Valley State University (GVSU), Florida International University (FIU), University of

Texas at El Paso (UTEP), and University of Alaska Anchorage (UAA). These universities monitor four research sites in northern Alaska: Utqiagvik, Atkasuk, Toolik Lake, and Innavait Creek. The goals of the project include understanding what drives ecosystem change in high latitude regions with special emphasis on the effects of long-term warming.

This thesis is funded under the ITEX-AON project, and includes data from over a decade of repeated plant cover samplings at each site. Studies documenting long-term plant cover datasets from these sites have found several common trends including increases in evergreen shrubs, deciduous shrubs, and graminoids and decreases in bryophytes and lichens (Elmendorf et al. 2012; Botting 2015; Hollister et al. 2015; Bjorkman et al. 2020; Harris 2020). This thesis incorporates historic cover data from ITEX-AON with a new dataset focusing on functional traits inspired by other studies within the ITEX network (Hudson et al. 2011; Bjorkman 2018a; Myers-Smith et al. 2019).

Purpose

The purpose of this thesis is to apply the species-specific approach to functional trait research in arctic tundra communities. This thesis quantifies intraspecific variation and explores the relationship between change in plant cover and functional traits. I measured ten functional traits important to ecosystem functioning on twelve focal species that occur across three regions spanning a latitudinal gradient in northern Alaska (Utqiagvik, Atkasuk, and Toolik Lake). Choosing species with a geographical range encompassing all three regions enables me to determine their individualistic responses to environmental conditions. The goals of this thesis are to compare species-level trends

with their corresponding growth forms, establish the amount of intraspecific variation within arctic communities, and establish whether there is a direct relationship between change in community composition and functional traits.

Scope

This thesis examines tundra plant communities representative of the Alaskan tundra by focusing on three regions spanning a latitudinal gradient (Utqiagvik, Atkasuk, and Toolik Lake). Results from this study should be applicable to similar communities found throughout the Alaskan arctic and areas in Siberia. Results will also provide insight on how arctic communities are adapted to surrounding environmental conditions and how communities may shift in composition as the climate changes.

Assumptions

My three study regions (Utqiagvik, Atkasuk, and Toolik Lake) have differences in climate (i.e., temperature, annual precipitation, etc.) and so I assume that functional trait trends in species populations are the result of mainly environmental differences. I also assume that a sample size of ten individuals adequately represents the whole population for each region. Finally, I assume that three plant cover samplings spanning ten years are representative of trajectories for each species and growth form, and that those trajectories are the result of changes in climate for each region.

Hypotheses

Chapter II focuses on quantifying the amount of ITV in traits across the three populations spanning a latitudinal gradient. The goals are to 1) establish if mean trait values vary among populations, 2) determine if species-level patterns match those of their

growth form, and 3) quantify the amount of ITV within each population and compare it to the amount of variation at different taxonomic levels. One hypothesis is that trait values will increase or decrease with latitude (depending on the trait) and reflect findings from previous studies. It is also expected that some species will exhibit individualistic responses to changes in latitude (i.e., some species will show a positive response to increased temperature while other species will show a negative response). Research has shown that some species (particularly deciduous shrubs) show strong species-specific responses to changes in environmental conditions, so we expect the same result in our study (Saccone et al. 2017). We also predict that Utqiagvik will have less ITV than the two southern sites (Atkasuk and Toolik Lake). The harsher conditions at Utqiagvik will cause individuals to converge on a single optimal trait value that promotes the greatest fitness. Toolik Lake, where conditions are more favorable and allow for greater niche partitioning, will have the greatest amount of ITV.

Chapter III looks at the direct relationship between plant cover and specific functional trait values and determines whether changing cover is correlated with certain traits. The goals of Chapter III are 1) to determine whether there is a direct relationship between shifts in species cover and specific trait values and 2) to assess whether community-weighted trait mean values (CWM) are shifting in response to climate change over time at each region. One hypothesis is that species increasing or decreasing in cover over time will be associated with at least one functional trait. It is also expected that CWM will shift at regions that are experiencing significant changes in cover.

Significance

These chapters will build upon existing knowledge surrounding the role of ITV in arctic communities and provide insight as to how they will continue to change as the climate warms. All data will be contributed to the Tundra Trait Team (TTT) database to further our knowledge of each species and of arctic population dynamics (Bjorkman 2018b). Focusing on species-level responses and contributing functional trait data to publicly available databases will also be valuable contributions to future trait-based studies. Additionally, providing evidence for strong species-specific responses will hopefully discourage future studies from using the traditional growth form approach to analysis. Highlighting differences in species populations of arctic plants will help us have a better grasp on inter-population trends in functional traits, thus providing a more complete picture of how the Arctic will respond to changing environmental conditions and facilitating more accurate forecasts of future vegetation change as the region warms.

Definitions

Functional trait – any characteristic of an individual that influences its fitness or performance

Intraspecific variation (ITV) – the amount and magnitude of differences between individuals within the same species

Local adaptation – occurs when a population of individuals adapts to its local environment and has a higher mean fitness than other individuals within the same species

Phenotypic plasticity – the capacity of an individual genotype to alter its phenotype in response to its environment

Chapter II

Comparing traditional growth form with species-specific trends in functional traits along a latitudinal gradient in northern Alaska

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Abstract

The Arctic is experiencing warming rates more than twice the global average. Previous studies have documented changes in plant cover in response to a warming climate. Generally, studies have shown that graminoids, deciduous shrubs, and evergreen shrubs increase with warming, but not all regions show the same response. The mixed response has been partially attributed to differences in species within growth forms across regions. Recent studies have shifted from a growth form emphasis toward an analysis of plant functional types based on specific plant traits. Many of these studies have examined trends in plant traits along environmental gradients. The amount of intraspecific variation (ITV) within populations of species is often unknown and unaccounted for in these analyses. Here, we examine trends in eight plant functional traits for twelve arctic plant species in three regions spanning a latitudinal gradient in northern Alaska. Comparison of mean trait values across the three regions for each species showed considerable variability within a growth form. Within deciduous shrubs, for example, one species increased in specific leaf area (SLA) with latitude while another species decreased. We also quantify the amount of ITV for each trait at each location and compare it to the amount of variation within taxonomic levels. Results differed among functional traits. Plant height, leaf area, SLA, leaf thickness, and leaf dry matter content (LDMC) had relatively low amounts of ITV (<15%) while NDVI and photosynthetic capacity (A_{max}) had high amounts of ITV (>50%). All traits showed significant differences across regions for at least some species. We therefore emphasize the need to investigate ITV in trait-based studies spanning multiple regions. Incorporating ITV in studies investigating vegetation change with warming will provide more robust and reliable predictions.

Introduction

The rate of global climate change has been steadily increasing over the last several decades (IPCC 2018). Climate change is occurring even faster in the northernmost latitudes, with temperatures increasing at twice the rate of the global average (ACIA 2004; AMAP 2019). The Arctic is also experiencing reduced snow cover and duration, continuous thawing of the permafrost, and rapid declines in sea ice extent (AMAP 2019). Observed changes are due to rapidly rising temperatures, making the Arctic an early indicator of future environmental change in other regions. The Arctic has been the forefront of research on climate change impacts for several decades, and will likely continue to be for decades to come.

Plant communities have been shown to change with temperature (Callaghan et al. 2011; Elmendorf et al. 2012; Hollister et al. 2015; Bjorkman et al. 2020). The Arctic is a harsh environment with cool summer temperatures, low nutrient availability, and a short growing season. Arctic plant species therefore fall under Grime's stress-tolerant life strategy and are commonly short-statured evergreen shrubs and low-growing forbs (Grime 1977). In the lower Arctic, however, deciduous shrubs and graminoids are dominant. Documented change in community composition in association with decadal warming trends have consistently found increases in evergreen shrubs, deciduous shrubs, and graminoids and decreases in bryophytes and lichens (Callaghan et al. 2011; Elmendorf et al. 2012; Hollister et al. 2015; Bjorkman et al. 2020). Responses to increased temperature are not consistent at all sites and analysis by growth form may mask species-specific responses. Species within growth forms exhibit a broad range of

responses to environmental manipulations, providing support for functional trait- and species-focused studies (Hudson et al. 2011; Saccone et al. 2017).

Many studies have also observed trends in functional traits along various environmental gradients (de Villemereuil et al. 2018; Gao et al. 2018; Halbritter et al. 2018; Amartuvshin et al. 2019). In general, size-related traits such as plant height and leaf area decrease with increased latitude and elevation (i.e., temperature) (de Villemereuil et al. 2018; Gao et al. 2018; Halbritter et al. 2018). Environmental gradient-based studies are often used as indicators for how functional traits will shift with climate warming since long-term data does not yet exist for many traits. Short-term simulated warming experiments using open-top chambers (OTCs) provide some evidence for temperature-trait relationships, but results are mixed (Hudson et al. 2011; Bjorkman et al. 2018a). Some species mirror results expressed by growth forms, but other species exhibit more individualistic responses. For example, the deciduous shrub *Arctostaphylos alpina* showed a decrease in survival rate compared to another deciduous shrub *Vaccinium myrtillus* (Saccone et al. 2017). Furthermore, temperature-trait relationships vary between species, making it difficult to understand each species-specific response to various environmental changes.

Shifts in community composition and, by result, shifts in plant functional traits with climate change can have important implications for ecosystem functioning. Functional traits such as plant height and specific leaf area (SLA) are strong predictors of primary productivity, and studies show increases in both with temperature (Hudson et al. 2011; Bjorkman et al. 2018a; de Villemereuil et al. 2018; Gao et al. 2018). Projections based on current community distributions predict that annual gross primary productivity

(GPP) will increase by 31% in northern biomes (Madani et al. 2018). Increased GPP coupled with potential increases in litter decomposition rates have the potential to offset the rate of carbon exchange in the Arctic (McLaren et al. 2017; Parker et al. 2018). Changes in ecosystem processes are coupled with changes in vegetation community structure including shifts in species abundances and diversity. Characteristics of individual populations (e.g., ITV) also shift, further affecting ecosystem functioning.

The role of intraspecific variation (ITV) in ecosystem functioning is important to consider because ITV can affect extinction risk, equilibrium densities, and other factors that determine population densities of various species (Bolnick et al. 2011; Kraft et al. 2015). The amount of variation between species (i.e., interspecific variation) is often assumed to be greater than the amount within species, making the effect of ITV negligible. For studies at regional and local scales that focus on individual species, however, it is important to quantify and consider ITV (Albert et al. 2011). The amount of ITV varies among populations, and can influence ecological interactions through several mechanisms including altering the number and strength of interactions between species (Bolnick et al. 2011). Intraspecific variation is also an important component of community assembly. In general, populations with high ITV have a broad niche breadth (i.e., habitat generalists) and therefore have a large geographical range; whereas populations with low ITV have a narrower niche breadth (i.e., habitat specialists) and therefore have smaller geographical ranges (Parkhurst and Loucks 1972; Laughlin et al. 2012; He et al. 2018a). It has been speculated that populations with high ITV will be more resistant to environmental changes, and be able to keep pace with the current rate of climate change (Malyshev et al. 2016; Henn et al. 2018). Conversely, populations with

low ITV may be more at risk of local extinction, leading to shifts in community composition and changes in community level functional traits over time. Due to high amounts of gene flow in the Arctic, it is possible that migration of more plastic individuals will help populations at risk of local extinction to survive. Migration and emigration of these individuals will also influence the amount of ITV that exists within a population. The role ITV plays in shifting community compositions also depends partially on the source of ITV. Whether the amount ITV within a population is fixed or plastic will determine the rate at which that population can respond to changing environmental conditions as well as how it will interact with other populations of species.

A functional trait-based approach to community ecology is thus critical in understanding impacts from global climate change. Specifically, looking at variation in functional traits along environmental gradients will indicate how communities are affected by the environment, enabling us to make predictions on future community change (McGill et al. 2006; Kamiyama et al. 2014). Having a better grasp on inter-population trends in plant functional traits will provide a more complete picture of how the Arctic will respond to changing environmental conditions. Here, we investigate variation in eight functional traits for twelve arctic species across three regions spanning a latitudinal gradient (Utqiagvik, Atkasuk, and Toolik Lake, Alaska). We aim to 1) document how much mean trait values vary between locations, 2) determine if species-level patterns match those of other members within the same growth form, and 3) quantify the amount of ITV within each location relative to the amount of variation within the growth form and across different taxonomic levels (family, genus, species). We hypothesize that trait values for growth forms will increase or decrease with latitude

(depending on the trait) and reflect findings from previous studies (**Table 2.1**). We also hypothesize that some species possessing equivalent growth forms will exhibit results differing in direction and/or magnitude from the overall growth form response. Finally, we hypothesize that Utqiagvik will have less ITV than the two southern regions (Atqasuk and Toolik Lake) because we expect the harsher conditions at Utqiagvik to cause individuals to converge on a single optimal trait value that promotes the greatest fitness. We expect Toolik Lake, where conditions are more favorable and allow for greater niche partitioning, to have the greatest amount of ITV.

Materials and Methods

Study Area

Three regions span a latitudinal gradient stretching from the northern foothills of the Brooks mountain range to the coast of the Chukchi Sea in Alaska, USA (**Fig. 2.1**). Utqiagvik, Alaska (71°19'N, 156°36'W) has been classified as high arctic tundra because of the lack of erect shrubs (however that is changing) and abundance of sedge species (e.g., *Carex aquatilis* and *Eriophorum* spp.). It has a mean July temperature of ~4°C and snowmelt occurs early to mid-June. Atqasuk (70°27'N, 157°24'W) and Toolik Lake (68°37'W, 149°35'N), Alaska are classified as low arctic tundra and are dominated by deciduous shrubs (e.g., *Betula nana* and *Salix* spp.) and sedge species (e.g., *Eriophorum vaginatum* and *Carex* spp.). Atqasuk has a mean July temperature of ~9°C and snowmelt occurs in late May. Toolik Lake has a mean July temperature of ~11°C and snowmelt occurs in early to mid-May.

Plant Trait Collection

Species were chosen for functional trait analysis based on their relative abundance at a location with special emphasis on species that occurred at all three locations. Species that occurred across all regions include *Carex aquatilis*, *Eriophorum angustifolium*, *Eriophorum russeolum*, *Eriophorum vaginatum*, *Luzula confusa*, *Pedicularis kanei*, *Petasites frigidus*, *Cassiope tetragona*, *Vaccinium vitis-idaea*, and *Salix pulchra* (**Table 2.2**). *Ledum palustre* and *Betula nana* were not present at Utqiagvik, but were dominant species at Atqasuk and Toolik Lake; including these two species creates a more representative sample for the southern two regions. Functional traits were measured on ten individuals for each species at each location. Individuals collected were spaced at least one meter apart to prevent duplicate sampling of the same individual.

The following plant traits were measured directly on the same ten individual plants (**Table 2.3**). Plant height (cm) was the vertical distance between the ground and highest vegetative structure on the plant. A LI-6400XT Portable Photosynthesis System (Licor Inc., Lincoln, Nebraska, USA) was used to measure photosynthetic capacity (A_{max} ; $\mu\text{mol CO}_2/\text{m}^2/\text{sec}$). Area was calculated for leaves placed in the IRGA (infrared gas analyzer) chamber using ImageJ software (Schneider et al. 2012). Leaf thickness (mm) was measured using a dial caliper on the largest leaf of each individual, and then the leaf was placed in a coin envelope and saved for further analysis. Leaf area was also calculated for the largest leaf on each individual using Image J software (Schneider et al. 2012). Each leaf was photographed on 1 cm^2 grid paper for scale. Normalized difference vegetation index (NDVI) and water band index (WBI) were calculated from reflectance measurements obtained using a single channel Unispec spectroradiometer (PP Systems,

Amesbury, Massachusetts, USA). Fresh weights for each leaf were taken to the nearest milligram immediately upon returning from the field. Leaves were dried at 45°C for 48 hours in a drying oven and again measured to the nearest milligram. The traits explained above were also used to calculate other traits such as specific leaf area (SLA) and leaf dry matter content (LDMC).

Statistical Analyses

All statistical analyses were performed using the R statistical software version 3.6.2 (R Core Team 2018). Individuals that had multiple trait values more than 2.2 standard deviations away from the trait mean were identified as outliers and removed (about one to two individuals per species). Because removed individuals had multiple outliers (several traits for a single individual), we assumed they were either unhealthy individuals or there were errors made during measurements. All variables were tested for normality using the Shapiro-Wilk test. Plant height, leaf area, leaf thickness, and LDMC were log-transformed in order to fulfill normality requirements. Box and whisker plots were made to visualize the amount of variation among and within species for each functional trait. To identify which traits were different across regions, one-way ANOVAs were performed for each species and growth form. P-values were adjusted for multiple comparisons using the Benjamini-Hochberg procedure. Trait means were also plotted against region to compare trends in growth forms with individual species.

In order to assess the population as a whole based on our samples, kernel density plots were used to estimate the population density function for each trait. We also performed a nested ANOVA using the ‘varcomp’ function within package ‘ape’ (Paradis and Schliep 2019) in R. The function first calculates the mean of each group, then

compares the variance around the group mean to the mean of the next level (Messier et al. 2010; Henn et al. 2018). Variance was partitioned into growth form, family, genus, region, across species, and within species. Variance partitioning of functional traits allows us to quantify ITV and identify at which taxonomic level the majority of variation occurs.

Results

Plant traits varied between species and between regions (**Fig. 2.2**). Results from one-way ANOVA showed that all traits are significantly different across regions for some species and growth forms (**Table 2.4**). All traits differed across regions for graminoids ($P < 0.01$) and five traits differed across regions for deciduous shrubs ($P < 0.01$). LDMC differed across regions for ten of the twelve species ($P < 0.04$). All other traits differed across regions for at least seven species ($P < 0.05$). For all species combined, seven traits differed across regions (excluding SLA).

For some traits, most species within a growth form follow the same general trend (**Fig. 2.3**). For example, most species and growth forms increase in plant height and leaf area between Utqiagvik and Toolik Lake. Some species, however, show individualistic responses for some functional traits. SLA increases from north to south for *S. pulchra*, but decreases for *B. nana*. LDMC also increases from north to south for *P. frigidus*, but not for *P. kanei*. Differences in species-specific responses within growth forms can also be found within WBI, leaf thickness, and photosynthetic capacity (A_{max}). In some cases, significant results for growth forms are driven by a single species (e.g., SLA, LDMC, and A_{max} in forbs). In other cases, trends emerge for individual species, but combined results

for multiple species within a growth form are non-significant (e.g., SLA, WBI, and NDVI in evergreen shrubs, SLA in deciduous shrubs, LDMC in forbs).

Kernel density plots show a large amount of overlap in population density curves across regions (**Fig. 2.4**). Two exceptions are WBI and photosynthetic capacity (A_{max}), which show a large amount of variation within Toolik Lake and far less variation within Utqiagvik. SLA shows the greatest amount of variation across all three regions and leaf area shows the least amount of variation.

Results from the nested ANOVA are similar to trends shown in the kernel density plots. Regional differences account for most of the variation within WBI (70.5%; **Fig. 2.5**). ITV accounts for most of the variation within photosynthetic capacity (A_{max} ; 81.1%) and NDVI (52.1%). Conversely, there was little ITV within plant height (9.5%), leaf area (7.4%), SLA (13.6%), leaf thickness (8.4%), and LDMC (12.6%). Genus and family accounted for relatively small portions of total variation for most traits, but growth form accounted for much of the variation within plant height (37.4%), SLA (63.6%), and LDMC (52.3%).

Discussion

Comparison of Growth Forms and Species

General trends in functional traits across regions were consistent with previous findings (**Table 2.1**). Plant height and leaf area were larger in the southern populations for most species (**Fig. 2.2, 2.3**). Increased plant size with temperature is common in most studies, and is attributed to slower growth rates restricted by colder temperatures (Caldwell et al. 1978; Hudson et al. 2011; Bjorkman et al. 2018a; de Villemereuil et al.

2018; Gao et al. 2018). Photosynthetic capacity decreased with latitude, which contradicts studies showing a positive relationship with temperature (Reich et al. 2018; Sanhueza et al. 2019; Zhou et al. 2019). SLA and LDMC increased for some species with latitude, but not for others. Previous studies have shown that changes in SLA and LDMC are more apparent at wetter than drier regions (Baruah et al. 2017; Bjorkman et al. 2018a). Since this study takes place at the regional scale rather than the local scale, effects of community type (namely soil moisture) on results are masked. Individuals collected from multiple community types (e.g., *Carex aquatilis*) were grouped together for analysis. Future analysis incorporating differences in variation and trait means across community types will better reflect what role ITV plays in temperature-trait relationships.

Trends in individual species across regions often varied within a growth form. For example, SLA significantly increased between Atqasuk and Toolik Lake for *S. pulchra*, but significantly decreased for *B. nana* (**Table 2.4; Fig. 2.3**). The overall net change for deciduous shrubs, however, was insignificant. In this case, opposite trends in individual species result in a null response when grouped together, making it appear as though SLA in deciduous shrubs is the same across multiple populations. A similar situation is found in LDMC in deciduous shrubs. Opposite trends in *S. pulchra* and *B.nana* result in a null response when grouped together. NDVI responses are extremely species-specific, which aligns with previous studies showing both browning and greening trends throughout the Arctic (Li et al. 2016; McPartland et al. 2019; Rastogi et al. 2019). In other cases, a single species drives the overall growth form response. Leaf thickness decreases from north to south for *P. frigidus*, but not for *P. kanei*, which is consistent with previous findings (He et al. 2018b; Wang et al. 2016).

Contrasting results in species responses within a growth form to environmental changes along a latitudinal gradient suggest that the traditional approach of grouping species by growth form may be insufficient in describing community-level changes (Epstein et al. 2001; Kamiyama et al. 2014; Saccone et al. 2017; Thomas et al. 2019; Prager et al. 2020). Saccone et al. (2017) showed especially strong species-specific responses in deciduous shrubs, which mirrors our own findings (*S. pulchra* and *B. nana* showed opposite trends SLA and LDMC). Investigating species-specific responses rather than broad growth form responses to changing environmental conditions, especially when the species in question are relatively abundant, will help better our understanding of how overall ecosystem functioning will change.

It is important to consider species abundance when observing trends in functional traits. Species with higher relative abundances have a stronger effect on ecosystem functioning (Baruah et al. 2017). Sedge *C. aquatilis* is the most abundant species at Utqiagvik; however, if Utqiagvik's plant community eventually shifts to more resemble Atqasuk and Toolik Lake, *E. vaginatum* and deciduous shrubs will dominate the landscape. Shrubification in the Arctic will lead to greater carbon sequestration, which may offset the amount of carbon being released into the atmosphere by thawing permafrost (Mekonnen et al. 2018). Shifts in plant traits for common species may therefore be more indicative of how the ecosystem as a whole will respond to changing environmental conditions. Soudzilovskaia et al. (2013) showed evidence that plant traits predict relationships between species abundance and temperature, suggesting selection for specific traits rather than species under certain environmental conditions. Other studies have also shown that functional traits are strong predictors for community

assembly (Alsos et al. 2007; Laughlin et al. 2012; Henn et al. 2018). The relationships between functional traits, environmental conditions, and species abundances all play a role in ecosystem interactions, and understanding these relationships is critical in predicting future ecosystem change.

Intraspecific Variation in Functional Traits

The role ITV plays in community ecology is complex and often ignored in functional trait-based studies. ITV is associated with niche breadth, and one hypothesis is that harsh environments cause populations to converge on a single optimal trait value that best reflects plant performance under those environmental conditions as long as there is no migration from other populations with significantly different conditions (Laughlin et al. 2012; Henn et al. 2018). We hypothesized that harsher conditions at Utqiagvik would cause individuals to follow this pattern, and that more optimal conditions at Toolik Lake would facilitate greater diversification and thus niche partitioning. Additionally, the presence of fewer community types at Utqiagvik (i.e., the landscape is more homogenous) and more community types at Toolik Lake (i.e., the landscape is more heterogenous) would lead to greater variation at Toolik due to the presence of more microhabitats. Kernel density plots showing the spread of functional traits for each region, however, do not support this hypothesis (**Fig. 2.4**). WBI follows the pattern outlined in our hypothesis, but most other traits show similar amounts of variation across regions. It is possible that our regions are too close together to see obvious differences in trait variability, and that a larger geographical scale would better support the trait convergence hypothesis.

It is often assumed that the amount of variation between species is greater than the amount of variation within species, but results show that ITV can be much greater than expected (Albert et al. 2011; Bolnick et al. 2011; Henn et al. 2018). Within-species variation accounted for more than 50% of the total variation in two functional traits (NDVI and A_{max} ; **Fig. 2.5**). Variance partitioning across taxonomic levels is also different for each functional trait. Region accounted for most of the variation within WBI, indicating that environmental conditions greatly affect this trait. For SLA and LDMC, growth form accounted for most of the variation. It has been established that both SLA and LDMC are important indicators of leaf strategies; leaves with low SLA and high LDMC have better resource retention, which is important in resource-poor environments such as the Arctic (Reich et al. 1992; Wilson et al. 1999). Little ITV within SLA and LDMC suggests that a single set of trait values is optimal for each species, but that these values are different for each growth form. More variation across growth forms for SLA and LDMC suggests that resource acquisition strategies change more with growth strategies than with individual species.

There is some speculation as to whether ITV is linked with phenotypic plasticity. It has been suggested that populations with little ITV may be less plastic than populations with greater ITV, but there is little evidence to support this hypothesis (Kichenin et al. 2013; He et al. 2018a; Henn et al. 2018). There is evidence, however, that level of plasticity changes between populations exposed to different environmental conditions, with harsher environments resulting in lower levels of plasticity (de Villemereuil et al. 2018). It is possible that the populations in this study spanning a latitudinal gradient

would show a similar trend, however, without performing a common garden or reciprocal transplant experiment level of plasticity cannot be determined.

In addition to plasticity, level and rate of local adaptation should be measured in arctic populations. Significant differences in functional traits between populations suggest that different ecotypes may exist throughout the Arctic (Alsos et al. 2007; Bennington et al. 2012; Laughlin et al. 2012). The existence of ecotypes would imply that local adaption is more responsible for differences in functional traits than phenotypic plasticity. Determining levels of plasticity and local adaptation is important because locally adapting populations may have more trouble keeping up with the current rate of global climate change than populations that are more plastic. Additionally, plasticity itself is adaptive and has been linked with environmental heterogeneity (Laughlin et al. 2012; Herrera 2017). As harsh environments become more complex, the ability to adapt and simultaneously become more plastic will enable species to survive as the climate changes. High amounts of gene flow between arctic populations may facilitate migration of more plastic individuals, helping prevent local extinction of at-risk populations (Laughlin et al. 2012; Eidesen et al. 2013). Establishing levels of plasticity and the amount of ITV within populations is the first step in understanding how different populations respond to local environmental conditions, and should be considered in all functional trait-based studies occurring at the local and regional scales (Albert et al. 2011; Bolnick et al. 2011; Kichenin et al. 2013; Siefert et al. 2015). Because ITV varies among functional traits, it is also important to focus on multiple traits related to ecosystem functioning.

Future Directions

It is important to collect functional trait data on not just species, but different populations of species as well. The Tundra Trait Team (TTT) database includes functional trait measurements for multiple species from several regions scattered throughout the Arctic (Bjorkman et al. 2018b). However, it is also important to establish the amount of ITV for each functional trait at each region. Additionally, filling in gaps in the database (to include all tundra species) and incorporating more functional traits will provide enough data to carry out a more comprehensive analysis of the amount of ITV in tundra populations as well as differences in functional traits across various environmental gradients.

Establishing more long-term functional trait datasets will also help determine how traits are shifting with changing environmental conditions. While many trait-based studies have been conducted on a very broad geographical scale (Reich et al. 1999; Diaz et al. 2004; Wright et al. 2005; Díaz et al. 2016), few studies have been conducted over a temporal scale (Tolvanen and Henry 2001; Baruah et al. 2017). Establishing how functional traits shift in response to long-term environmental manipulations will help predict changes in ecosystem functioning over time.

Finally, establishing the amount of gene flow and genetic variation in arctic populations is key to determining whether they are locally adapted to their environment or are demonstrating phenotypic plasticity. It is likely that populations experience a combination of the two, and that plasticity itself is an adaptive trait. Without determining rates of local adaptation, however, it is difficult to predict just how plant communities will respond to changing environmental conditions. Implementing more wide-spread

reciprocal transplant experiments will help reconcile the local adaptation versus plasticity debate, and advance our knowledge of plant-climate interactions.

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Table 2.1. General trends in plant functional traits as summarized in the literature. Due to a limited number of studies spanning latitudinal gradients, sources include studies spanning elevation gradients and warming experiments. Superscripts correspond to citations supporting each trend and are listed below the table.

Trait	General Trend
Plant Height	Increase with temperature in response to latitude ¹² , elevation ^{3,4,5,12} , and warming ^{1,2,8,12}
Leaf Area	Increase with temperature in response to latitude ¹² , elevation ^{3,7,9} , and warming ^{2,8,12}
Specific Leaf Area (SLA)	Increase with temperature in response to latitude ¹² , elevation ^{7,9} , and warming ^{2,8,12} but strong species-specific responses
Water Band Index (WBI)	Decrease with temperature in response to soil temperature ¹³
Normalized Difference Vegetation Index (NDVI)	Mixed responses to temperature in response to elevation ¹⁰ and soil temperature ^{11,13}
Leaf Thickness	Decrease with temperature in response to latitude ^{6,16}
Leaf Dry Matter Content (LDMC)	Decrease with temperature in response to latitude ¹² , elevation ^{7,9} , and warming ^{2,8,12}
Photosynthetic Rate	Increase with temperature in response to warming ^{14,15,17}

¹Baruah et al. 2017, ²Bjorkman et al. 2018a, ³de Villemereuil et al. 2018, ⁴Gao et al. 2018, ⁵Halbritter et al. 2018, ⁶He et al. 2018b, ⁷Henn et al. 2018, ⁸Hudson et al. 2011, ⁹Kichenin et al. 2013, ¹⁰Li et al. 2018, ¹¹McPartland et al. 2018, ¹²Myers-Smith et al. 2018, ¹³Rastogi et al. 2019, ¹⁴Reich et al. 2018, ¹⁵Sanhueza et al. 2019, ¹⁶Wang et al. 2016, ¹⁷Zhou et al. 2019

Table 2.2. Categorical abundance of the plant species measured at each region (Utqiagvik, Atqasuk, and Toolik Lake). Species were classified as not present, rare, locally abundant, or common. Locally abundant species are found only in specific habitat types while common species are found in most habitats.

Species	Family	Utqiagvik	Atqasuk	Toolik Lake
Graminoids				
<i>Carex aquatilis</i>	Cyperaceae	Common	Common	Common
<i>Eriophorum angustifolium</i>	Cyperaceae	Common	Common	Common
<i>Eriophorum russeolum</i>	Cyperaceae	Locally abundant	Locally abundant	Rare
<i>Eriophorum vaginatum</i>	Cyperaceae	Rare	Common	Common
<i>Luzula confusa</i>	Juncaceae	Locally abundant	Locally abundant	Locally abundant
Forbs				
<i>Pedicularis kanei</i>	Orobanchaceae	Rare	Rare	Rare
<i>Petasites frigidus</i>	Asteraceae	Common	Common	Common
Evergreen Shrubs				
<i>Cassiope tetragona</i>	Ericaceae	Locally abundant	Locally abundant	Common
<i>Ledum palustre</i>	Ericaceae	<i>Not present</i>	Common	Common
<i>Vaccinium vitis-idaea</i>	Ericaceae	Locally abundant	Common	Common
Deciduous Shrubs				
<i>Betula nana</i>	Betulaceae	<i>Not present</i>	Common	Common
<i>Salix pulchra</i>	Salicaceae	Locally abundant	Common	Common

Table 2.3. Summary of measured plant traits with corresponding units and replicates as well as a short description of how each trait was measured. Replicates indicate the number of measurements taken for each species at each region.

<i>Trait</i>	<i>Units</i>	<i>Reps</i>	<i>Description</i>
Plant Height	cm	10	Individual was measured from the ground to the highest vegetative structure
Leaf Area	cm ²	10	Calculated using ImageJ software using photographs taken on 1cm ² grid paper
Specific Leaf Area (SLA)	cm ² /mg	10	Calculated by dividing the leaf area (cm ²) by its dry mass (mg)
Water Band Index (WBI)	—	10	Collected using a single channel Unispec and calculated using Multispec software ($WBI = \rho_{900} / \rho_{970}$; $\rho = reflectance$)
Normalized Difference Vegetation Index (NDVI)	—	10	Collected using a single channel Unispec and calculated using Multispec software ($NDVI = (NIR - Red) / (NIR + Red)$)
Leaf Thickness	mm	10	Collected using a dial caliper
Leaf Dry Matter Content (LDMC)	mg/g	10	Calculated by dividing the dry mass (mg) by the fresh mass (g)
Photosynthetic Capacity (A_{max})	μmol CO ₂ /m ² /sec	10	Collected using a LI-6400XT Portable Photosynthesis System

Table 2.4. Statistical significance of differences in functional traits across regions (Utqiagvik, Atqasuk, and Toolik Lake). Traits include plant height (cm), leaf area (cm²), specific leaf area (SLA; cm²/mg), water band index (WBI), normalized difference vegetation index (NDVI), leaf thickness (mm), leaf dry matter content (LDMC; mg/g), and photosynthetic capacity (A_{max} ; $\mu\text{mol CO}_2/\text{m}^2/\text{sec}$). P-values and F statistics are from one-way ANOVAs; significant p-values (<0.05) are indicated in bold. Analyses were conducted for each functional group, species, and all species combined for each trait.

	Plant Height		Leaf Area		SLA		WBI		NDVI		Leaf Thickness		LDMC		A_{max}	
	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F
Deciduous Shrubs	0.15 (2.27)		<0.01 (21.1)		0.11 (2.58)		<0.01 (30.9)		<0.01 (15.9)		<0.01 (19.3)		0.06 (3.41)		<0.01 (10.6)	
<i>Betula nana</i>	0.21 (2.01)		0.04 (5.81)		0.01 (13.0)		<0.01 (112)		<0.01 (41.7)		0.08 (4.31)		0.04 (6.31)		0.15 (2.79)	
<i>Salix pulchra</i>	0.13 (2.55)		<0.01 (10.0)		0.03 (4.47)		<0.01 (96.6)		<0.01 (37.2)		<0.01 (24.3)		0.01 (6.18)		<0.01 (32.2)	
Evergreen Shrubs	<0.01 (9.55)		0.18 (1.96)		0.68 (0.44)		0.09 (2.78)		0.20 (1.82)		0.01 (5.48)		<0.01 (7.85)		<0.01 (22.2)	
<i>C. tetragona</i>	<0.01 (26.6)		0.34 (1.24)		<0.01 (8.12)		<0.01 (13.1)		0.85 (0.18)		<0.01 (58.6)		<0.01 (9.84)		<0.01 (32.5)	
<i>Ledum palustre</i>	<0.01 (24.3)		0.25 (1.71)		0.59 (0.37)		0.01 (9.73)		0.02 (8.73)		<0.01 (46.3)		0.01 (12.6)		0.42 (0.82)	
<i>V. vitis-idaea</i>	<0.01 (9.44)		0.13 (2.50)		0.08 (3.34)		<0.01 (22.3)		0.06 (3.55)		0.16 (2.27)		<0.01 (9.36)		<0.01 (83.9)	
Forbs	<0.01 (50.2)		0.02 (4.75)		0.01 (5.78)		0.87 (0.14)		0.79 (0.28)		0.06 (3.29)		0.82 (0.23)		0.06 (3.36)	
<i>Pedicularis kanei</i>	<0.01 (31.9)		0.01 (8.00)		<0.01 (19.2)		0.41 (1.05)		0.95 (0.05)		0.10 (2.85)		0.50 (0.81)		0.03 (4.51)	
<i>Petasites frigidus</i>	<0.01 (83.7)		<0.01 (13.3)		0.83 (0.21)		0.23 (1.74)		0.26 (1.60)		<0.01 (7.47)		<0.01 (12.9)		0.23 (1.72)	
Graminoids	<0.01 (11.0)		0.01 (6.05)		<0.01 (13.3)		<0.01 (54.6)		<0.01 (13.3)		0.01 (10.5)		<0.01 (20.0)		0.01 (6.24)	
<i>Carex aquatilis</i>	<0.01 (16.4)		0.59 (0.61)		0.09 (3.05)		0.78 (0.29)		0.04 (4.26)		0.02 (5.07)		0.03 (4.53)		<0.01 (42.5)	
<i>E. angustifolium</i>	<0.01 (45.7)		<0.01 (48.3)		<0.01 (264)		0.06 (3.98)		<0.01 (18.4)		0.01 (6.42)		0.01 (7.00)		<0.01 (29.3)	
<i>E. russeolum</i>	<0.01 (20.3)		<0.01 (13.0)		<0.01 (12.6)		<0.01 (50.4)		0.01 (6.47)		<0.01 (20.7)		0.01 (6.94)		<0.01 (47.1)	
<i>E. vaginatum</i>	<0.01 (23.6)		0.05 (3.90)		<0.01 (15.3)		<0.01 (132)		0.01 (7.31)		<0.01 (30.3)		0.28 (1.50)		<0.01 (21.0)	
<i>Luzula confusa</i>	0.21 (1.87)		0.01 (7.72)		<0.01 (9.24)		<0.01 (67.2)		<0.01 (30.1)		<0.01 (15.1)		<0.01 (21.3)		0.01 (7.08)	
All Species	<0.01 (9.67)		<0.01 (6.31)		0.51 (0.76)		<0.01 (35.2)		<0.01 (10.8)		<0.01 (7.84)		0.03 (3.94)		<0.01 (13.6)	



Fig. 2.1. Location of study regions near Utqiagvik, Atqasuk, and Toolik Lake, Alaska.

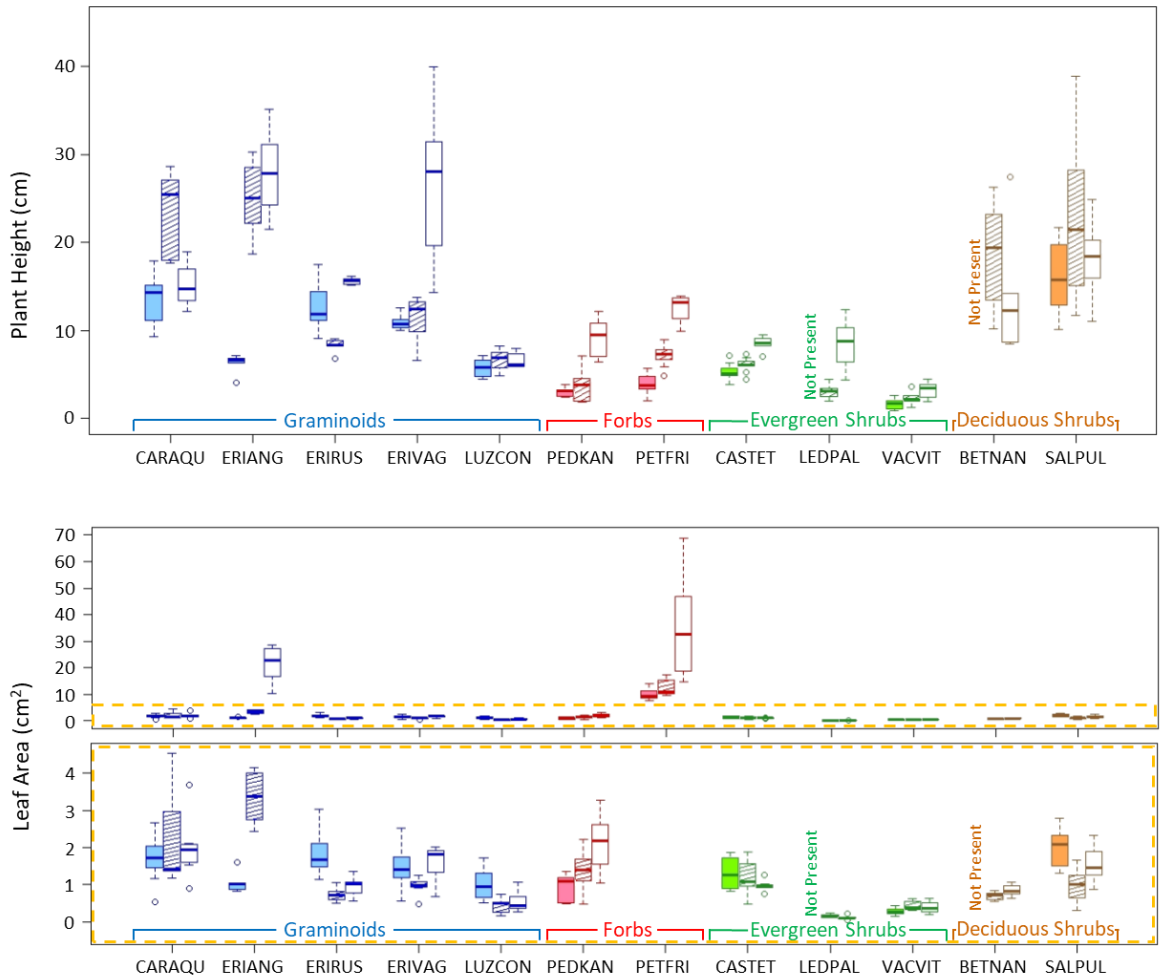


Fig. 2.2. Box and whisker plots for eight plant functional traits and twelve species across three regions in northern Alaska (Utqiagvik, Atqasuk, and Toolik Lake). Species are colored according to growth form (blue = graminoids, red = forbs, green = evergreen shrubs, brown = deciduous shrubs). Species codes are as follows: CARAQU = *Carex aquatilis*, ERIANG = *Eriophorum angustifolium*, ERIRUS = *Eriophorum russeolum*, ERIVAG = *Eriophorum vaginatum*, LUZCON = *Luzula confusa*, PEDKAN = *Pedicularis kanei*, PETFRI = *Petasites frigidus*, CASTET = *Cassiope tetragona*, LEDPAL = *Ledum palustre*, VACVIT = *Vaccinium vitis-idaea*, BETNAN = *Betula nana*, and SALPUL = *Salix pulchra*. Boxplots with a solid fill represent Utqiagvik, boxplots with a dashed fill represent Atqasuk, and boxplots with no fill represent Toolik Lake.

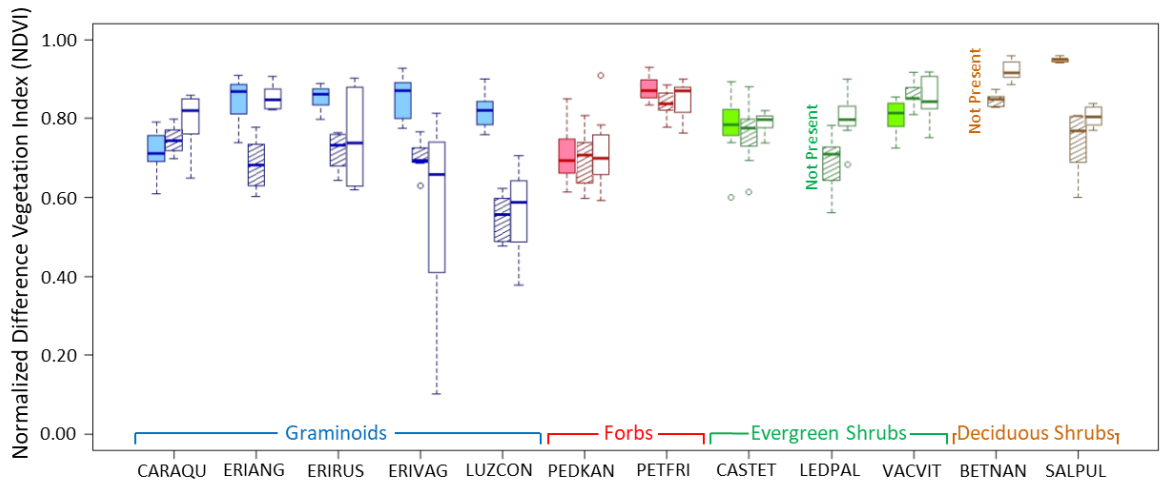
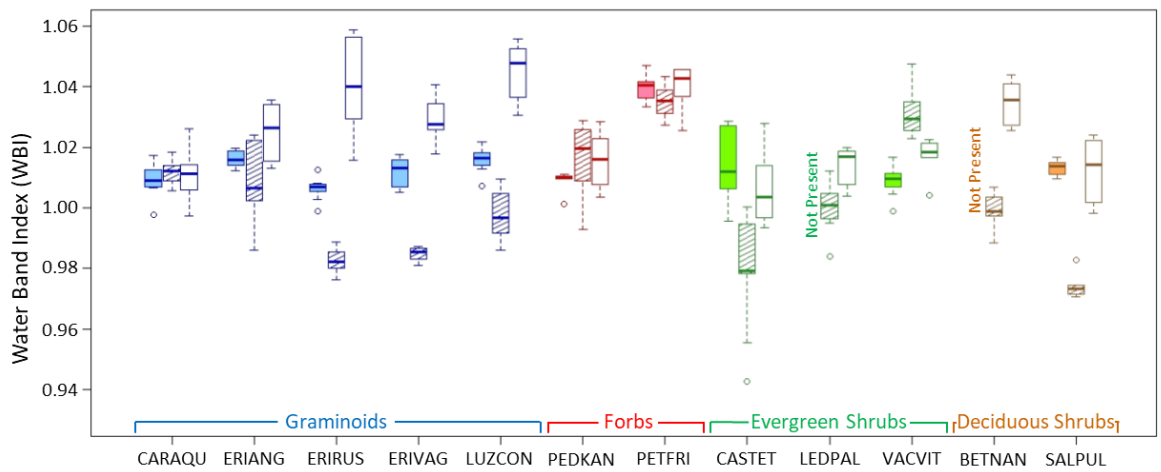
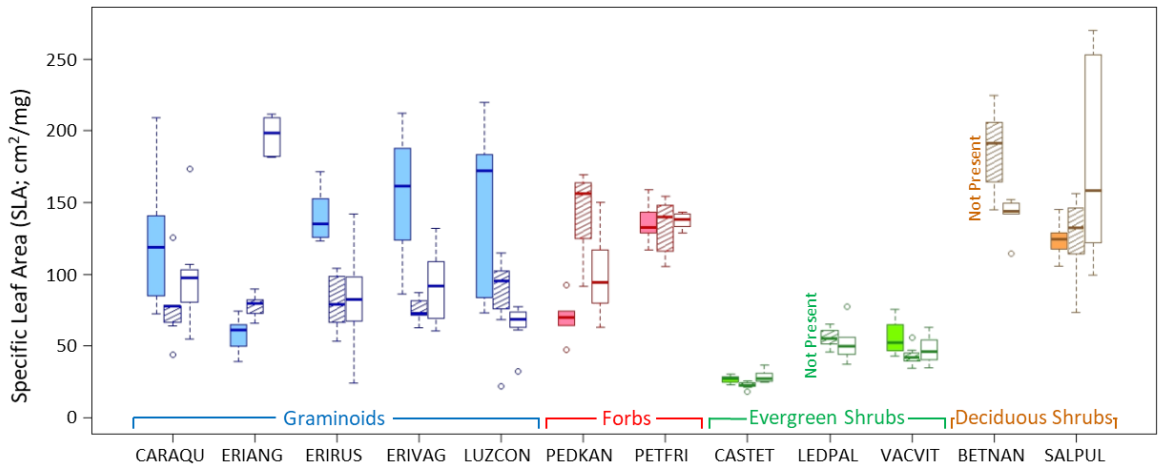


Fig. 2.2. Continued...

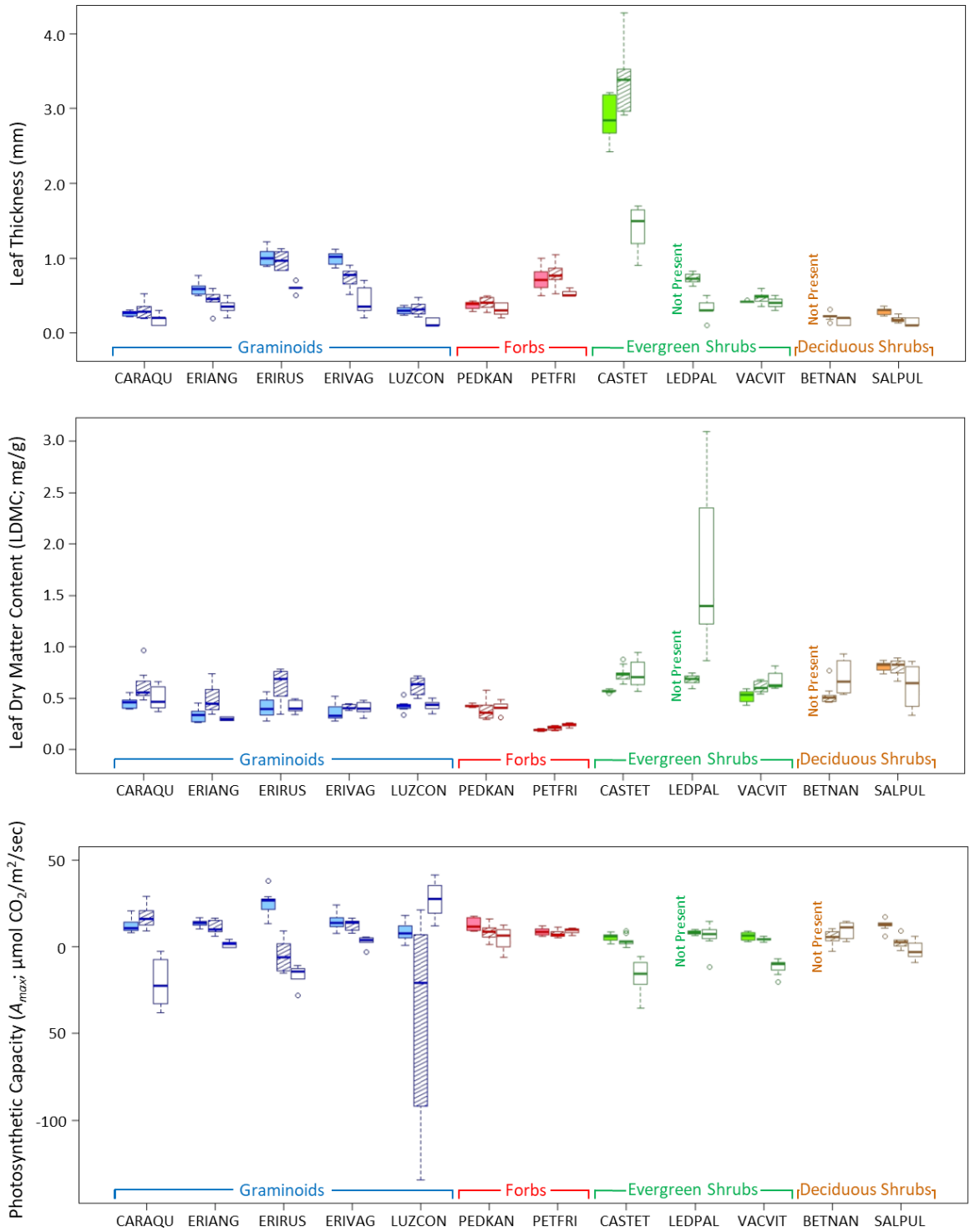


Fig. 2.2. Continued...

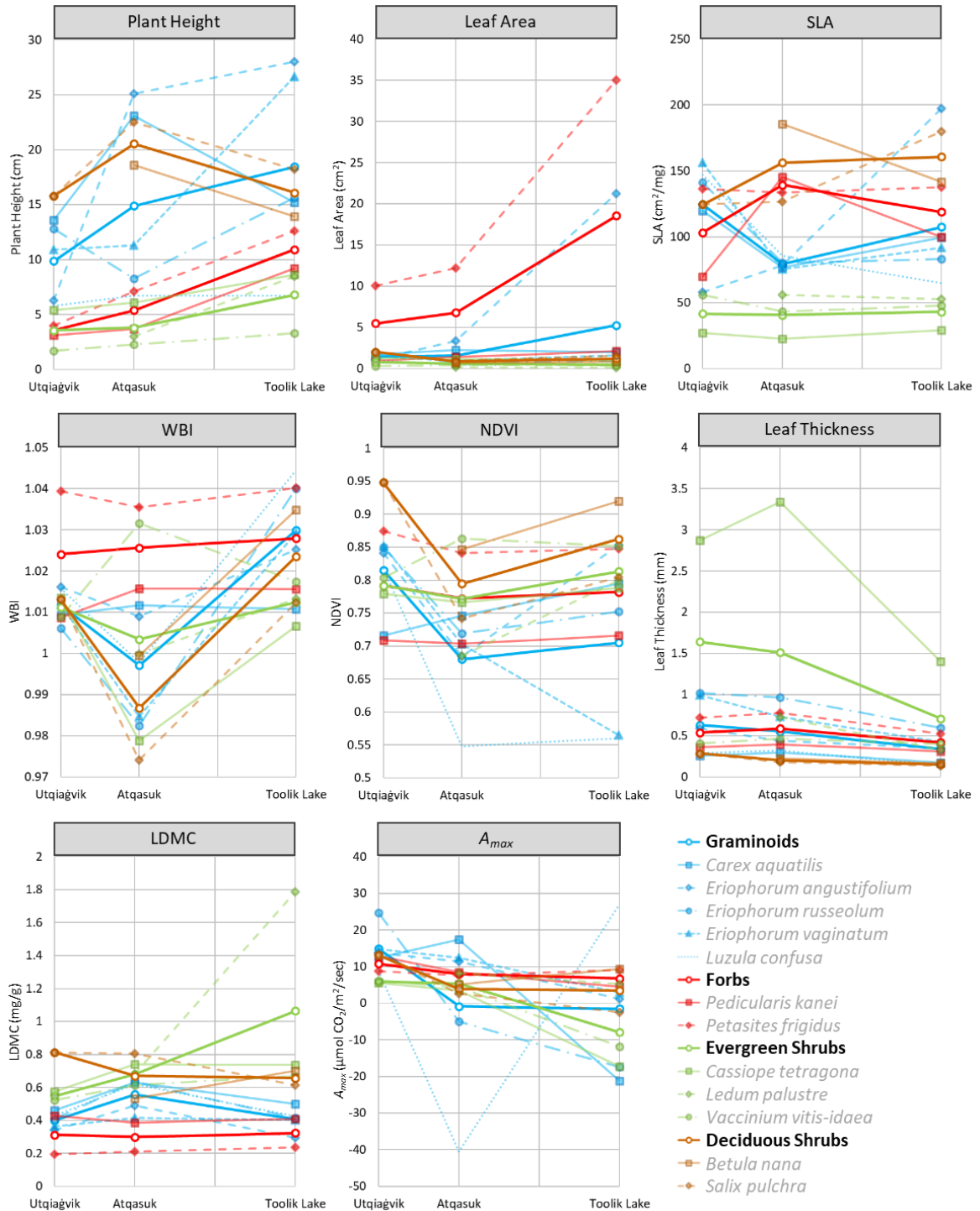


Fig. 2.3. Comparison of species-level average trait values with growth forms for eight functional traits and three populations spanning a latitudinal gradient. Dashed lines represent individual species and solid lines represent growth forms. Colors correspond with growth forms (blue = graminoids, red = forbs, green = evergreen shrubs, and brown = deciduous shrubs).

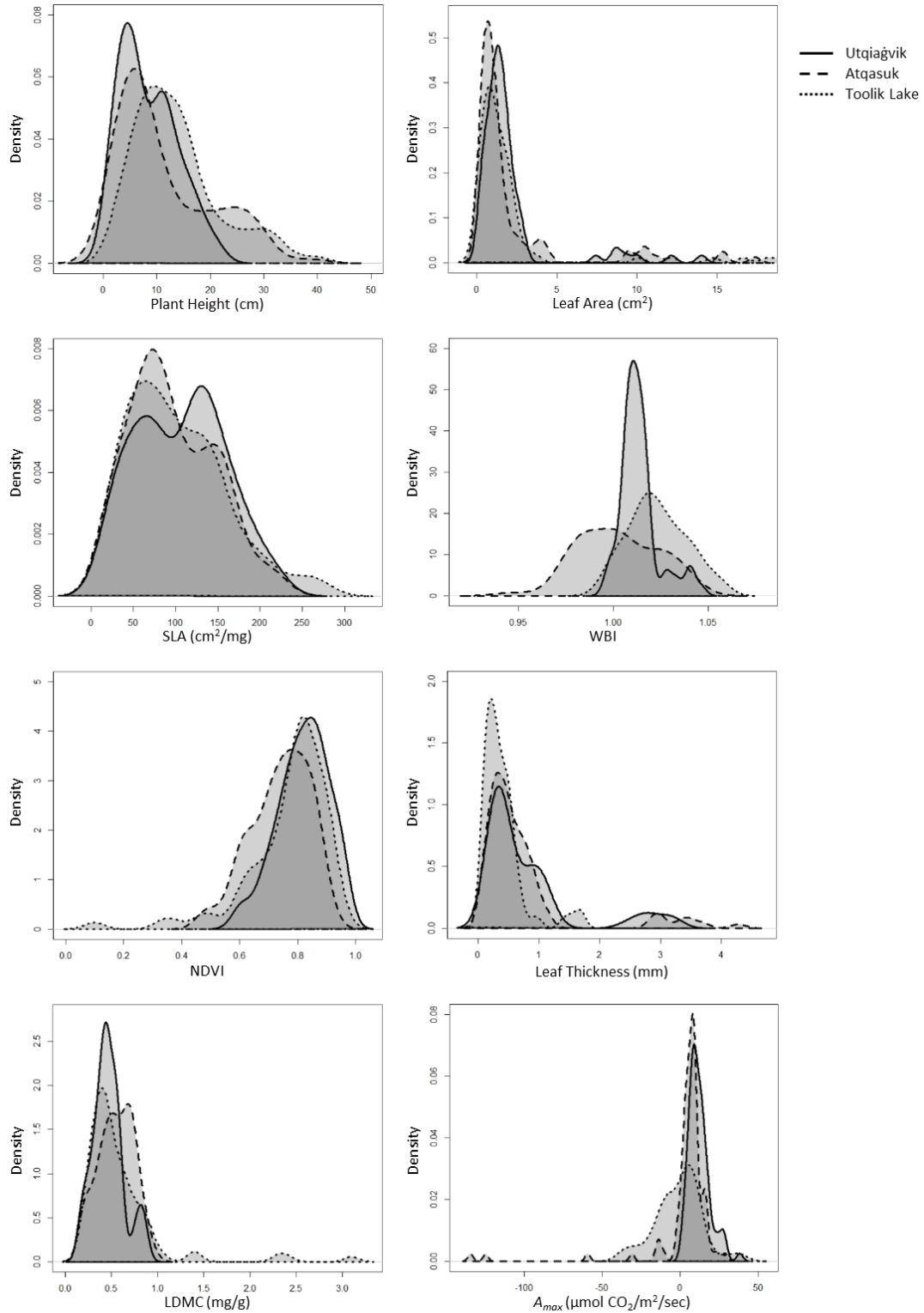


Fig. 2.4. Kernel density plots for eight functional traits across three regions: Utqiagvik (solid line), Atqasuk (dashed line), and Toolik Lake (dotted line). Kernel density plots allow visualization of data without assuming normality, thus providing distributions by smoothing out the noise.

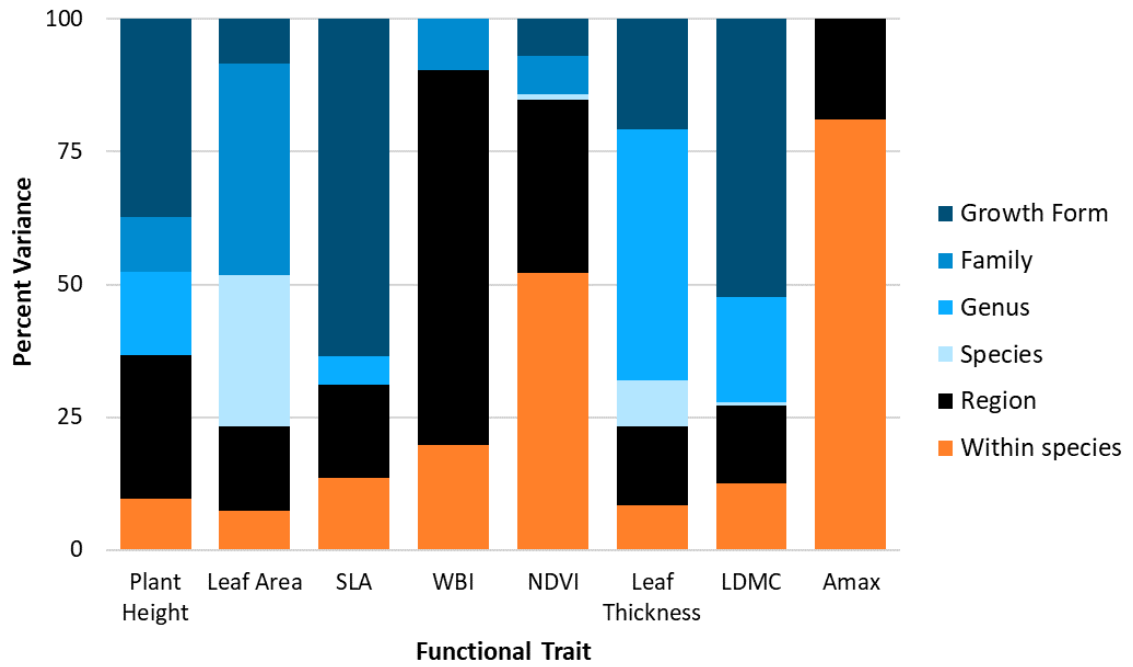


Fig. 2.5. Variance partitioning within species, across regions, and at different taxonomic levels for eight plant functional traits: plant height (cm), leaf area (cm²), specific leaf area (SLA; cm²/mg), water band index (WBI), normalized difference vegetation index (NDVI), leaf thickness (mm), leaf dry matter content (LDMC; mg/g), and photosynthetic capacity (A_{max} ; $\mu\text{mol CO}_2/\text{m}^2/\text{sec}$). Percent variance results are from a nested ANOVA comparing variance around one group mean to the mean of the next level.

Chapter III

Can plant functional traits explain shifts in community composition in a changing Arctic?

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Abstract

The Arctic is the fastest warming biome in the world, experiencing rates twice the global average. Graminoids, deciduous shrubs, and evergreen shrubs have been shown to increase at some regions, but not at others. To better understand why plant response varies across regions, we compared change in plant cover with functional traits of the dominant plant species. Ten plant functional traits were measured for twelve species at three regions in northern Alaska (Utqiagvik, Atqasuk, and Toolik Lake) and cover was measured three times from 2008 to 2018. Repeated measures ANOVA revealed that few species are significantly increasing in cover over time; *Carex aquatilis* and *E. vaginatum* are increasing at Atqasuk only. Canonical correspondence analysis suggested a relationship between shifts in species cover and functional traits, but Pearson and Spearman correlations did not yield any significant trends. Investigation of community-weighted trait means (CWM) revealed significant change over time for all traits at Utqiagvik and Atqasuk, but no change at Toolik Lake. The changes in CWM are primarily due to the change in cover of a few key species, namely *Carex aquatilis* and *Eriophorum* spp.; therefore, it is important that modeling efforts account for species-driven change. Major shifts in community level trait values affect ecosystem processes such as decomposition and carbon cycling, having the potential to affect the overall carbon budget in the Arctic.

Introduction

Global climate change is expected to cause major losses in biodiversity, and the Arctic is particularly susceptible to this threat (IPCC 2018). The Arctic is the fastest warming biome in the world, with average temperatures increasing at twice the rate of the global average (ACIA 2004; AMAP 2019). The Arctic has regularly broken historic record temperatures, experienced reduced snow cover and duration, and undergone continuous thawing of permafrost for several decades (AMAP 2019). The Arctic is therefore an indicator of future environmental change, placing it at the forefront of research on climate change impacts.

Plant communities are particularly sensitive to changes in temperature. In the Arctic where a short growing season and low average temperatures severely limit growth, plants are responsive to even small temperature increases (Hollister et al. 2015; Bjorkman et al. 2020). Changes in community composition with warming have been documented across the Arctic, with increases in evergreen shrubs, deciduous shrubs, and graminoids and decreases in bryophytes and lichens being the most consistent trends across regions (Callaghan et al. 2011; Elmendorf et al. 2012; Hollister et al. 2015; Bjorkman et al. 2020). As a persistently cold and severely nutrient limited system, the Arctic consists of plants characterized by slow growth rates and low reproductive outputs; however, studies have shown that rates for both of these traits have increased due to climate warming (Oberbauer et al. 2013; Hollister et al. 2015; Mekonnen et al. 2018). Shifts in plant performance may result in shifts in ecosystem functioning. The link between performance and ecosystem function has led to an increase in studies focusing on plant functional traits as a means to study vegetation responses to changing environmental conditions

(Chapin et al. 1996; Messier et al. 2010; Hudson et al. 2011; Soudzilovskaia et al. 2013; Baruah et al. 2017; Bjorkman et al. 2018a; Madani et al. 2018; Myers-Smith et al. 2019).

Plant functional traits strongly affect ecosystem functioning, specifically carbon cycling and ecosystem energy balance, which can further impact changes in climate (Lavorel and Garnier 2002; Cornelissen et al. 2007; Pearson et al. 2013; Myers-Smith et al. 2019). Changes in the rate of ecosystem processes such as net primary productivity and decomposition change the net amount of carbon added to the atmosphere, affecting the overall rate of climate change. A list of traits has been generally agreed upon as having important impacts on ecosystem processes (Cornwell et al. 2008; Hudson et al. 2011). For example, plant height is positively correlated with light capture ability (Westoby et al. 2002; Mekonnen et al. 2018). Tall-statured plants have greater access to sunlight and impose shade on short-statured plants. Additionally, leaf area is indicative of trade-offs concerning energy and water balance (Parkhurst and Loucks 1972). Large leaves experience more water loss through transpiration, which is especially important in environments prone to desiccation. Specific leaf area (SLA), on the other hand, is positively correlated with relative growth rate and negatively correlated with leaf life span (Reich et al. 1992). Leaves with a high SLA are thought to be more productive, but also relatively short-lived (Wilson et al. 1999). Finally, photosynthetic capacity (A_{max}) is a direct measure of maximum productivity (Johnson and Tieszen 1976) and is also inversely related to leaf longevity (Johnson and Tieszen 1976; Reich et al. 1999). All of these traits directly influence ecosystem processes such as net primary productivity. Individual traits have therefore been studied in great detail, and in recent years researchers have focused on linking functional traits with community level responses to

changing environmental conditions (Wright et al. 2005; Messier et al. 2010; Hudson et al. 2011; Soudzilovskaia et al. 2013; Baruah et al. 2017; Bjorkman et al. 2018a; Madani et al. 2018; Myers-Smith et al. 2019).

In this study we examine ten functional traits related to plant size and leaf economics (**Table 3.S1**). Many studies have investigated temperature-trait relationships along environmental gradients in order to understand how ecosystems respond to a changing environment, but few studies have looked at the direct relationship between changes in species abundance and specific trait values (Hudson et al. 2011; Muscarella and Uriarte 2016; Bjorkman et al. 2018a; Henn et al. 2018). The importance of plant functional traits to ecosystem processes makes it critical to understand how these traits are shifting in response to community changes as the climate warms. Additionally, looking at how shifts in community composition influence shifts in CWM may be indicative of how the arctic ecosystem as a whole is responding to a changing climate. In this study, we aim to 1) determine whether there is a direct relationship between shifts in species abundances and specific trait values and 2) assess whether community-weighted trait mean values (CWM) are shifting in response to climate change over time. We hypothesize that species increasing or decreasing in cover over time will be associated with at least one functional trait. It is expected that increasing species have a distinct competitive advantage that will be explained by functional traits. We also hypothesize that CWM will shift at regions that experience significant changes in cover.

Materials and Methods

Study Area

Regions are arranged along a latitudinal gradient on the North Slope of Alaska, USA (**Fig. 3.1**). Utqiagvik (71°19'N, 156°36'W) is located on the north coast of Alaska along the Arctic Ocean. Utqiagvik has a mean July temperature of ~4°C and snowmelt occurs in early to mid-June. The dominant plant species are *Salix* spp., *Carex aquatilis*, and *Eriophorum* spp. Atqasuk, Alaska (70°27'N, 157°24'W) is located approximately 100km south of Utqiagvik, has a mean July temperature of ~9°C, and snowmelt occurs in late May. The dominant species are *Betula nana*, *Salix* spp., *Eriophorum* spp., and *Carex* spp. Toolik Lake, Alaska (68°37'W, 149°35'N) is nestled in the foothills of the Brooks mountain range, has a mean July temperature of ~11°C, and snowmelt occurs in early to mid-May. The dominant plant species are *Salix* spp., *Betula nana*, and *Eriophorum* spp.

Plant Cover Sampling

Plant cover was measured at Utqiagvik, Atqasuk, and Toolik Lake on 30 1-m² plots spaced 100 m apart. Plots were sampled using the non-destructive point-frame method outlined in the ITEX Manual (Molau and Mølgaard 1996). A simplified version of the point-frame method was used because it was deemed equal in its ability to detect changes in vegetation cover (May and Hollister 2012). Sampling occurred in 2010, 2014, and 2018 for Utqiagvik and Atqasuk and in 2008, 2014, and 2018 for Toolik Lake. A 75 cm² grid with 100 points was leveled over each plot; three permanent markers that allowed for accurate repositioning of the grid every sampling were lined up with the corresponding crosshairs within the grid. At each point, a ruler was lowered until first contact within the plant canopy. The height was recorded as well as the status

(alive/dead) and species of the individual contacted. The same was recorded for the last species located just above the ground surface. The point-intercept method was repeated for the 100 points within the grid at the 30 plots for each of the three regions. Due to difficulties in identification, bryophytes and lichens were grouped by growth form.

Plant Trait Collection

Species were selected for functional trait analysis based on their relative abundance at a location with special emphasis on species that occur at all three locations (Chapter II). The species that occur across all three regions were *Carex aquatilis*, *Eriophorum angustifolium*, *Eriophorum russeolum*, *Eriophorum vaginatum*, *Luzula confusa*, *Pedicularis kanei*, *Petasites frigidus*, *Cassiope tetragona*, *Vaccinium vitis-idaea*, and *Salix pulchra* (**Table 3.1**). *Ledum palustre* and *Betula nana* are not present at Utqiagvik, but are dominant species at Atqasuk and Toolik Lake; including these two species creates a more representative sample for the southern two regions. Ten individuals from each species were sampled at each location (Utqiagvik, Atqasuk, and Toolik Lake). Individuals were selected by first encounter while searching around the center of each 30-plot grid. Individuals were also sampled at least one meter apart to prevent duplicate sampling of the same individual.

A series of measurements were taken for each individual in the field (measurements are outlined in **Table 3.S1**). Plant height was measured in centimeters from the ground to the highest vegetative structure on the plant. Photosynthetic capacity (A_{max}) was measured using a LI-6400XT Portable Photosynthesis System (Licor Inc., Lincoln, Nebraska, USA). Leaves placed in the IRGA (infrared gas analyzer) chamber were saved to calculate area. Leaf thickness was measured on the largest leaf of each

individual using a dial caliper; each leaf was then placed in a coin envelope and saved for further analysis.

In the lab, we took photographs of each individual leaf placed on 1 cm² grid paper. Surface area for each leaf was calculated using ImageJ software (Schneider et al. 2012). Reflectance measurements (normalized difference vegetation index (NDVI) and water band index (WBI)) were collected using a single channel Unispec spectroradiometer (PP Systems, Amesbury, Massachusetts, USA). Fresh weights were taken to the nearest milligram immediately upon returning from the field. Next, leaf samples were placed in a drying oven at 45°C for at least 48 hours. Dry weights were then taken using the same scale. The traits explained above were also used to calculate other traits such as specific leaf area (SLA) and leaf dry matter content (LDMC). A nutrient analysis determining nitrogen content and carbon to nitrogen ratio using the combustion method was conducted at Florida International University. Leaf samples were combined for each species at each region to conduct a single nutrient analysis.

Statistical Analyses

All statistical analyses were performed using the R statistical software version 3.6.2 (R Core Team 2018). Individuals that had multiple trait values more than 2.2 standard deviations away from the trait mean were identified as outliers and removed (about one to two individuals per species). Because removed individuals had multiple outliers (several traits for a single individual), we assumed they were either unhealthy individuals or there were errors made during measurements. Whole individuals rather than individual trait values were removed to preserve a complete data matrix without any missing values. All variables were tested for normality using the Shapiro-Wilk test. Plant

height, leaf area, leaf thickness, and LDMC were log-transformed to fulfill normality requirements. To identify which species were changing in cover over time, repeated measures ANOVAs were performed for each species at each region. P-values were adjusted for multiple comparisons using the Benjamini-Hochberg procedure.

To assess whether certain traits are associated with change in cover, canonical correspondence analysis (CCA) was conducted using package ‘vegan’ in R (Oksanen et al. 2019) using average cover values for each species for each sampling in relation to the average trait values for each species. For the CCA, we took the average percent cover for each species across all 30 sampled plots for each region; we also took the average trait value of all ten collected individuals at each region. CCA maximizes correlation between plant community composition and trait variables, revealing underlying trends in the data. Pearson and Spearman correlations between average trait values for each species and change in average cover values of that species from first (2010 for Utqiagvik and Atqasuk, 2008 for Toolik Lake) to last (2018) sampling were performed for each region and across all region in order to test individual relationships within the CCA. P-values for correlations were adjusted for multiple comparisons using the Benjamini-Hochberg procedure.

To detect changes in trait values with climate change over time, community-weighted trait means (CWM) were calculated for all traits for each plot for each sampling across all three regions using the formula:

$$\text{CWM} = \sum_{i=1}^n (p_i \times \text{trait}_i)$$

where p_i is the relative abundance of species i in the plot, and trait_i is the average trait value of species i (Duarte et al. 2018). Repeated measures ANOVA using plot-level

CWM values were performed to determine whether CWM values were changing over time at each region. P-values were again adjusted for multiple comparisons using the Benjamini-Hochberg procedure.

Results

Means and standard errors were calculated for each functional trait and species (**Table 3.S2**). Results from repeated measures ANOVA showed that only two species significantly increased in cover at one region (**Table 3.S3; Fig. 3.2**). *Carex aquatilis* ($P=0.02$, $F=10.60$) and *E. vaginatum* ($P=0.05$, $F=7.988$) increased at Atqasuk. No single species significantly increased or decreased at Utqiagvik or Toolik Lake. When analyzed by growth form, however, we found additional significant results: graminoids ($P<0.01$, $F=31.67$; $P<0.01$, $F=64.55$) increased at Utqiagvik and Atqasuk, respectively, and forbs ($P=0.02$, $F=10.34$) increased at Toolik Lake. Litter ($P<0.01$, $F=183.5$) also increased at Toolik Lake. Growth form analyses included all species found within each region rather than just our twelve focal species.

Canonical correspondence analysis (CCA) suggested patterns between change in cover and trait values (**Fig. 3.3**). Leaf nitrogen content was eliminated from the ordination due to variance inflation with carbon to nitrogen ratio. Once leaf nitrogen content was removed, all variance inflation factors were less than four. The proportion of constrained variance explained was 70.6%. Post-hoc permutations testing using the ‘anova.cca’ function in R revealed that the model ($P<0.01$) and first axis ($P<0.01$) were significant. Species increasing in cover were associated with high photosynthetic capacity (A_{max}) and species decreasing in cover were associated with high LDMC. No Pearson or

Spearman correlations between change in cover from first to last sampling and average trait values were significant.

Community-weighted trait means (CWM) consistently increased at Utqiagvik and Atqasuk, but not at Toolik Lake (**Table 3.S4; Fig. 3.4**). At Utqiagvik and Atqasuk every single CWM significantly increased over time while no CWM significantly changed over time at Toolik Lake.

Discussion

Change in Cover

Changes in species level abundances in response to a changing climate over time are consistent with more generalized trends focused on growth forms (Callaghan et al. 2011; Elmendorf et al. 2012; Hollister et al. 2015; Bjorkman et al. 2020). Graminoids are increasing at the two northern regions (Utqiagvik and Atqasuk). Not all species within each growth form are increasing the same, however. Within graminoids, *C. aquatilis* and *E. vaginatum* significantly increased in cover over time at one region but *E. angustifolium*, *E. russeolum* and *L. confusa* did not. Sedges *C. aquatilis* and *E. vaginatum* are common, dominant species as opposed to more locally abundant species, which may explain why they showed significant changes in cover. Species-level responses in our analyses are limited in that not all species present at each region occurred in at least one of the sampled plots (e.g., *P. kanei* is present at all three regions, but was not sampled in any plot). More rare species are therefore excluded from some analyses, limiting our focus primarily to common species. Due to the extremely small proportion of the landscape taken up by rare species compared to the overwhelming proportion by more

common species (e.g., *E. vaginatum* at the two southern regions; **Fig. 3.2**), we focused on the common species because shifts in abundances will have a much greater impact on overall ecosystem functioning.

Shifts in community composition were more pronounced at Utqiagvik and Atkasuk, and species-level responses were more dynamic. Two species at one of these regions increased in cover over time (*C. aquatilis* and *E. vaginatum*; **Table 3.S3**), but many species experienced small fluctuations in cover between samplings. Because our analyses only included three samplings over 8-10 years, a trend that would emerge from more consistent sampling may have been obscured, preventing the detection of more subtle responses. Therefore, our results are likely driven by the few species with large changes in cover between samplings.

Graminoid species, particularly *C. aquatilis* and *E. vaginatum*, are driving change in cover at Utqiagvik and Atkasuk. These are two species that retain their old growth in combination with new growth each growing season. Other species, including most forbs and some grasses, are herbaceous perennials that die back and regrow their leaves each year. Still others (e.g., evergreen shrubs) retain their growth over several years, resulting in slow relative growth rates (Reich et al. 1992; Mekonnen et al. 2018). Because graminoids retain their old growth in combination with new growth, they are able to quickly populate bare landscapes, possibly explaining the large increase in graminoids at the northern regions. An increase in graminoids is absent at Toolik Lake because the landscape is already densely populated with few bare patches available for colonization. Therefore, it is possible that combinations of traits linked with the ability to retain leaves for multiple growing seasons are most closely associated with change in cover.

Functional Traits and Change in Cover

Canonical correspondence analysis suggests significant increases in cover are associated with high photosynthetic capacity (A_{max}), particularly at Utqiagvik and Atkasuk (**Fig. 3.3**). Because arctic plants are constrained by such a short growing season, it is important they have the ability to photosynthesize at low temperatures while maximizing carbon fixation (Caldwell et al. 1978). Species that already have a high photosynthetic capacity will therefore respond more readily to warmer temperatures and a longer growing season. As these species increase in cover over time the overall functionality of the ecosystem will shift as well, causing productivity and net carbon exchange to increase over time with rising temperatures (Reich et al. 1999; Mekonnen et al. 2018).

Though photosynthetic capacity seems to be related to change in species cover, our results from Pearson and Spearman correlations do not support this relationship. It is possible that future analyses focusing on individual regions rather than all regions combined may have revealed more obvious underlying trends. The fact that no correlations were significant also emphasizes the need to focus on multiple traits in combination with each other rather than individual traits. Further analyses incorporating multivariate approaches (i.e., ordinations) are likely to better identify relationships between functional traits and other aspects of community dynamics (such as change in plant cover) and ecosystem functioning.

Community-Weighted Trait Means and Change in Cover

Because species level responses are so dynamic, many studies have investigated shifts in CWM (Kichenin et al. 2013; Muscarella and Uriarte 2016; Bjorkman et al.

2018a). A community-weighted approach considers overall species abundance in addition to species-specific responses. More dominant species therefore have a greater effect on the overall community trait value than rare species. Because our CWM values are calculated based on a single trait sampling (2018) and several cover samplings (2008/2010, 2014, 2018), however, shifts in CWM over time are driven solely by change in cover. Our results do not consider shifts in trait values over time, but several studies show that many traits are slow to respond to changing environmental conditions, if they change at all (Hudson et al. 2011; Kichenin et al. 2013; Bjorkman et al. 2018a). Therefore, we believe our results still have important implications with regard to shifts in ecosystem functioning in a changing environment.

Our results indicate that Utqiagvik and Atqasuk are experiencing consistent shifts in CWM for every measured trait in response to changing cover (**Table 3.S4; Fig. 3.4**). Toolik Lake, however, showed no significant trends in CWM over time. Because our results are driven by change in cover, it is logical that Utqiagvik and Atqasuk would yield more significant changes in CWM than Toolik Lake. Therefore, the observed shifts in CWM are driven by a few dominant species (i.e., *C. aquatilis* and *E. vaginatum*; **Fig. 3.S1**).

Because relatively few species are driving these changes, it is important that researchers account for species-specific responses to changing environmental conditions rather than relying solely on growth forms. There is a large amount of variation among species within a growth form resulting in overgeneralizations with regard to effects on ecosystem functioning (Saccone et al. 2017; Thomas et al. 2019). There is also large variation in traits at the population level within a species. For example, the SLA of *E.*

angustifolium at Toolik Lake is more than twice the SLA of *E. angustifolium* at Utqiagvik and Atkasuk. Therefore, it is also important to look at region-specific responses with regard to shifting community composition.

Shifts in CWM have been related to environmental gradients under the hypothesis that species converge on a locally optimal phenotype and that species abundance is related to proximity to an optimal trait value (Laughlin et al. 2012; Muscarella and Uriarte 2016; Henn et al. 2018). Convergence toward an optimal phenotype seems to occur in resource limited ecosystems driven by facilitation of species (e.g., the Arctic) rather than in resource abundant ecosystems driven by competition (Henn et al. 2018). Because we found significant results for several traits, however, it seems that investigating traits in multidimensional trait space is important to consider in future analyses. Multiple traits may interact to determine niche differentiation between species, indicating trade-offs regarding plant performance and function (Diaz et al. 2004; McGill et al. 2006; Kraft et al. 2015; Díaz et al. 2016). A multidimensional approach to trait-based studies may therefore be more indicative of cover-trait relationships and give us a better understanding of how future shifts in trait values will influence ecosystem functioning.

Future Directions

In order to capture a more comprehensive view of how plant communities in the tundra are responding to a changing climate, functional trait data must be collected for all species across multiple regions. The Tundra Trait Team (TTT) database includes tens of thousands of measurements for 18 plant traits collected from multiple regions throughout the Arctic (Bjorkman et al. 2018b); however, there are gaps for many regions and/or

species. Filling in data gaps and extending the trait list will facilitate countless studies investigating functional trait trends.

Additionally, collecting trait measurements over a long period of time will indicate whether trait values are changing or remaining constant. It is likely that traits are shifting as environmental conditions change, but data regarding shifts in traits are limited to very few studies. Because different regions are experiencing different environmental changes, it is important to conduct trait-based studies on a broader geographic scale.

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Table 3.1. Categorical abundance of the plant species measured at each region (Utqiagvik, Atqasuk, and Toolik Lake). Species were classified as absent, rare, locally abundant, or common. Locally abundant species are found only in specific habitat types while common species are found in most habitats.

Species	Family	Utqiagvik	Atqasuk	Toolik Lake
Graminoids				
<i>Carex aquatilis</i>	Cyperaceae	Common	Common	Common
<i>Eriophorum angustifolium</i>	Cyperaceae	Common	Common	Common
<i>Eriophorum russeolum</i>	Cyperaceae	Locally abundant	Locally abundant	Rare
<i>Eriophorum vaginatum</i>	Cyperaceae	Rare	Common	Common
<i>Luzula confusa</i>	Juncaceae	Locally abundant	Locally abundant	Locally abundant
Forbs				
<i>Pedicularis kanei</i>	Orobanchaceae	Rare	Rare	Rare
<i>Petasites frigidus</i>	Asteraceae	Common	Common	Common
Evergreen Shrubs				
<i>Cassiope tetragona</i>	Ericaceae	Locally abundant	Locally abundant	Common
<i>Ledum palustre</i>	Ericaceae	<i>Not present</i>	Common	Common
<i>Vaccinium vitis-idaea</i>	Ericaceae	Locally abundant	Common	Common
Deciduous Shrubs				
<i>Betula nana</i>	Betulaceae	<i>Not present</i>	Common	Common
<i>Salix pulchra</i>	Salicaceae	Locally abundant	Common	Common



Fig. 3.1. Location of study regions near Utqiagvik, Atkasuk, and Toolik Lake, Alaska.

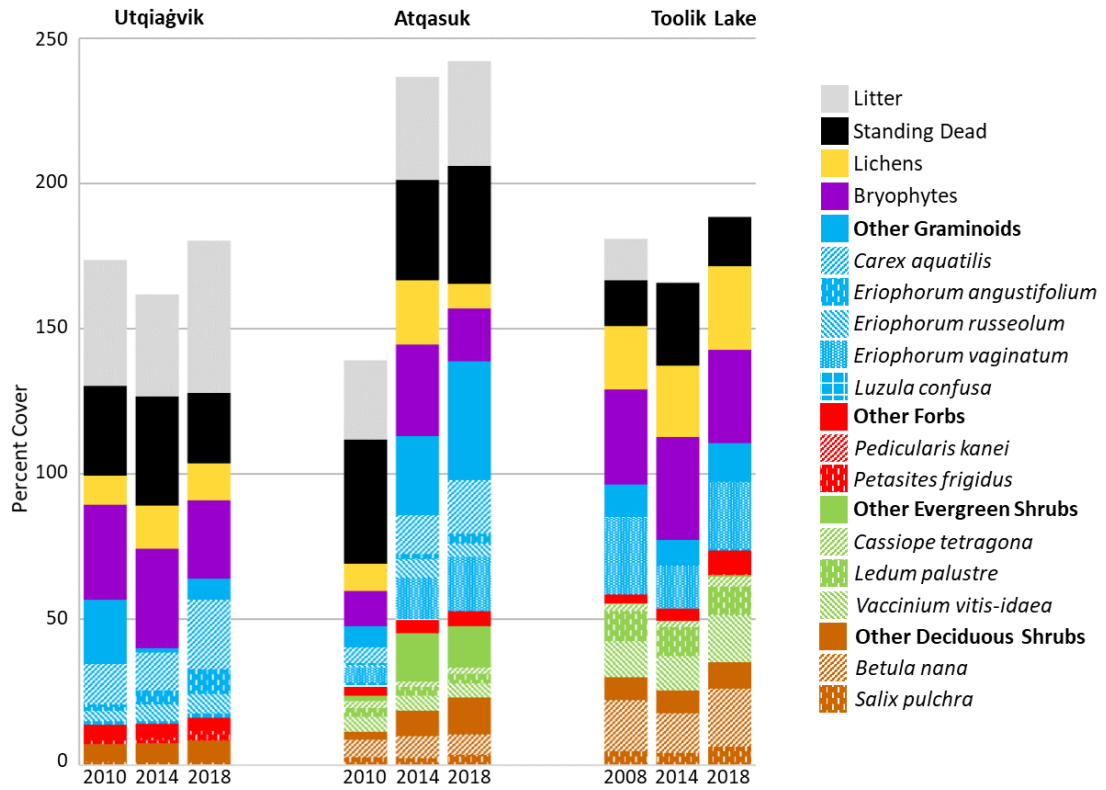


Fig. 3.2. Average plant cover at Utqiagvik, Atqasuk, and Toolik Lake, sampled between 2008 and 2018. Cover data were collected using the non-destructive point frame sampling method. The species which were measured for plant traits are denoted, other plants are grouped by growth form.

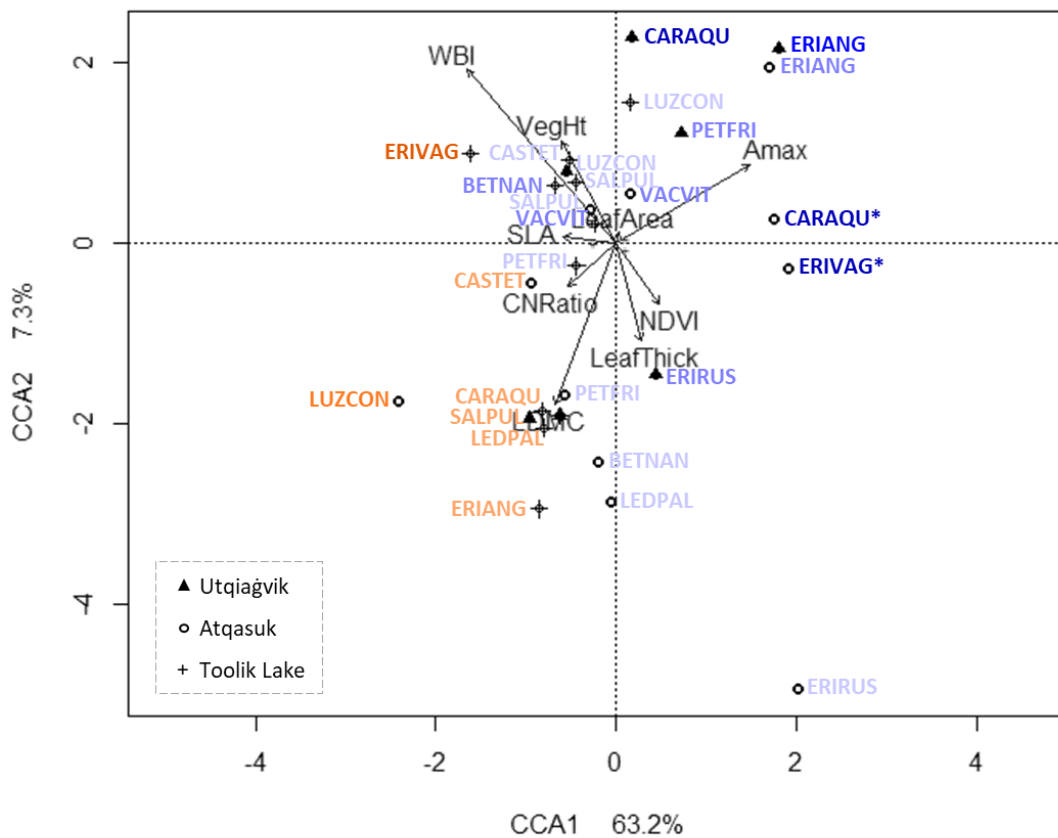


Fig. 3.3. Canonical correspondence analysis (CCA) of average cover values from each year of sampling and average trait values (“VegHt” = plant height (cm), “LeafArea” = leaf area (cm²), “SLA” = specific leaf area (cm²/mg), “WBI” = water band index, “NDVI” = normalized difference vegetation index, “LeafThick” = leaf thickness (mm), “LDMC” = leaf dry matter content (mg/g), “Amax” = photosynthetic capacity (μmol CO₂/m²/sec), and “CNRatio” = carbon to nitrogen ratio) for twelve arctic plant species (species codes follow the pattern of *Genus species* = GENSPE) at each region (represented by different symbols for Utqiagvik, Atqasuk, and Toolik Lake). The proportion of constrained variation explained was 70.6%. Results from post hoc analysis (999 permutations) indicate that the model (P<0.01) and first axis (P<0.01) are significant. Species in blue increased in cover from the first to last sampling with darker shades increasing the most and lighter shades increasing the least. Species in orange decreased in cover from the first to last sampling with darker shades decreasing the most and lighter shades decreasing the least. Species that significantly increased (repeated measures ANOVA; P<0.05) are indicated with an asterisk (*).

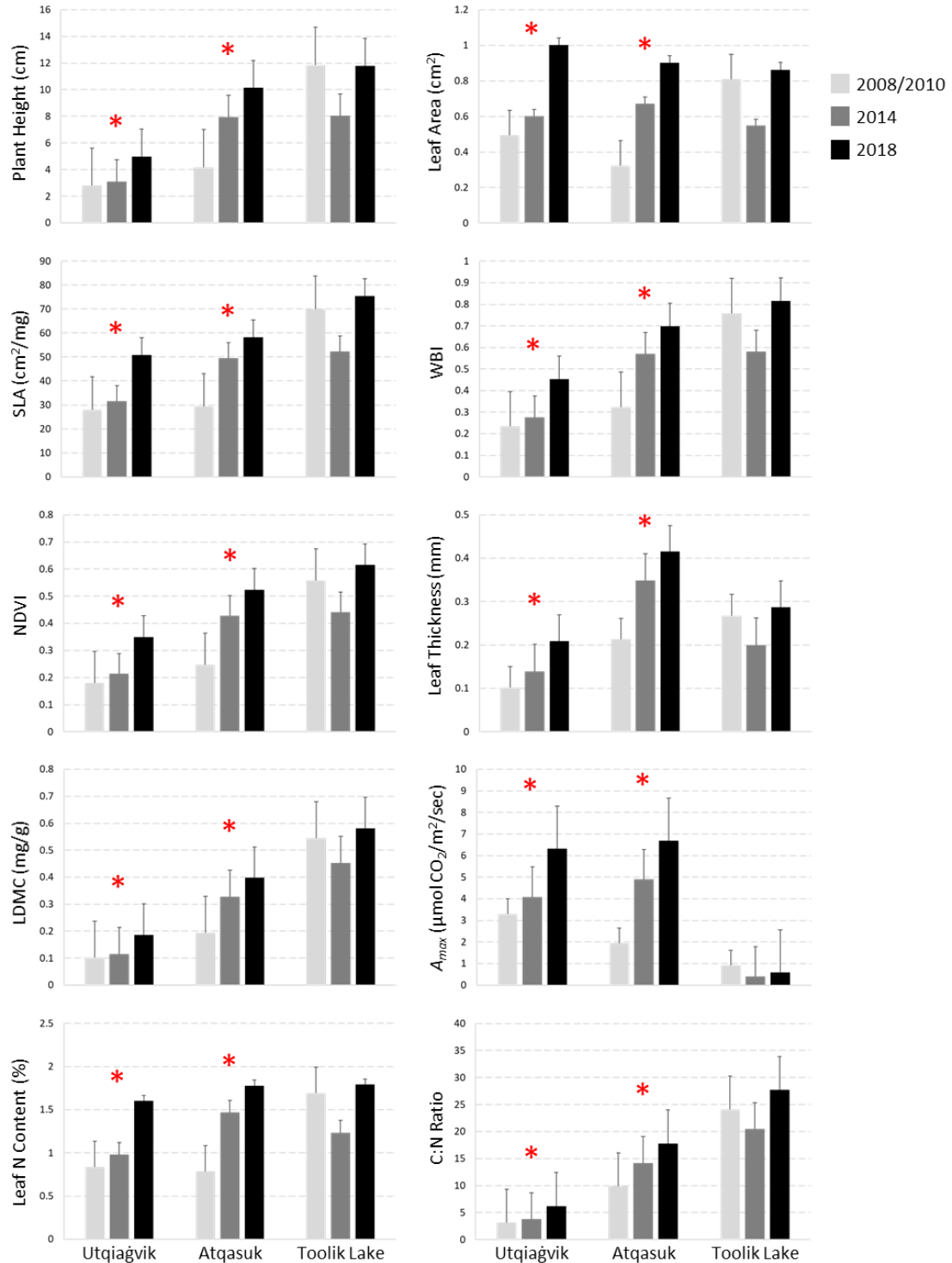


Fig. 3.4. Shifts in community-weighted trait means (CWM) for ten different functional traits from first (2008/2010) to last (2018) sampling at Utqiaġvik, Atqasuk, and Toolik Lake. Regions denoted with a red asterisk (*) were considered different based on a repeated measures ANOVA ($P < 0.05$).

Supplementary Table 3.S1. Summary of collected plant traits with corresponding units and number of replicates as well as a short description of how each trait was measured. Replicates indicate the number of measurements taken for each species at each site.

<i>Trait</i>	<i>Units</i>	<i>Reps</i>	<i>Description</i>
Plant Height	cm	10	Individual was measured from the ground to the highest vegetative structure
Leaf Area	cm ²	10	Calculated using ImageJ software using photographs taken on 1cm ² grid paper
Specific Leaf Area (SLA)	cm ² /mg	10	Calculated by dividing the leaf area (cm ²) by its dry mass (mg)
Water Band Index (WBI)	—	10	Collected using a single channel Unispec and calculated using Multispec software ($WBI = \rho_{900} / \rho_{970}$; $\rho = reflectance$)
Normalized Difference Vegetation Index (NDVI)	—	10	Collected using a single channel Unispec and calculated using Multispec software ($NDVI = (NIR - Red) / (NIR + Red)$)
Leaf Thickness	mm	10	Collected using a dial caliper
Leaf Dry Matter Content (LDMC)	mg/g	10	Calculated by dividing the dry mass (mg) by the fresh mass (g)
Photosynthetic Capacity (A_{max})	μmol CO ₂ /m ² /sec	10	Collected using a LI-6400XT Portable Photosynthesis System
Leaf Nitrogen Content	%	1	Leaf nutrients were processed at Florida International University (FIU)
C:N Ratio	—	1	Calculated by taking the ratio of leaf N content and leaf C content

Supplementary Table 3.S2. Means and (*standard error*) of 10 leaf traits (plant height (cm), leaf area (cm²), specific leaf area (SLA; cm²/mg), water band index (WBI), normalized difference vegetation index (NDVI), leaf thickness (mm), leaf dry matter content (LDMC; mg/g), photosynthetic capacity (*A*_{max}; μmol CO₂/m²/sec), leaf nitrogen content (Leaf N; %), and carbon to nitrogen ratio) for twelve arctic plant species at Utqiagvik, Atqasuk, and Toolik Lake, Alaska. All samples were collected during peak growing season 2018. Standard error is not included for leaf nitrogen content and carbon to nitrogen ratio because all leaf samples were pooled to obtain a single value (*n*=1).

	Plant Height	Leaf Area	SLA	WBI	NDVI	Leaf Thickness	LDMC	<i>A</i> _{max}	Leaf N	C:N Ratio
Utqiagvik										
<i>Carex aquatilis</i>	13.6 (0.94)	1.77 (0.20)	119.8 (13.3)	1.01 (0.00)	0.72 (0.02)	0.26 (0.01)	0.46 (0.02)	12.49 (1.35)	3.64 -	13.56 -
<i>C. tetragona</i>	5.4 (0.33)	1.29 (0.14)	27.0 (1.0)	1.01 (0.00)	0.78 (0.03)	2.87 (0.09)	0.57 (0.00)	5.54 (0.77)	1.15 -	49.47 -
<i>E. angustifolium</i>	6.3 (0.56)	1.09 (0.14)	58.1 (6.1)	1.02 (0.00)	0.84 (0.03)	0.59 (0.05)	0.34 (0.04)	13.76 (1.05)	3.20 -	15.53 -
<i>E. russeolum</i>	12.8 (0.93)	1.84 (0.20)	141.2 (6.0)	1.01 (0.00)	0.85 (0.01)	1.02 (0.04)	0.41 (0.03)	24.74 (2.56)	3.77 -	13.14 -
<i>E. vaginatum</i>	10.9 (0.30)	1.49 (0.20)	156.2 (15.6)	1.01 (0.00)	0.85 (0.02)	0.99 (0.03)	0.36 (0.03)	14.70 (1.75)	3.77 -	13.03 -
<i>Luzula confusa</i>	5.8 (0.37)	1.02 (0.15)	147.0 (20.2)	1.02 (0.00)	0.82 (0.02)	0.29 (0.02)	0.43 (0.02)	8.77 (1.97)	3.46 -	15.13 -
<i>Pedicularis kanei</i>	3.1 (0.21)	0.96 (0.15)	69.9 (5.9)	1.01 (0.00)	0.71 (0.03)	0.36 (0.02)	0.43 (0.01)	12.80 (1.61)	2.75 -	17.51 -
<i>Petasites frigidus</i>	4.0 (0.50)	10.06 (0.87)	136.5 (5.4)	1.04 (0.00)	0.87 (0.01)	0.72 (0.07)	0.19 (0.00)	8.80 (0.84)	3.71 -	12.70 -
<i>Salix pulchra</i>	15.8 (1.35)	2.03 (0.18)	124.5 (3.8)	1.01 (0.00)	0.95 (0.00)	0.29 (0.02)	0.81 (0.01)	13.09 (1.13)	3.64 -	14.21 -
<i>V. vitis-idaea</i>	1.7 (0.22)	0.30 (0.03)	56.2 (4.2)	1.01 (0.00)	0.80 (0.02)	0.41 (0.00)	0.52 (0.02)	6.18 (0.82)	1.01 -	51.07 -

Supplementary Table 3.S2. Continued...

	Plant Height	Leaf Area	SLA	WBI	NDVI	Leaf Thickness	LDMC	A_{max}	Leaf N	C:N Ratio
Atqasuk										
<i>Betula nana</i>	18.6 (1.84)	0.70 (0.03)	185.7 (9.2)	1.00 (0.00)	0.85 (0.01)	0.23 (0.02)	0.53 (0.03)	5.11 (1.55)	3.68 -	14.30 -
<i>Carex aquatilis</i>	23.1 (1.90)	2.26 (0.49)	76.7 (9.4)	1.01 (0.00)	0.75 (0.01)	0.30 (0.05)	0.63 (0.06)	17.32 (2.78)	2.83 -	15.96 -
<i>C. tetragona</i>	6.1 (0.29)	1.16 (0.15)	22.9 (0.8)	0.98 (0.01)	0.77 (0.03)	3.34 (0.15)	0.74 (0.03)	3.54 (1.03)	0.78 -	72.67 -
<i>E. angustifolium</i>	25.1 (1.47)	3.36 (0.24)	78.2 (2.7)	1.01 (0.00)	0.68 (0.02)	0.44 (0.04)	0.49 (0.05)	11.43 (1.37)	2.73 -	17.86 -
<i>E. russeolum</i>	8.3 (0.32)	0.74 (0.08)	80.2 (8.0)	0.98 (0.00)	0.72 (0.02)	0.97 (0.05)	0.63 (0.07)	-4.97 (4.22)	2.50 -	19.18 -
<i>E. vaginatum</i>	11.3 (1.01)	0.96 (0.09)	75.5 (3.2)	0.98 (0.00)	0.70 (0.02)	0.73 (0.05)	0.42 (0.01)	12.38 (1.29)	2.77 -	17.64 -
<i>Ledum palustre</i>	3.0 (0.30)	0.16 (0.02)	56.0 (2.6)	1.00 (0.00)	0.69 (0.03)	0.73 (0.03)	0.68 (0.02)	8.21 (0.49)	1.41 -	39.39 -
<i>Luzula confusa</i>	6.7 (0.40)	0.43 (0.07)	85.5 (10.3)	1.00 (0.00)	0.55 (0.02)	0.32 (0.03)	0.62 (0.03)	-40.58 (21.4)	1.87 -	25.83 -
<i>Pedicularis kanei</i>	3.7 (0.52)	1.40 (0.16)	145.2 (8.0)	1.02 (0.00)	0.70 (0.02)	0.40 (0.02)	0.39 (0.03)	8.43 (1.30)	4.19 -	11.20 -
<i>Petasites frigidus</i>	7.1 (0.36)	12.20 (0.89)	133.4 (5.8)	1.04 (0.00)	0.84 (0.01)	0.78 (0.05)	0.21 (0.01)	7.52 (0.58)	3.03 -	15.70 -
<i>Salix pulchra</i>	22.5 (3.22)	0.98 (0.15)	126.8 (9.5)	0.97 (0.00)	0.74 (0.03)	0.18 (0.01)	0.81 (0.03)	2.68 (1.20)	4.04 -	11.86 -
<i>V. vitis-idaea</i>	2.3 (0.28)	0.44 (0.05)	43.3 (2.6)	1.03 (0.00)	0.86 (0.01)	0.47 (0.03)	0.61 (0.02)	4.43 (0.39)	0.79 -	67.14 -

Supplementary Table 3.S2. Continued...

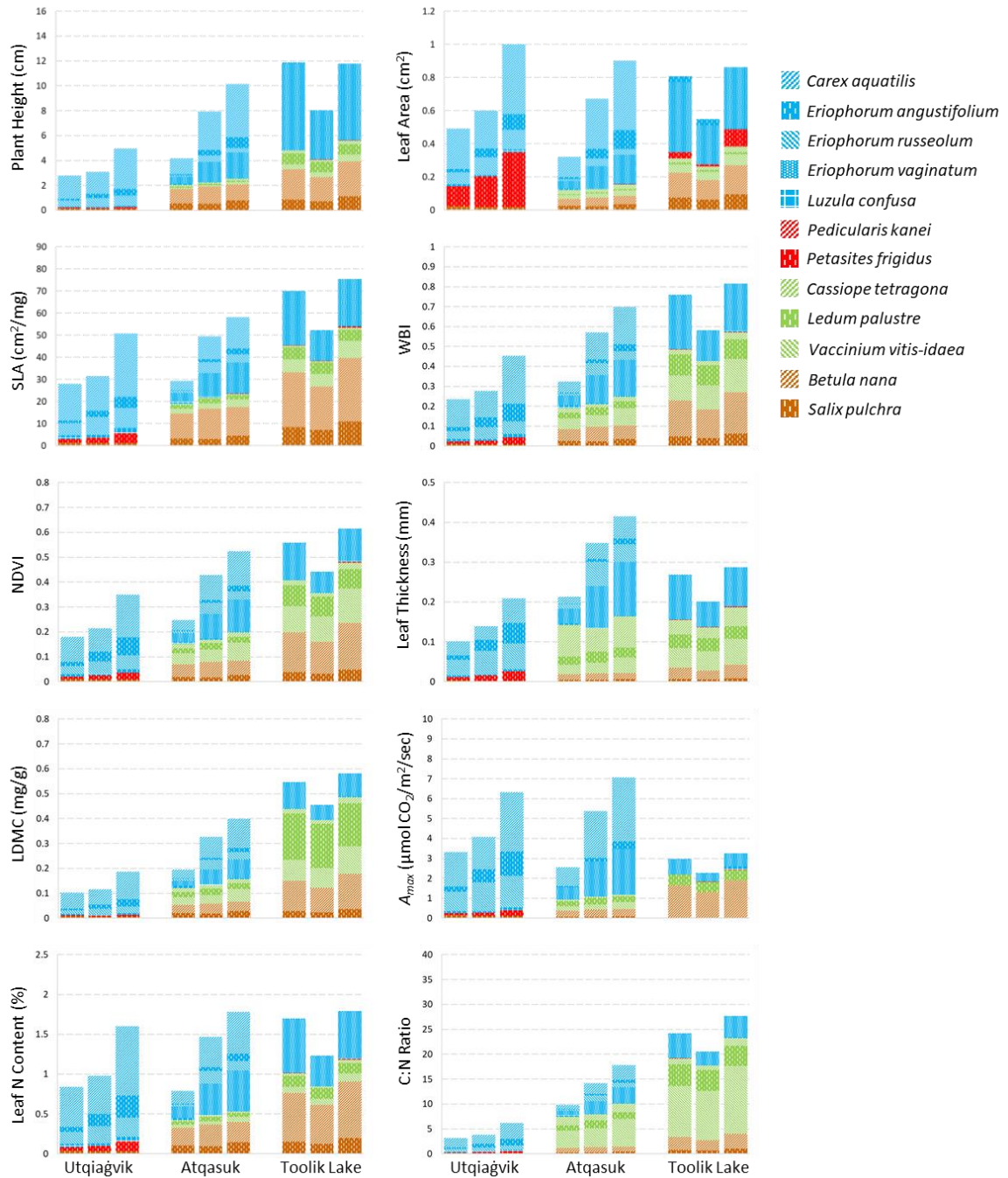
	Plant Height	Leaf Area	SLA	WBI	NDVI	Leaf Thickness	LDMC	A_{max}	Leaf N	C:N Ratio
Toolik Lake										
<i>Betula nana</i>	14.0 (2.89)	0.86 (0.06)	141.5 (5.5)	1.03 (0.00)	0.92 (0.01)	0.17 (0.02)	0.70 (0.07)	9.39 (2.11)	3.50 -	15.14 -
<i>Carex aquatilis</i>	15.2 (0.83)	1.99 (0.28)	99.4 (12.1)	1.01 (0.00)	0.79 (0.03)	0.18 (0.03)	0.50 (0.04)	-21.29 (4.88)	3.25 -	15.01 -
<i>C. tetragona</i>	8.6 (0.32)	0.99 (0.06)	29.2 (1.7)	1.01 (0.00)	0.79 (0.01)	1.40 (0.12)	0.74 (0.05)	-17.31 (4.09)	1.23 -	46.52 -
<i>E. angustifolium</i>	28.0 (2.15)	21.27 (2.82)	197.4 (5.5)	1.03 (0.00)	0.85 (0.01)	0.35 (0.04)	0.30 (0.01)	1.11 (0.79)	3.61 -	13.34 -
<i>E. russeolum</i>	15.7 (0.19)	0.97 (0.13)	83.3 (19.2)	1.04 (0.01)	0.75 (0.06)	0.60 (0.03)	0.42 (0.03)	-17.48 (3.10)	3.85 -	12.60 -
<i>E. vaginatum</i>	26.7 (2.95)	1.61 (0.18)	91.9 (8.7)	1.03 (0.00)	0.57 (0.09)	0.43 (0.07)	0.40 (0.02)	2.87 (1.00)	2.57 -	18.71 -
<i>Ledum palustre</i>	8.5 (1.07)	0.13 (0.02)	52.6 (5.0)	1.01 (0.00)	0.80 (0.03)	0.33 (0.05)	1.79 (0.31)	5.28 (3.21)	1.34 -	41.95 -
<i>Luzula confusa</i>	6.7 (0.35)	0.56 (0.11)	65.1 (5.8)	1.04 (0.00)	0.56 (0.04)	0.14 (0.02)	0.42 (0.02)	27.11 (4.05)	2.15 -	21.92 -
<i>Pedicularis kanei</i>	9.2 (0.76)	2.14 (0.26)	99.9 (10.0)	1.02 (0.00)	0.72 (0.03)	0.31 (0.03)	0.41 (0.02)	4.46 (2.42)	3.51 -	13.64 -
<i>Petasites frigidus</i>	12.6 (0.52)	35.01 (6.61)	137.6 (1.8)	1.04 (0.00)	0.85 (0.02)	0.53 (0.02)	0.24 (0.01)	9.01 (0.52)	3.42 -	13.79 -
<i>Salix pulchra</i>	18.2 (1.47)	1.57 (0.17)	180.0 (24.5)	1.01 (0.00)	0.80 (0.01)	0.14 (0.02)	0.61 (0.07)	-2.46 (1.87)	3.21 -	16.38 -
<i>V. vitis-idaea</i>	3.3 (0.31)	0.40 (0.06)	47.8 (3.5)	1.02 (0.00)	0.85 (0.02)	0.40 (0.03)	0.67 (0.03)	-11.81 (1.58)	0.64 -	82.62 -

Supplementary Table 3.S3. Statistical significance of change in cover over time at Utqiaġvik, Atqasuk, and Toolik Lake. P-values and F statistics from repeated measures ANOVAs; significant p-values (<0.05) are indicated in bold.

	Utqiaġvik		Atqasuk		Toolik Lake	
	P	F	P	F	P	F
Deciduous Shrubs	0.84	(0.095)	0.31	(2.906)	0.42	(1.298)
<i>Betula nana</i>	<i>Not present</i>		0.87	(0.066)	0.69	(0.451)
<i>Salix pulchra</i>	0.88	(0.048)	0.76	(0.276)	0.62	(0.685)
Evergreen Shrubs	-		0.12	(5.266)	0.42	(1.994)
<i>Cassiope tetragona</i>	-		0.98	(0.001)	0.76	(0.241)
<i>Ledum palustre</i>	<i>Not present</i>		0.76	(0.243)	0.76	(0.204)
<i>V. vitis-idaea</i>	-		0.31	(2.868)	0.29	(3.228)
Forbs	0.76	(0.204)	0.42	(1.513)	0.02	(10.34)
<i>Pedicularis kanei</i>	-		-		-	
<i>Petasites frigidus</i>	0.42	(1.314)	0.42	(1.509)	0.42	(1.545)
Graminoids	<0.01	(31.67)	<0.01	(64.55)	0.68	(0.513)
<i>Carex aquatilis</i>	0.12	(5.727)	0.02	(10.60)	0.42	(1.697)
<i>E. angustifolium</i>	0.07	(6.903)	0.23	(3.959)	0.62	(0.649)
<i>E. russeolum</i>	0.42	(1.926)	0.36	(2.327)	-	
<i>E. vaginatum</i>	-		0.05	(7.988)	0.42	(1.281)
<i>Luzula confusa</i>	0.69	(0.414)	0.42	(1.643)	0.42	(1.450)
Bryophytes	0.42	(1.434)	0.42	(1.288)	0.97	(0.004)
Lichens	0.69	(0.440)	0.90	(0.030)	0.36	(2.447)
Standing Dead	0.29	(3.378)	0.81	(0.134)	0.48	(1.049)
Litter	0.36	(2.470)	0.12	(5.409)	<0.01	(183.5)

Supplementary 3.S4. Statistical significance of change in community-weighted trait means (CWM) over time at Utqiagvik, Atqasuk, and Toolik Lake. P-values and F statistics from repeated measures ANOVAs; significant p-values (<0.05) are indicated in bold. CWMs were calculated based on 2018 trait measurements and 2008/2010, 2014, and 2018 percent cover estimates.

	Utqiagvik		Atqasuk		Toolik Lake	
	P	F	P	F	P	F
Plant Height	< 0.01	(11.62)	< 0.01	(44.87)	0.80	(0.149)
Leaf Area	0.01	(7.979)	< 0.01	(41.47)	0.89	(0.028)
SLA	< 0.01	(15.84)	< 0.01	(26.33)	0.80	(0.103)
WBI	< 0.01	(19.00)	< 0.01	(57.61)	0.80	(0.148)
NDVI	< 0.01	(19.41)	< 0.01	(52.68)	0.66	(0.439)
Leaf Thickness	< 0.01	(17.99)	< 0.01	(16.70)	0.80	(0.120)
LDMC	< 0.01	(13.87)	< 0.01	(59.59)	0.80	(0.152)
Amax	< 0.01	(15.77)	< 0.01	(38.62)	0.64	(0.520)
Leaf N	< 0.01	(18.28)	< 0.01	(54.98)	0.89	(0.018)
C:N Ratio	< 0.01	(19.32)	< 0.01	(17.72)	0.29	(1.648)



Supplementary Fig. 3.S1. Contributions of species to community-weighted trait means (CWM) for ten different functional traits. CWM were calculated for three samplings between 2008 and 2018 at Utqiaġvik, Atqasuk, and Toolik Lake. Cover data were collected at each sampling and trait data were collected in 2018. CWM were calculated by multiplying the trait mean (2018) by the average cover of each species for each sampling at each site.

Chapter IV

Extended Review of Literature

Why the Arctic?

Global climate change is expected to cause major losses in biodiversity and the Arctic is particularly susceptible to this threat (IPCC 2018). The Arctic is the fastest warming biome in the world, with the melting of glaciers and sea ice and thawing of permafrost primary evidence of rising air temperatures. Over the last 50 years winter temperatures in the Arctic have increased by 3-4°C, twice the rate of the rest of the world (ACIA 2004; AMAP 2019). The Arctic is therefore an indicator of future environmental change, making it the forefront of research on climate change impacts.

Anthropogenic increases in greenhouse gas emissions are the primary drivers behind rising global mean air temperatures (ACIA 2004; IPCC 2018; AMAP 2019). Historically the Arctic has been a sink for atmospheric carbon dioxide with the permafrost playing an integral role in maintaining the global carbon balance (Billings 1987). Over 97% of carbon in the tundra is stored in the soil with much of it trapped in the permafrost layer. This, coupled with cold temperatures limiting decomposition, makes the tundra a carbon sink, an important aspect of maintaining global carbon balance (Billings 1987). However, with climate warming and the thawing of the permafrost, evidence shows that the Arctic is becoming a carbon source rather than a carbon sink (Oechel et al. 1993). Carbon trapped within the permafrost is released and made available to soil microbes which fuel decomposition and thus release of carbon as carbon dioxide into the atmosphere. Warmer temperatures also cause increases in net primary productivity and rates of ecosystem carbon dioxide exchange (Oberbauer et al. 2007).

There is already evidence of net carbon losses in tundra ecosystems with increased net primary productivity (Oechel et al. 1993; Oberbauer et al. 2007), upsetting the carbon balance that has been maintained throughout the Holocene (Billings 1987). Release of carbon through increased rates of decomposition and net primary productivity contributes to rises in air temperatures, creating a positive feedback loop and further propelling global climate change.

Arctic Vegetation Community Assembly

Plant communities are particularly sensitive to changes in temperature. The Arctic is described by a short growing season with low average temperatures that limit growth and soil microbial activity (Bliss 1962; Billings and Mooney 1968). In addition to carbon, most soil nutrients are trapped within the permafrost and are unavailable for uptake by plants. As a persistently cold and severely nutrient limited system, the Arctic consists of plants characterized by slow growth rates and low reproductive outputs (Bliss 1962; Billings and Mooney 1968; Bell and Bliss 1980). This is in line with Grime's stress-tolerant life strategy, which most closely describes arctic plants (Grime 1977). In addition to dealing with low temperatures and nutrient limitations, arctic plants are prone to desiccation. If exposed during the winter months when water in the soil is frozen and unavailable to roots, the aerial parts of plants are damaged by dry, heavy winds. Plants in the Arctic are therefore specially adapted to harsh climate conditions (i.e. perennial evergreens of low stature) (Bliss 1962; Billings and Mooney 1968; Savile 1972).

Species that currently occupy the Arctic are remnants of large oscillations in climate and recurrent glaciations throughout the Pleistocene. The Arctic biome is relatively young and therefore a fairly simple ecosystem, making it ideal for phylogenetic

studies that incorporate large-scale gene flow patterns and dispersal barriers. Arctic ecosystems are less complex than temperate areas and harbor fewer species with wider ecological niches (Callaghan et al. 2004; Eidesen et al. 2013). The simplicity of arctic ecosystems is largely due to major glaciation events expelling any former vegetation, forcing community assembly processes to start over again and again with primary succession. The temporal scale necessary for a complex ecosystem to arise is therefore currently lacking in arctic systems.

During the last glacial maximum (*c.* 21,000 years ago), however, much of the Arctic was unglaciated. Within these refugia, species specially adapted to withstand extremely harsh conditions were able to persist. Beringia, the area around the Bering Strait, was one major glacial refugium for the Arctic, and is shown to be a hotspot of species diversity and endemism (Hultén 1937; Eidesen et al. 2013). Recent studies show that Beringia also holds some of the highest degrees of genetic diversity and distinctiveness in the Arctic, suggesting that most arctic plants initially radiated outward from Beringia and reached full circumpolar distributions before the onset of the Pleistocene glaciations (Hultén et al. 1937; Alsos et al. 2007; Eidesen et al. 2013). Today's arctic species distributions therefore originated from Beringia and other refugia, with extreme stress-tolerance driving many of the characteristics shared by arctic (particularly high arctic) species.

A unique characteristic of arctic plants is winter seed dispersal. Due to the short growing season, many plants don't set seed until after the first snowfall. Therefore, some arctic plants will dramatically increase in height at the very end of the growing season in order to reach above the snow line in winter (Savile 1972). *Potentilla hyparctica* and

Papaver hultenii are two species that demonstrate this adaptation. Seeds can then travel much greater distances with the combination of high winds and smooth surface of packed down snow. Arguably the dispersal distance of many arctic plants is indefinite, as seeds travel across slick sheets of snow until they hit a geographical barrier (Savile 1972; Laughlin et al. 2012; Eidesen et al. 2013). High amounts of gene flow in the Arctic help maintain genetic diversity and therefore hopefully the ability to adapt with the changing climate.

Perhaps more important than dispersal is the ability to establish in a new area. There is evidence that the ability of an individual to germinate, survive, and locally reproduce is more limiting than an individual's ability to disperse (Laughlin et al. 2012; Eidesen et al. 2013). Successful colonization is strongly correlated with temperature requirements of the species (Alsos et al. 2007) and there is evidence that some species (or ecotypes of species) are more successful at establishing in a new area than others (Bennington et al. 2012; Laughlin et al. 2012). Assuming that community assembly is stochastic in nature, plant communities will then be built based not on which species arrive first, but on which species arrive first *and* successfully establish and propagate. Since dispersal distances are, in theory, unlimited, it is logical to assume that mechanisms and traits related to establishment are more important than dispersal ability when predicting long-term shifts in arctic ecosystems.

It may be appropriate, then, to describe the process of community assembly in terms of functional traits rather than individual species. Functional traits influence performance; thus, environments often consist of species with similar trait values. Competition for limiting resources prevents species from being too functionally similar,

promoting species coexistence rather than competition. Laughlin et al. (2012) proposed a predictive model of community assembly. Their model begins with an environmental filter that selects for traits that can tolerate the environmental conditions. The likelihood of a species appearing based on its range and dispersal ability is then calculated, also considering the species ability to proliferate once it's established. These two steps are integrated to calculate relative abundances of species. The authors reported that the model successfully chose the correct most abundant species 51% of the time. Instances of mismatches were species with similar trait values and were therefore functionally redundant.

At least in extreme environments, it can therefore be argued that community assembly is largely based on selection of traits that can best tolerate harsh arctic conditions rather than individual species. Arctic communities are driven by facilitation, and can thus be described by convergence on the mean trait value (and therefore loss of variance) that best reflects an optimal phenotype for those local environmental conditions (Laughlin et al. 2012; Muscarella and Uriarte 2016; Henn et al. 2018). Individuals closest to the mean trait value therefore have the highest fitness. Communities that are not resource limited are driven by competition rather than facilitation, which leads to divergence from the mean trait value (and therefore increase in variance) (Henn et al. 2018). Individuals become specialized to fill a specific niche space, broadening the niche breadth of the population (McGill et al. 2006; He et al. 2018b; Thomas et al. 2020). As surrounding environmental conditions change, however, optimal trait values shift and thus cause shifts in species abundances. Functional redundancy among species makes it difficult to accurately predict shifts in species composition, but observing shifts in

functional traits over time can provide insight on how ecosystem functioning might change in coming decades (Laughlin et al. 2012; He et al. 2018b; Henn et al. 2018).

Intraspecific Variation (ITV) in Arctic Populations

The range of trait values a species can have and still survive is related to the amount of heritable intraspecific variation (ITV) within a population. ITV is important to consider in many trait-based studies, but is not always appropriately accounted for. Albert et al. (2011) provide an excellent guide for when and how ITV should be considered. They state that many trait-based studies assume the amount of ITV is insignificant compared to the amount of interspecific variation, but this is often not the case. Albert et al. (2011) pose four questions that help establish whether ITV should be considered: (1) “Is ITV explicitly encompassed?”, (2) “What is the study spatial scale?”, (3) “How have species been selected for the study?”, and (4) “What are we interested in?”. If ITV is not explicitly encompassed, then spatial scale plays a large part in determining ITV effect. At the global scale, ITV is probably negligible due to the vast array of species included. At the regional and local scales, however, species- versus site-centered studies and questions regarding response traits versus effect traits all play a part in determining the role of ITV. Because this study takes place at the regional scale and is focused on a few key species rather than all species, ITV was measured and considered when conducting analyses and drawing conclusions. Both ITV and interspecific variation can have significant ecological effects, including amount of species interactions, rate of adaptation, and level of phenotypic fitness and should therefore be carefully considered in trait-based studies (McGill et al. 2006; Bolnick et al. 2011; Thomas et al. 2020).

It has been proposed that severity of environmental conditions is related to level of ITV (He et al. 2018b; Henn et al. 2018). It is thought that species in harsh environments have a narrow habitat range and therefore low ITV (McGill et al. 2006; He et al. 2018b). Individuals with low ITV could be characterized as habitat specialists, with a narrow niche breadth and geographical range (Sultan 2000; He et al. 2018b). Low ITV individuals would then possess a fitness advantage in their preferred habitats, outperforming generalists only when specific environmental conditions are met (Caley and Munday 2003; Thomas et al. 2020). Generalist species, on the other hand, would be able to persist over a broader range of conditions, but never reach the level of performance of a specialist (Caley and Munday 2003; Thomas et al. 2020). More generalist species would therefore have higher ITV and a much broader geographical range. High ITV individuals would also have a better chance of colonization across a largely heterogenous landscape. The relationship between ITV, phenotypic plasticity, and habitat specialists versus generalists is not well supported, but further investigation of the concept is needed to see whether it can be applied to arctic ecosystems.

There are, however, specialist and generalist species that occur in the Arctic. Species that occupied unglaciated areas during the last glacial maximum were likely specialists with a high stress tolerance (Alsos et al. 2007; Eidesen et al. 2013). Stress-tolerant species are characterized as high arctic species and currently occupy the northernmost regions. Populations of high arctic species likely have low ITV and a narrow geographical range. High arctic populations are restricted to regions with very specific environmental conditions, but have higher overall fitness than other more generalist species in the area (Sultan 2000; He et al. 2018b). High arctic species would,

however, fail to persist as environmental conditions change, resulting in greater abundances of generalist species over time.

Conversely, many low arctic species likely invaded these areas after the glaciers receded and conditions were more favorable. Low arctic species are likely more generalist species with lower stress tolerance. Due to increased competition and more widely available niche space, low arctic species likely have higher ITV and a much broader geographical range. A wider niche breadth enables these species to persist as environmental conditions change. It is therefore expected that high arctic species such as *Cassiope tetragona* will eventually disappear over time, while more generalist, low arctic species such as *Salix pulchra* and *Carex aquatilis* will become more abundant. Changes in species abundance as a result of ITV depends (at least in part) on the amount of genetic variation present versus the amount environmental variation, but further research is needed to differentiate between the underlying components of ITV.

As the climate changes, community composition and overall species abundances shift as well. Mean trait values as well as the amount of ITV within these communities will also shift, which has important implications for ecosystem functioning. Many studies have investigated the role specific traits play in community ecology (Messier et al. 2010; Bolnick et al. 2011; Kichenin et al. 2013; Díaz et al. 2016). Most studies agree that trade-offs involving plant form and function are involved, limiting the amount of trait combinations that can exist on a global scale. Díaz et al. (2016) performed an analysis involving 46,085 species and showed that 75% of trait variation is explained within two dimensions: one involving plant size and the other the leaf economics spectrum. Relationships between traits that lie along these two spectra have been thoroughly

investigated and support this claim (Reich et al. 1999; Wilson et al. 1999; Diaz et al. 2004; Vile et al. 2005). Additionally, the amount of variability within a population can affect ecosystem processes. Functional traits are directly related to species fitness, and increased ITV can either improve or inhibit performance. Species performance influences how different species interact with each other (i.e., competition, facilitation, etc.), affecting the dynamic of the entire community. Investigating the importance and influence of ITV is therefore fundamental in understanding how ecosystem functioning will change in coming decades.

Plasticity vs. Local Adaptation

There is some evidence that populations with low ITV are less plastic than populations with high ITV. De Villemereuil et al. (2018) investigated patterns of phenotypic plasticity and local adaptation in populations of *Arabis alpina*, an alpine plant that occupies areas up to the highest elevations. Through a set of common garden experiments, the authors found that populations at the highest elevations were less plastic than populations at lower elevations. Absence of gene flow between populations and relative consistency of environmental conditions confirmed that each population was locally adapted to its environment. For species lacking phenotypic plasticity such as *A. alpina*, then, the rate of local adaptation must be able to keep up with the rate of global climate change in order for the species to persist.

Populations that are plastic will likely be able to shift their trait values to match changing environmental conditions. Reciprocal transplant experiments across elevation gradients show evidence for this (de Villemereuil et al. 2018; Gao et al. 2018; Henn et al. 2018). When transplanted to a location with a vastly different mean trait value,

individuals tended to converge toward that value. In cases where the new location had a similar mean trait value, however, individuals diverged from that value. Henn et al. (2018) also did not find a strong link between phenotypic plasticity and intraspecific variation. In theory, populations with high intraspecific variation are also more plastic, but there was little evidence for this. Instead, the authors linked plasticity to leaf lifespan, suggesting that longer lived species might be more plastic. Perhaps, then, shorter lived species are less plastic because they are instead able to locally adapt at a faster rate.

It is also possible, if not probable, that plasticity itself is adaptive. While evidence shows that high elevation populations (and, comparably, high latitude populations) have relatively low levels of phenotypic plasticity (de Villemereuil et al. 2018; Gao et al. 2018; Henn et al. 2018), it is possible that over time more plastic individuals will be selected for and increase overall plasticity for the population. Rather than asking whether populations are plastic or locally adapted to their environment, it is better to consider a combination of both and accept that responses to gradual changes in climate will be more complex than previously thought. Establishing levels of phenotypic plasticity and local adaptation in arctic populations is an important step in future studies looking at community responses to a changing climate.

Plant-Temperature Interactions and Functional Traits

Many studies are devoted to understanding how arctic communities will respond to increased temperatures. The International Tundra Experiment (ITEX) is a network of researchers from more than eleven countries that has been studying plant-temperature relationships for decades. Many sites throughout arctic and alpine ecosystems have established long-term warming experiments using open-top chambers (OTCs).

Manipulation experiments have revealed general trends in plant responses to elevated temperatures including increased cover of deciduous shrubs, evergreen shrubs, and graminoids and decreased cover of bryophytes and lichens (Callaghan et al. 2011; Elmendorf et al. 2012; Hollister et al. 2015; Bjorkman et al. 2020). Not all trends are consistent across regions, however. Some studies have reported varying responses with community types, with wet/moist communities being more responsive than dry communities (Elmendorf et al. 2012; Bjorkman et al. 2020). Some studies have speculated that mixed responses are due to mixed species responses within growth forms (Hudson et al. 2011; Saccone et al. 2017). Large variation in individual species responses to temperature indicate that the traditional growth form approach may be insufficient in evaluating overall community change. Saccone et al. (2017) reported vast differences in species-specific responses to snow manipulation experiments within deciduous shrubs. Some species interacted more strongly with neighboring species, and other species showed greater sensitivity to environmental extremes. Such dynamic responses show that a species-specific approach to evaluating community change will be more insightful than grouping species into traditional growth forms.

Many studies have shifted from cover-focused community responses to functional trait responses to temperature manipulations. Plant functional traits have been shown to strongly affect ecosystem functioning which can further impact changes in climate (Lavorel and Garnier 2002; Cornelissen et al. 2007; Pearson et al. 2013; Myers-Smith et al. 2019). Many functional traits have been studied in detail, and a list of traits has been generally agreed upon to be important to ecosystem processes (Cornwell et al. 2008; Hudson et al. 2011). Plant height is the most intensively studied trait, and is positively

correlated with light capture ability (Westoby et al. 2002; Mekonnen et al. 2018). Tall-statured plants have earlier access to sunlight upon snowmelt and impose shade on short-statured plants. Other size-related traits, such as leaf area, are also commonly studied. Leaves with greater surface area have increased photosynthetic rates, but also increased water loss (Parkhurst and Loucks 1972; Wang et al. 2019). Conversely, smaller, thicker leaves have better water retention and are therefore resistant to desiccation. Size related traits are therefore indicative of trade-offs related to plant performance, which is especially important in harsh environments. Certain indices are also good indicators of plant strategies. Water band index (WBI) is an indicator of leaf water content (Peñuelas et al. 1993) and normalized difference vegetation index (NDVI) is a valuable tool for monitoring productivity (Kriegler et al. 1969; Posse and Cingolani 2004; Xu et al. 2012). Specific leaf area (SLA) and leaf dry matter content (LDMC), two other commonly studied traits, are generally associated with leaf life span and relative growth rate (Reich et al. 1992; Wilson et al. 1999). Leaves with a high SLA are thought to be more productive, but also relatively short-lived (Wilson et al. 1999). While traits such as leaf area, NDVI, and SLA can be indicative of plant productivity, photosynthetic capacity (A_{max}) can also be directly measured and correlated with other traits such as leaf longevity (Johnson and Tieszen 1976).

How functional traits change with increased temperature is a relatively recent approach to community change studies. Many studies focus on trends in traits along environmental gradients (most commonly elevational gradients) and report how different populations of the same species respond to different environmental conditions (Hudson et al. 2011; Muscarella and Uriarte 2016; Bjorkman et al. 2018a; Henn et al. 2018). A few

general trends in temperature-trait relationships are supported by several studies.

Increased plant height is the most common response to increased temperature (Hudson et al. 2011; Bjorkman et al. 2018a; de Villemereuil et al. 2018; Gao et al. 2018). Studies also show increases in SLA and decreases in LDMC, but suggest that these responses are strongly driven by community type (Baruah et al. 2017; Bjorkman et al. 2018a).

Responses of other functional traits are mixed across sites (Hudson et al. 2011; Bjorkman et al. 2018a).

The number of studies investigating temperature-trait relationships is rapidly increasing. Trends in functional traits have been documented along environmental gradients (de Villemereuil et al. 2018; Gao et al. 2018; Halbritter et al. 2018; Amartuvshin et al. 2019) and several others have explored how community-weighted trait means (CWM) respond to increases in temperature (Kichenin et al. 2013; Muscarella and Uriarte 2016; Bjorkman et al. 2018a). While most studies support general trends in temperature-trait relationships for some functional traits, mixed results for other traits suggest that a different approach to trait-based studies is necessary to better understand community-level responses to changing environmental conditions. Research suggests that a stronger focus on species-level responses to environmental changes may be more indicative of future community change (Saccone et al. 2017; Myers-Smith et al. 2019). While functional trait data exists for many arctic species within the Tundra Trait Team database (TTT), we lack data on differences in functional traits between populations of the same species (Bjorkman et al. 2018b). It is important to establish whether species-level functional trait values are uniform across populations, or if they are altered by

environmental conditions. Information on individual populations of species will further our understanding of community-level responses to future environmental change.

Extended Methodology

ITEX-AON History and Measurements

Established in 1990, ITEX is a network of researchers from more than eleven countries that seeks to understand plant-temperature interactions in cold adapted species. Strict protocols outlining the assembly of open-top chambers (OTCs) to simulate climate warming are in place as well as procedures for accurately measuring plant cover (Molau and Mølgaard 1996). There are currently over 30 active ITEX sites carrying out official protocols covering individual growth rates, phenology changes, inflorescence counts, abundance measurements, and many others.

The ITEX sites in the United States were originally funded separately in the early to mid 1990's; however eventually they joined together. Currently Grand Valley State University (GVSU) along with Florida International University (FIU), University of Texas at El Paso (UTEP), and University of Alaska Anchorage (UAA) form the ITEX-AON (International Tundra Experiment-Arctic Observing Network) with funding from the National Science Foundation (NSF). The work is funded as part of the NSF Arctic Observing Network (AON). These universities monitor four research sites on the North Slope of Alaska: Utqiagvik, Atkasuk, Toolik Lake, and Imnavait Creek (**Fig. 4.1**). All project sampling occurs within Arctic System Science (ARCSS) grids established in the early 1990s. ARCSS grids include 100 control plots spaced evenly over 1 km², OTC plots with corresponding control plots that make up the established ITEX sites, and a mobile-instrumented sensor platform (MISP) covering a 50-m transect that collects abiotic and spectral data.

The ITEX plots have been the most intensely and consistently monitored. Each ITEX site consists of two sub-sites: a wet meadow/moist acidic site and a dry heath site. At Utqiagvik and Atqasuk, phenology, reproductive effort, and growth rates have been measured since the mid-1990s and have yielded significant responses to experimental warming (Oberbauer et al. 2013; Barrett et al. 2015; Kremers et al. 2015; Prev y et al. 2017). Carbon flux measurements at all four sites have also showed major differences in carbon exchange over time (Welker et al. 2000; Oberbauer et al. 2007). Long-term monitoring of plant cover using the point-frame method outlined in the ITEX manual (Molau and M lgaard 1996) has been conducted at all four research sites and has generally shown that graminoids and shrubs increase and mosses and lichens decrease (Elmendorf et al. 2012; Hollister et al. 2015). Snow manipulation experiments at Toolik Lake have given insight on how changes in hydrology affect ecosystem functioning (Welker et al. 2000; Leffler et al. 2016; Jespersen et al. 2018). Overall, the ITEX sites have a long history of vegetation monitoring that has provided valuable information on how arctic communities are responding to a changing climate.

One mobile-instrumented sensor platform (MISP) is installed at each location. The MISP collects daily abiotic and spectral data along a 50-m transect. Specifically, responses of albedo (Healey et al. 2014) and NDVI (May et al. 2017; May et al. 2020) to daily fluctuations in temperature have allowed detection of changes in growing season length and intensity.

Finally, close monitoring of 100 control plots within each ARCSS grid has showed differences in vegetation change across landscape types (Elmendorf et al. 2012; Gregory 2014, Botting 2015, Hobbie et al. 2017; Harris 2020). Aerial kite photography

has also revealed landscape-level vegetation changes through various remote-sensing platforms (Vargas et al. 2017). Continuous monitoring at several spatial scales has allowed the ITEX-AON network to capture many aspects of tundra ecosystem dynamics over several decades. This thesis uses vegetation change observations collected on a subset of plots from the ARCSS grid (**Fig. 4.1**).

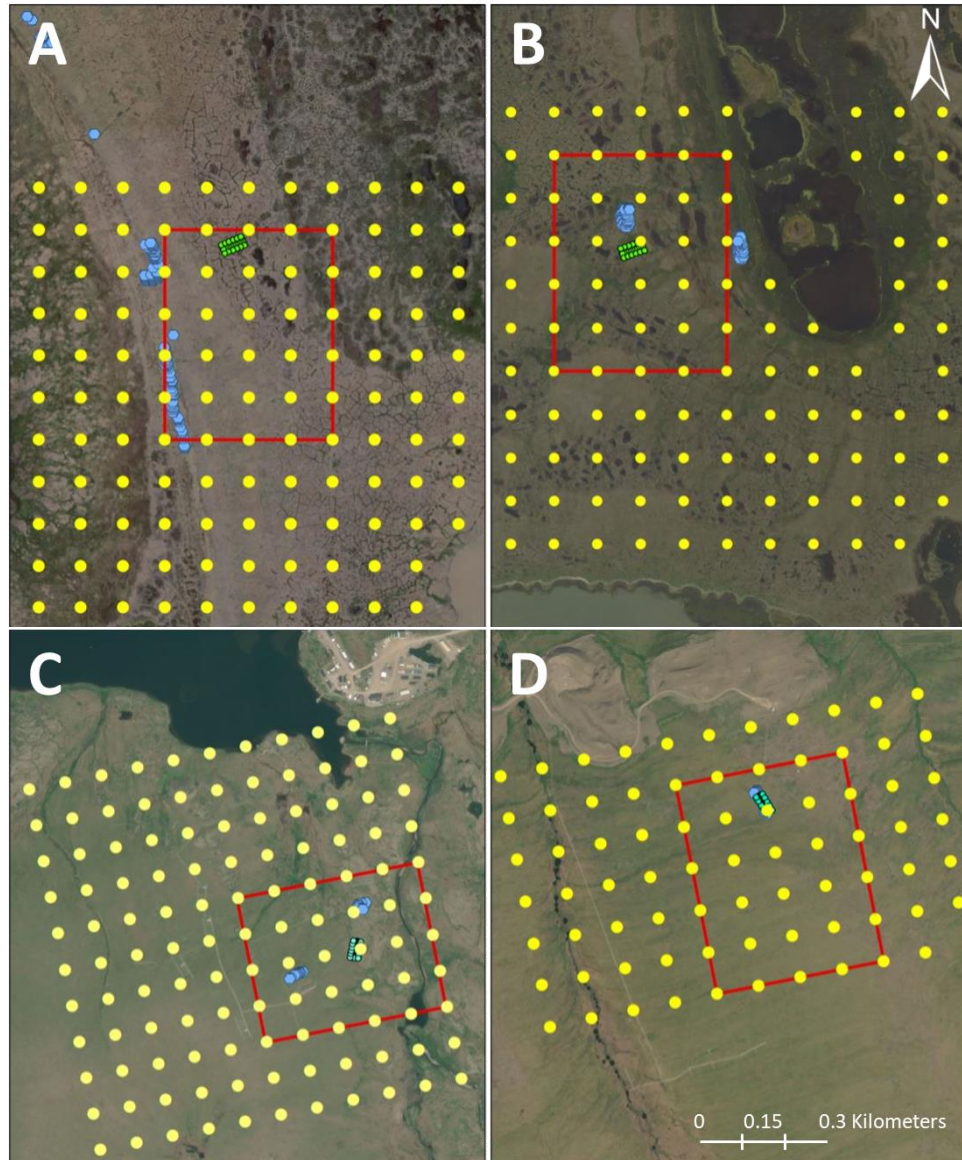


Fig. 4.1. Site maps for (A) Utqiagvik, (B) Atqasuk, (C) Toolik Lake, and (D) Innavait Creek showing the location of the ARCSS grid plots (yellow circles) with 30-plot subsets (red rectangle), ITEX plots (blue circles) for the dry heath and wet meadow/moist acidic sub-sites, and MISP transect (green circles). Figure credit goes to Sergio Vargas with the Systems Ecology Lab (SEL) at the University of Texas at El Paso (UTEP).

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:

TRAIT: each trait (plant height, leaf area, SLA, WBI, NDVI, leaf thickness, LDMC, *A_{max}*)

SPECIES: each species (*C. aquatilis*, *E. angustifolium*, *E. russeolum*, *E. vaginatum*, *L. confusa*, *P. kanei*, *P. frigidus*, *C. tetragona*, *L. palustre*, *V. vitis-idaea*, *B. nana*, and *S. pulchra*)

COVER: Years of sampling (2008/2010, 2014, and 2018) for the average cover of each species at each site

Site: Utqiagvik, Atqasuk, and Toolik Lake

Year: years of plant cover sampling (2008/2010, 2014, and 2018)

GrowthForm: species were classified as graminoids, forbs, deciduous shrubs, or evergreen shrubs

Family: each species was classified according to family

Genus: each species was classified according to genus

One-Way and Repeated Measures ANOVAs

These tests were used to identify (1) which traits are different across regions (**Table 2.4**), (2) which species are changing in cover over time (**Table 3.S2**), and (3) whether community-weighted trait means (CWM) values were changing over time (**Table 3.S4, Fig. 3.4**). All tests used a variation of the ‘aov’ function in R.

(1) `aov(TRAIT ~ Site, data=dataset1)`

dataset1: each species was a separate observation (repeated for each site; $n=34$) with each functional trait as a separate variable

(2) `aov(SPECIES ~ Year, data=dataset2)`

dataset2: observations consisted of cover values for 30 plots at each site and for three years of sampling (2008/2010, 2014, and 2018; $n=270$) with each species as a separate variable

(3) `aov(TRAIT ~ Year, data=dataset3)`

dataset3: observations consisted of calculated community-weighted trait means for 30 plots at each site and for three years of sampling (2008/2010, 2014, and 2018; $n=270$) with each functional trait as a separate variable

Nested ANOVA

This test uses the ‘varcomp’ function within package ‘ape’ (Paradis and Schliep 2019). The function first calculates the mean of each group, then compares the variance around the group mean to the mean of the next level (Messier et al. 2010; Henn et al. 2018) (**Fig. 2.5**). The option “*random=~1/GrowthForm/Family/Genus/Species/Site*” indicates that each level is treated as a random variable and has its own intercept in the

model. The option “*na.action = na.omit*” removes any missing observations from the dataset.

```
varcomp.[TRAIT] <- varcomp(lme(TRAIT)~1,  
  random=~1|GrowthForm/Family/Genus/Species/Site,  
  data=dataset1, na.action = na.omit), 1)
```

Canonical Correspondence Analysis (CCA)

This test uses package ‘vegan’ in R (Oksanen et al. 2019) and uses average cover values for each species for each sampling in relation to the average trait values for each species (**Fig. 3.3**). The following lines of code (1) perform the CCA, (2) test the model and (3) each individual axis for significance, and (4) provides the variance inflation factors for each variable. “*Name.cca*” names the CCA function for the next lines of code.

```
(1) Name.cca <- cca(dataset4 ~ ., dataset1)  
(2) anova.cca(Name.cca, step=1000)  
(3) anova.cca(Name.cca, by="axis", step=1000)  
(4) vif.cca(Name.cca)
```

dataset4: observations consisted of average cover values for each species at each site ($n=34$) with each year of sampling as a separate variable

Pearson and Spearman Correlations

These test whether change in cover over time is correlated with specific traits. This line of code was repeated for each trait at each region and for all regions combined.

```
cor.test(dataset1$TRAIT), dataset4$COVER, method =  
  "pearson/spearman")
```

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