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EXAMINING THE ROLES OF SMALL MAMMAL HERBIVORY AND SOIL NUTRIENT ADDITION IN STRUCTURING ARCTIC PLANT COMMUNITIES USING EXPERIMENTS AND REMOTE SENSING

by

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A thesis/dissertation

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of Towson University

in partial fulfillment

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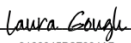

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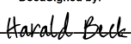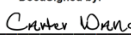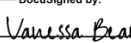
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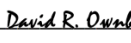# OFFICE OF GRADUATE STUDIES

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ABSTRACT

EXAMINING THE ROLES OF SMALL MAMMAL HERBIVORY AND SOIL

NUTRIENT ADDITION IN STRUCTURING ARCTIC PLANT COMMUNITIES

USING EXPERIMENTS AND REMOTE SENSING

Nicole Williamson

Climate warming affects arctic tundra plant communities in many potential ways, including increasing soil nutrient availability and changing herbivory pressure. This study uses a fertilization experiment in tussock tundra to examine how different levels of nutrients affect plant community greenness, species composition, diversity, and recovery from herbivory. Results indicate that under high levels of fertilization, one deciduous shrub species (*Betula nana*) dominates, reducing species richness and diversity. Simulated herbivory resulted in less growth although greater nutrients aided recovery for plants subjected to herbivory just one time. Community greenness was correlated with *Betula nana* abundance, however, the direction of this relationship was dependent on the time of season. These results suggest that under increased soil nutrient conditions as occurs as a result of climate warming, the interaction between plant competition and herbivory may be important in affecting tundra plant populations.

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Introduction

Arctic ecosystems are critical regions of the Earth for many reasons, including

because they store massive amounts of carbon (C) in their soils (Gorham, 1991; Zimov et

al., 2006b). Northern soils are nutrient-poor (Tuomi et al., 2018), and are characterized

by an upper active layer of soil that is frozen for only part of the year and a lower inactive

layer which remains frozen year-round called permafrost (Zimov et al., 2006a). Organic

matter accumulates in these soils over time as decomposition is limited by low

temperatures and short summer seasons (Zimov et al., 2006a), allowing arctic soils to

store ~268 gigatons of C, approximately 16% of the terrestrial C (Tarnocai & Kimble,

2003). In addition to soil, plants play an important role in the earth's carbon cycle.

Globally, terrestrial plants are a major component of Earth's carbon budget, storing about

550 gigatons of C per year (Riebeek, 2011). Therefore, how plants in different regions,

including the Arctic, respond to climate change is a key component for predicting how

both regional and global carbon cycles may be impacted in the future.

Plant-herbivore interactions

Plant-herbivore interactions are another critical aspect of the C cycle in northern

regions. Small herbivores like tundra voles (*Microtus oeconomus)* or lemmings

(*Dicrostonyx* spp.) can exhibit strong top-down controls on arctic ecosystems by directly

affecting plant communities (Tuomi et al., 2018). The body weight of individual voles

ranges from only 40-120g, but they can have a big effect on plant communities as they

are active year-round and tend to have high metabolisms and low digestive efficiencies,

meaning they must consume several times their body weight in food per day (Ims &

Fuglei, 2005). These rodents also tend to have 3-4 year boom-bust population cycles (Ims

& Fuglei, 2005; Olofsson et al., 2012) which can stochastically, and sometimes dramatically, impact plant communities.

The cyclic nature of rodent populations in northern hemispheres leads to varying levels of herbivory pressure across years. During a population boom, rodents can cause a significant amount of damage to plants through herbivory and other activities. Following a population boom, plant biomass can be as much as 12-24% lower than the previous year, the effects of which can be observable from satellites in space (Olofsson et al., 2012). Rodent populations then return to a much lower level for 3-4 years where they have minimal impact on the plant community. This short-term high-level herbivory pressure followed by several years of sustained low-level herbivory can be considered as a `pulse` event. By contrast a `press` event would occur if there were several years of sustained high rodent populations and high-level herbivory pressure. Short bursts of herbivory pressure could potentially promote more growth following the herbivory event through compensatory growth mechanisms (Belsky, 1986). Prolonged periods of high herbivory rates however may suppress growth over time if the plant is unable to cope with the rate of herbivory. Small mammal herbivores therefore can have significant effects on C stocks in arctic tundra (e.g., Olofsson et al., 2012) through direct and indirect plant-herbivore interactions.

Climate change impacts

This vital C sink is under threat as climate change causes the Arctic to warm at twice the global average rate (Pithan & Mauritsen, 2014). A warming Arctic is projected to have far-reaching consequences on the C cycle in this region as well as globally. Climate change is predicted to cause longer, warmer summers which will increase

permafrost thaw (Zimov et al., 2006a) and the subsequent expansion of the active layer (Pithan & Mauritsen, 2014). A deeper active layer will support greater microbial activity as microbes begin to break down stores of carbon-rich organic material that were previously less accessible to them while frozen. As this organic material is consumed by microbes, it will increase C loss from Arctic soils to the atmosphere as a byproduct of cellular respiration. In addition, this increased decomposition of organic material will mineralize inorganic nutrients and thus increase soil nutrient availability (Schuur et al., 2015, Figure 1). Some studies predict a reversal of the Arctic acting as a C sink to becoming a source (Natali et al., 2011; Schuur et al., 2009). Others predict that warmer temperatures and greater nutrient availability will increase C storage in the Arctic by promoting plant growth (carbon fertilization hypothesis) which will increase C storage both above and below ground (Camill et al., 2001). Therefore, observing how greater soil nutrient availability affects plant communities is an important component of understanding and predicting how C fluxes and stores may change in the future.

Climate change is further predicted to cause approximately half of the present-day vegetated regions in the Arctic to shift to a different physiognomic class by 2050 (Pearson et al., 2013) which will also affect tundra C dynamics. In the last serval decades, average plant canopy heights have been increasing along with plant litter abundance, while the amount of bare ground has been decreasing (Elmendorf et al., 2012). Some plants, especially woody species like trees and shrubs, tend to store more C within their structures compared to non-woody plants and are more resilient to decomposition.

Woody plant species have historically made up a relatively small fraction of plant abundance in several arctic tundra communities. In recent decades, however, woody

shrubs have been increasing across many areas of the Arctic (Kleinhesselink et al., 2014; Myers-Smith et al., 2019). One potential explanation for these patterns is that rising temperatures caused by climate change and subsequent increased soil nutrient availability are promoting woody-shrub growth (Stow et al., 2004; Sturm et al., 2001). Not all plant species, however, respond the same way to these climatic changes. In nutrient addition experiments in moist acidic tundra (MAT) communities, most vascular plant species were found to increase in abundance over the short-term in response to fertilization (Shaver et al., 2001). Over the long-term, however, one or two vascular plant species (one of which is a deciduous shrub, *Betula nana*) grew to dominate over all others (Hobbie et al., 2005, Shaver et al., 2014). These experimental results and observations of shrubs increasing across the Arctic indicate shrubs have a competitive advantage over other plant species in a changing Arctic. Likely, deciduous shrubs are able to outcompete graminoids and other lower lying plants for access to light (Bret-Harte et al., 2001, Bret-Harte et al., 2004, Fetcher, 1985). This suggests that over the long-term, climate change in the Arctic may significantly impact tundra plant communities by altering competitive relationships among plant species, and by shifting to a shrubbier tundra, may alter patterns of C stocks.

Climate change will not only impact arctic plant communities but is also expected to negatively affect small rodent populations that rely on this vegetation for food and shelter (Batzli and Henttonen 1990). Voles and lemmings do not hibernate over the winter, and thus rely on the safety and insulation of the subnivean zone (the area between the top of the snowpack and the surface of the ground) for survival. The subnivean zone allows these small rodents to move around freely to access their food while under a layer of protection against harsh winter weather conditions like frigid temperatures, wind, and

rain (Figure 2). For these reasons they favor areas that accumulate a thicker snow pack in the winter (Fauteux et al., 2015; Reid et al., 2012). As the Arctic continues to warm, winter conditions will become less favorable by becoming warmer and more variable (Ims & Fuglei, 2005). Warming temperatures contribute to increased rainfall which can reduced snowpack depths by melting existing snowpacks and decreasing snow accumulation. Reduced snowpack depth increases small mammal exposure to extreme winter weather conditions which is detrimental to their survival (Aars and Ims, 2002; Pitelka & Batzli, 2007). While small in stature, these rodents play an important role in the tundra ecosystem and can have big impacts on plant communities.

Plant species vary greatly in their susceptibility to herbivory by these small mammals. *Eriophorum vaginatum* (hereafter, *Eriophorum*) is a well-studied tussock forming sedge that accounts for a significant portion of the biomass in moist acidic tundra ecosystems (Shaver et al., 1986). Tundra voles rely on this species for both food and shelter (Batzli & Lesieutre, 1991, Figure 2). Tundra voles have been found to selectively forage for sedges (particularly *Eriophorum*) over woody shrubs (Batzli & Lesieutre, 1991; Christie et al., 2015). *Eriophorum* tolerates herbivory well by increasing leaf production after a defoliation event (e.g., Archer & Tieszen, 1983). However, tolerance to herbivory and recovery after defoliation is reduced when subjected to fertilization (Johnson & Gough, 2013), likely because of a shift in competitive interactions with other plant species. While *Eriophorum* can tolerate both nutrient addition (Heskel et al., 2012) and warmer temperatures (Tissue & Oechel, 1987), this species can be outcompeted by other plants, especially woody shrubs, under those conditions (Heskel et al., 2013; Shaver et al., 2014), potentially due to reduced light availability (Fetcher, 1985). Fertilization

enriches *Eriophorum* leaf nitrogen (N) content, which can lead to increased herbivory rates (Tuomi et al., 2018; Gough et al., 2007, 2008, and 2012; Figure 1). This suggests that climate change may lead to compounding negative effects on *Eriophorum's* photosynthetic capacity and overall success by increasing interspecific plant competition for light availability and herbivory rates.

Monitoring and predicting changes with NDVI

One potential way to monitor changes to arctic plant communities caused by climate change and herbivore activity is by utilizing spectral reflectance data. One common tool for assessing plant health is the normalized difference vegetation index (NDVI). NDVI essentially is a measure of how green plants are, but these values can be used to predict other plant productivity measures such as gross primary production (GPP) (Street et al.,2007, Shaver et al.,2013). NDVI has also been shown to be higher in fertilized treatments compared to unfertilized ones in tundra communities (Arens et al.,2008). On a larger scale, satellite imagery has been used to detect vole population cycles and their subsequent effect on vegetation by monitoring changes to estimated NDVI values (Olofsson et al.,2012). Satellite imagery and NDVI have also been used to observe and quantify trends in Arctic greening and its links to increasing shrub cover in parts of the Arctic (e.g., Mekonnen et al., 2021).

Overview of Thesis

The goal of this study was to investigate the response of a tundra plant community to experimental manipulations to better understand the effects of climate change and repercussions for the C cycle. In the next chapter I describe the impacts of a gradient of nutrient additions on moist acidic tussock tundra plant community composition after 15 years. Paired with this nutrient gradient is a simulated herbivory experiment which explores the impacts of small mammal herbivory on a preferred forage species' (*Eriophorum)* growth. In my second chapter, I explore the use of NDVI for predicting *Betula* abundance in the fertilization experiment and a small mammal density manipulation experiment. Finally, a general conclusion section summarizes both chapters.

Chapter 1:

Effects of Simulated Herbivory and Added Nutrients in Moist Acidic Tussock Tundra

Research questions and hypotheses

Previous nutrient addition studies on MAT have been limited to one very high level of nutrient addition. This study utilized a nutrient addition gradient to determine (1) how do soil nutrients affect arctic tussock tundra plant community composition under a range of nutrient addition. I hypothesized that (a) above a certain threshold, additional soil nutrients alter competitive relationships and shift the plant community towards the dominance of shrubs, and (b) *Eriophorum* abundance is negatively correlated with greater soil nutrients and increased dominance of other plant species. In addition to the plant community at large, I wanted to quantify (2) how do simulated press and pulse herbivory interact with fertilization to affect the growth of a preferred forage species' (*Eriophorum)* tiller height. I hypothesized that (a) *Eriophorum* tiller height will increase with the level of fertilization, (b) simulated pulse herbivory stimulates *Eriophorum* tiller heights while press herbivory reduces *Eriophorum* tiller heights, and (c) after herbivory, *Eriophorum* tillers will grow taller when fertilized compared to unfertilized individuals.

Methods

Study site

A nutrient addition gradient experiment in MAT (06MAT) was established by the Arctic Long-Term Ecological Research project in 2006 at Toolik Field Station located in the northern foothills of the Brooks Range, Alaska, USA (68° 38′ N, 149° 43′ W, Figure 3). Soils in this region are moist and mainly glacial till and outwash from two different glacial advances 10,000 and 60,000 years before the present (Hobbie and Kling, 2014). The region is snow covered for two-thirds of the year, and maximum thaw depth ranges from ~0.25-1.0 m during summers. The growing season in this region is short, typically ranging between 120-126 days starting around mid-May until mid-September (Cherry et al.,2014). Tussock forming sedges (*Eriophorum vaginatum*), deciduous shrubs (*Betula nana*), ericaceous evergreens (*Rhododendron palustre* and *Vaccinium vitis-idaea*), and mosses (*Sphagnum* spp.) dominate the vegetation at this site (Shaver et al.,2014). Most of the previous nutrient addition experiments conducted on MAT have included only one, high level of fertilization (N 10 $g/m^2/yr$, and P 5 $g/m^2/yr$) to test plant response to nutrient addition (e.g., Boelman et al., 2003; Gough et al., 2012; Heskel et al., 2013; Shaver et al., 1998). This amount of fertilization does not realistically reflect the level of nutrient availability that would be expected on the tundra under future warming scenarios. To address this issue, this MAT nutrient addition gradient study was established to monitor the response of the plant community to a range of nutrient addition levels. This newer experiment aims to provide a better understanding of how the plant community will respond to increased soil nutrient availability at levels that more accurately mimic current and future conditions in a warming Arctic.

Nutrient addition

The MAT nutrient addition gradient experiment was designed with four blocks, each containing seven 5x20m plots that were randomly assigned treatments within each block, described in detail in Heskel et al., (2012). For this study only blocks 1-3 and four treatments: CT, F2, F5, and F10 fertilization treatments were used (Figure 4). The plots are fertilized yearly with granular ammonium nitrate and superphosphate after the snow melts in the spring. Control plots (CT) receive no fertilizer, F2 receive 2 gN/m^2 + 1 gP/m^2, F5 receive 5 gN/m^2 + 2.5 gP/m^2, and F10 receive 10 gN/m^2 + 5 gP/m^2 (Prager et al., 2017; Suchocki, 2020). A 5x5m area at the eastern end of each of these plots was dedicated for destructive sampling, while the remaining 5x15m of the plot was left for non-destructive sampling to help preserve the long-term integrity of the plots.

Plant community sampling

Relative abundance was estimated in mid-late July each year beginning in 2008 to species level, when possible, for all plant forms except for mosses and lichen which were lumped within each category. Other categories included litter (all species), bare ground (including frost boils and standing water), and woody-standing dead (mainly deciduous shrub die off). Relative abundance was measured using standardized percent cover. Each fertilization plot has a permanent 8x1m long monitoring area that was established in 2008. Along this area, eight $1m^2$ quadrats are aligned 0.2m in from the edge of the plots, and aerial percent cover is estimated for each species/group every year in mid-late July (only 4 quadrats/plot in 2008, and 5 quadrats/plot in 2015 and 2020). To standardize values to 100% percent cover within quadrats, percent cover of individual species/group were divided by the sum of all percent cover values within a given quadrat. Species were

then consolidated into growth forms (deciduous shrubs, evergreen shrubs, graminoids, and forbs, see Table 1 for species breakdown). *Eriophorum* was left out of the graminoid category and evaluated independently. Average relative cover was calculated by first averaging across the eight quadrats within a given plot, then by averaging across blocks. Diversity was calculated using the Shannon Diversity Index (Equation 1). Species richness and diversity were calculated at a $1m^2$ level from the cover quadrats.

Equation 1: Where H is diversity, *i* is one species, P_i is the proportion of the entire community made up of species *i, S* is the total number of species in the plot.

$$H = -\sum_{i=1}^{S} p_i \ln p_i$$

Simulated herbivory

Within each plot, a simulated herbivory experiment was established in 2018 to examine the effects of photosynthetic biomass removal due to vole herbivory on the tussock forming sedge species *Eriophorum* (Suchocki 2020). Six *Eriophorum* tussocks were randomly selected from each plot (total of 72 individuals) by throwing a pencil over the shoulder and picking the tussock closest to the tip of the pencil that did not have any visible signs of vole activity (no severed leaves, missing rhizomes, winter nests, or hay piles). Four *Eriophorum* tussocks were selected within the destructive portion of the plots, and two individuals were selected from the non-destructive portion. The four *Eriophorum* individuals selected within the destructive portion of the plots were then randomly assigned an herbivory treatment (PU: Pulse or PR: Press) so that there were two *Eriophorum* assigned to each of the herbivory treatments. The two individuals

selected within the non-destructive region of the plots experience no simulated herbivory (NH – no herbivory). This provided 6 replicates for each of the 12 possible combinations of fertilization and simulated herbivory treatments (Figure 4).

Pulse and Press treatments were subjected to a simulated herbivory event in late June of 2018 when all leaves (and any other species of plants growing from the tussock) were cut down to the base of the tussock mound. All severed biomass was subsequently collected, sorted by species, dried, and weighed (data not shown). Press individuals were subjected to additional herbivory events in 2019, 2020, and 2021, while Pulse individuals were allowed to recover.

Starting in 2018, each tussock in the experiment had 6 tillers (10 tillers in 2021) randomly selected by dropping a pencil onto the tussock and identifying a tiller closest to the pencil tip. If a tiller was within 5cm of the outer edge of the tussock, a new tiller was selected. Selected tillers were then fitted with metal tags, given unique IDs and monitored for the duration of the experiment. If a tag fell off a tiller, then a new one was randomly selected. Press tussocks had all tags removed before the leaves are cut, and new tillers were selected once the leaves were long enough to re-tag. Following an herbivory event, the height of the tallest green leaf within a tiller was measured every two weeks for a period of 8 weeks for all herbivory treatments (NH, PU, and PR). In the summer of 2020 however, recovery measurements were only recorded one time after the herbivory event, in late July (when plant growth peaks), due to staffing and travel limitations during the COVID-19 pandemic. Mean tiller heights were calculated by averaging across the 6 tillers on a given tussock, then across the two tussocks of the same simulated herbivory treatment within a given fertilized plot, then averaged across the three blocks.

Statistics

All statistical analyses were performed with R version 4.0.3 (2020), except for Non-metric Multidimensional Scaling (NMDS) which was preformed using PC-ORD (version 7). Statistical significance was cut off at $p < 0.05$. A multivariate analysis of variance (MANOVA) was used to test for significant differences among average living plant growth forms cover between fertilization treatments for the years 2008 and 2021 (years were run independently of each other). NMDS ordination with Bray-Curtis (Sørensen) dissimilarity measure was used to analyze differences in plant growth forms relative abundance between fertilization treatments for the years 2008-2021, as well as 2008 and 2021 run independently. A Multi-response permutation procedure (MRPP) was then used to test for significant difference between two or more groups of sampling units. Linear regressions were used to test the relationships between relative cover of some growth forms among the fertilization treatments. Two-way analysis of variance (ANOVA) with interaction was used to test differences in final tiller heights among simulated herbivory and fertilization treatments (each year tested independently of the others). If the ANOVA showed significant differences among treatments or the interaction, the means were compared using Tukey's honestly significant difference (Tukey's HSD).

Results

Plant community response to nutrient addition

Over the12-year monitoring period (2008-2021) the plant community shifted in response to fertilization, most dramatically in the F10 treatment (Figure 5). In 2008, moss (p = 0.01) and *Eriophorum* (p = 0.03) were found to have significantly different mean relative cover across fertilization treatments (Tables 2 and 3). *Eriophorum* cover was highest in the F10 treatment with an average of 0.25 ± 0.05 (SD), compared to the control with 0.14 ± 0.01. Moss had the opposite trend and was highest in the control plots with 0.12 ± 0.04 and lowest in the F10 with 0.03 ± 0.01 (Table 2).

In 2021, deciduous shrubs (p = <0.001), evergreen shrubs (p = <0.01), and moss (p = <0.01) had significantly different relative cover across the fertilization treatments (Table 3). Mean deciduous shrub cover was much greater in the F10 treatment (0.59 ± 0.03) compared to the control (0.23 ± 0.03) and the other fertilization treatments (0.23-0.32, Table 2). Evergreen shrubs however were much lower in the F10 treatment (0.02 ± 0.0) compared to the control (0.25 ± 0.05) and the other fertilized treatments (0.34-0.27, Table 2). Mean forb cover, driven by one species, *Rubus chamaemorus*, was also much greater in the F10 treatment (0.14 ± 0.09) compared to the control (0.04 ± 0.04); however, this difference was not found to be significant.

Mean species richness was similar across the control and all fertilization treatments in 2008 (Table 4). By 2021 however, richness had declined in the F5 and F10 treatments while the control remained unchanged. This effect was most pronounced within the F10 treatment which declined from a mean of 12 ($\pm$ 2) to 5 ($\pm$ 1) species. Within the F10 treatment plots, there were two deciduous shrub species (*Arctostaphylos*

alpina and *Vaccinium uliginosum*), one evergreen shrub (*Cassiope tetragona*), and one forb (*Pedicularis* sp.) that went extinct by 2021. Diversity showed a similar trend from 2008 to 2021. This reduction was again most pronounced in the F10 treatment (Table 4).

All fertilization treatments were found to have negative correlations between deciduous shrub and *Eriophorum* relative cover (Figure 6), however they were only found to be significant in the F5 ($p = <0.001$) and F10 ($p = <0.001$) fertilization treatments (Table 5). Notably, the range of deciduous shrub cover increased with the level of fertilization (0.15 - 0.75 in the F10 treatment compared to 0.14 - 0.34 in the CT). By highlighting cover values from 2008 and 2021 in the graphs, the increase in shrub cover over time in the fertilized treatments (particularly in the F5 and F10 treatments) can be seen to be driving this trend. This is not observed in the CT plots, as values from 2008 and 2021 seem to be clustered together.

Results from the NMDS Sorenson (Bray-Curtis) distance summaries indicate that there are differences in growth form cover between fertilization treatments for all years ($p = 0.02$) and for just 2021 ($p = 0.02$, Figure 7). When comparing across all years, deciduous shrubs, forbs, and standing dead are strongly correlated with axis 1, were all greater in F10 treatments relative to controls in both 2008 and 2021, and were greater overall in fertilized plots in 2021 compared to 2008 (Table 2). In 2021, deciduous shrubs, *Eriophorum*, evergreen, and graminoids were all strongly correlated with axis 2. Deciduous shrub cover is greatest in the F10 and F5 treatments. Evergreen shrubs and *Eriophorum* were greatest in the CT and F2 treatments (also see Figure 5).

Eriophorum recovery from herbivory

Measured average tiller heights fluctuated within the growing seasons as a result of new leaves being selected if tags fell off or the tip of a leaf starting to senesce. In general however, tillers increase in height throughout the growing season among all simulated herbivory treatments (Figure 8). In 2018, a marginally significant interaction effect was found between herbivory and fertilization treatments (p = 0.06, Table 6, Figure 9). This occurred because the NH tillers grew longer with greater nutrients whereas the PR tillers were of similar heights regardless of fertilization treatment. Tiller heights were found to be significantly different among the simulated herbivory treatments as well (p < 0.001). PR and PU were significantly shorter than the NH (p < 0.001 for both treatments) but were not significantly different from each other (p = 0.26, Table 7). Tiller heights were also significantly affected by fertilization (p < 0.01, Table 6). F10 and F5 fertilization treatments had significantly taller final tiller heights compared to the control (p = 0.01), but were not significantly different from each other or the F2 treatment (Table 6).

In both 2019 and 2020, no interaction effect was found between simulated herbivory and fertilization (Table 6). Both years did have significant differences in final tiller heights among herbivory treatments (p < 0.001, Table 6). In both years PR and PU treatments were significantly shorter compared to the NH (p < 0.001, Table 7). Unlike in 2018, PU and PR were significantly different from each other (p = 0.02 and p <0.001 for 2019 and 2020 respectively) with average final tiller heights being lower in the PR treatment when compared to PU. No significant differences among fertilization treatments were found in either year.

In 2021, a significant interaction effect was found between simulated herbivory and fertilization (p = 0.01, Figure 9). This was caused by differences in tiller height with fertilization occurring in the PU treatment but not the NH or PR treatments. In the PU herbivory treatment, *Eriophorum* in the F10 fertilization plot produced significantly taller tillers compared to CT and F2, but none were significantly different from F5. PR herbivory *Eriophorum* produced significantly shorter tillers compared to all other simulated herbivory-fertilization treatments. Tiller heights were also found to be significantly different among the main effect of simulated herbivory treatments overall in 2021 (p < 0.001, Table 6). PR and PU were significantly shorter than the NH (p < 0.001 for both treatments) but were not significantly different from each other (p = 0.59, Table 7). Tiller heights were also found to be significantly different among the main effect of fertilization (p = 0.04, Table 6). *Eriophorum* in F10 fertilization plots produced significantly taller tillers compared to the CT (p = 0.04), but not when compared to any other fertilization treatment (Table 7).

Discussion

Plant community composition shifts towards the dominance of shrubs in response to fertilization

The MAT plant community significantly changed in response to fertilization over the course of a 13-year period. The amount of change, however, was dependent on the level of fertilization. I hypothesized that above a certain threshold, additional soil nutrients would alter competitive relationships and shift the plant community towards the dominance of shrubs. This hypothesis was supported by the results and agrees with

similar studies of the F10 level of nutrient addition (Hobbie et al., 2005, Mack et al., 2004, and Shaver et al., 2001). By 2021, relative cover of deciduous shrubs was significantly different across fertilization treatments and was greatest in the F5 and F10 treatments while deciduous shrub cover was not different between the CT and F2 treatments. This suggests that the threshold for significant plant community shifts towards the dominance of shrubs is determined by a combination of the amount of fertilization received. After 13 years, the fertilization threshold for shifting the plant community towards the dominance of shrubs must lie somewhere between F2 ($2gN/m^2$ + $1.5gP/m^2$) and F5 ($5gN/m^2$ + $2.5gP/m^2$).

In response to fertilization, the only other growth forms to increase in relative cover were forbs and standing dead (dominated primarily by deciduous shrubs), though this change was not statistically significant for forbs. Deciduous shrubs are woody (contain lignin) and have a high C:N ratio and therefore will take longer to breakdown compared to other growth forms. Thus, increased standing dead in the F5 and F10 plots is most likely due to increased deciduous shrub cover and subsequent die off from winter frost exposure or disease. Most of the other growth forms (evergreen shrubs, *Eriophorum*, lichen, moss, and bare ground) were found to significantly decrease in response to fertilization. This is likely due to increased understory shading from deciduous shrubs. Moss and lichen are also sensitive to osmotic stress caused by direct contact with fertilizers which could further contribute to their decline in fertilized treatments. The decline of most growth forms under high levels of fertilization explains why species richness and diversity decline in moist acidic tundra over time under nutrient addition.

Other nutrient addition studies have found that short term (2-3 years) fertilization initially increases graminoid (including *Eriophorum*) and most other vascular species abundance before deciduous shrubs began to dominate over the long-term (Shaver et al., 2001). This initial increase in abundance was seen in 2008 where *Eriophorum* had significantly greater cover in the F10 treatment compared to the control. The initial positive response of vascular plants to fertilization suggests that the limiting factor for these species was nutrient availability. Once that limitation is alleviated through nutrient addition, the plants respond positively until a new limitation (light) occurs and begins to cause declines.

Though only significant in the F5 and F10 treatment, *Eriophorum* abundance was negatively associated with deciduous shrub cover, and this relationship became stronger as the level of fertilization increased. These results support my hypothesis that *Eriophorum* productivity is negatively correlated with greater soil nutrients and increased dominance of other plant species. Deciduous shrubs, including *Betula nana,* can quickly accumulate a significant height advantage over many other MAT species after just a few growing seasons due to rapid branching and sturdy wooden structures (Bret-Harte et al., 2001). This means that as deciduous shrubs increase in fertilized plots, most other species will decline due to light limitations created by shrubs. Studies where light intensity was artificially manipulated using shade cloths have shown that *Eriophorum* growth was reduced when shaded (Chapin and Shaver 1985). This is further supported by species removal studies that have found that graminoid productivity increases more under fertilization when neighboring species were removed (Bret-Harte et al., 2004).

Eriophorum leaves do not consistently grow taller with more fertilization

The effect of fertilization on tiller heights was mixed. *Eriophorum*'s response to fertilization varied interannually in both direction and magnitude. When the main effect of fertilization was significant (2018 and 2021), average tiller heights tended to be greater among the highest fertilization levels (F5 and F10). These results are consistent with similar studies that reported greater tiller heights under fertilization (Johnson and Gough 2013, Shaver and Laundre et al., 1997, Shaver et al., 1986). However, in 2019 and 2020, no significant effect of fertilization was found which contradicts these findings. One potential reason for not seeing consistently strong responses in tiller heights to fertilization is that *Eriophorum* was increasing it production in other ways. Some studies have shown that in response to fertilization, *Eriophorum* will increase the number of tillers (Shaver and Laundre 1997) and overall biomass. While tiller heights typically also increased in these cases, *Eriophorum' s* overall productivity might be greater in fertilized plots compared to unfertilized plots, but we may have missed this signal by only measuring tiller heights.

Given the presence of interannual variation however, another explanation is that natural environmental variables such as climate, herbivory, and/or interspecific plant competition may be interacting with fertilization to cause the suppressed or negative response to fertilization we observed. *Eriophorum* has reduced growth when exposed to higher air temperatures, but increased growth when exposed to elevated temperatures and fertilization (Chapin and Shaver 1985). Interannual variation in air temperature therefore would likely not explain the trends we found. As discussed in the previous section, woody shrubs often grow to dominate over other species in fertilized plots and can lead

to understory shading that limits *Eriophorum* growth. In addition to increased competition for light, natural vole herbivory of *Eriophorum* also increases with fertilization (Gough et al., 2012). Preliminary snap trap and mark recapture estimates suggest that vole populations in this area were low in 2017 and 2018 and were higher in 2019-2021 (Steketee, J., personal communication). This suggests that natural vole activity could potentially have muddled our results. The combined negative impacts on *Eriophorum* growth from competition and increased vole activity could lead to suppressed growth responses in fertilized plots.

Eriophorum leaves do not grow taller after herbivory

Pulse *Eriophorum* tillers did not grow taller compared to NH, nor were they able to recover to the same height as the NH within the same season. These results do not support the hypothesis that PU herbivory will stimulate tillers to grow taller. PU tillers did not recover to the same heights as the NH treatment until the 4th growing season and only in the F5 and F10 treatments. Similar studies have also observed this reduced production of *Eriophorum* in years following herbivory treatments (Grogan & Zamin 2018, Johnson & Gough 2013). PR *Eriophorum* were consistently shorter compared to both the PU and NH every year after 2018. While it appears that *Eriophorum* subjected to herbivory did not quickly recover to heights similar to NHs, other metrics could be looked at in the future to better access overall impacts of herbivory on productivity. For example, changes to the number of leaves per tiller group or the density of tillers per tussock could compensate for the reduction in average height. *Eriophorum* has been found to increase the number of tillers it produces in response to simulated herbivory, but this generally came at the cost of reduced tiller height (Shaver et al., 1986).

Fertilization does not always interact with herbivory to affect tiller height

Following herbivory, fertilization was predicted to produce greater tiller heights. This trend was not consistently observed in every year. Apart from a marginally significant interaction effect detected in 2018, no significant interaction between fertilization and herbivory occurred until 2021. Even then, only among the PU herbivory treatment were there any significant differences in tiller heights across fertilization treatments. As expected, the F10 fertilization treatment produced the tallest tillers, but these were not significantly taller than tillers in the F5 or F2 treatments. The lack of a consistent strong interaction between fertilization and herbivory again suggests that other environmental factors may be influencing tiller heights. Additionally, this result suggests that other measures of productivity and compensatory growth should be incorporated in the future for a more robust evaluation of the impact of these manipulations on *Eriophorum.*

Chapter 2:

Exploring the Use of NDVI for Detecting Differences Among Experimental Treatments and Predicting *Betula nana* Abundance in Moist Acidic Tussock Tundra

Research questions and hypotheses

Based on previous work that has been successful at utilizing NDVI to monitor changes to plant communities, I wanted to test if NDVI could be used as a tool for predicting plant species abundance and detecting experimental treatment differences. As previous work has already established links between NDVI and shrub cover (Mekonnen et al., 2021), I specifically asked (1) can NDVI be used to predict *Betula* (a deciduous shrub) cover, and if so (2) when in the growing season is the strongest correlation between NDVI and *Betula* abundance. From these two questions I hypothesized that (a) there will be a significant positive relationship between *Betula* cover and NDVI at peak season, and (b) the relationship between NDVI and *Betula* cover will be stronger in the start of the season than during the peak season. I also wanted to know if (3) NDVI can be used to detect plant community responses to experimental treatments. I hypothesized that (a) NDVI will be greater in fertilized plots compared to unfertilized ones, and (b) NDVI will decrease as herbivory pressure increases. I expected changes in community composition to drive changes to NDVI values among treatments, therefore, I also compared mean relative plant cover for each experiment to determine if any community level changes had occurred.

Methods

Study sites

See Chapter 1: *Study sites* for a description of the LTER 06MAT nutrient addition gradient experiment site. In 2018, an experimental small-mammal herbivore manipulation was established on moist acidic tussock tundra near Toolik Field Station. The experiment is a part of a larger project, known as Team Vole, with sites in other regions of Alaska (Utqiagvik and Nome) characterized, respectively, by the dominant tundra types wet graminoid tundra and MAT. At each of these three tundra ecosystems, three replicate sites were selected. The moist acidic tussock tundra sites at Toolik are known as Pipeline (PL), South Toolik (ST), and Imnavait (IM, Figure 1, Table 8). At each of these sites, two 20 x 20m enclosures were erected, along with one 8 x 8m exclosure (EX), and an 8 x 8m control plot (CT; Figure 11). Control plots are used to assess ambient/natural herbivory effects, while exclosures are used to assess the effects of no herbivory. One of the enclosure fences (pulse: PU) was stocked with a high density of tundra voles (*Microtus oeconomus,* 3 females, 1 male) for just one year (2019) to simulate a short-term high herbivory pressure event. The other enclosure fence (Press: PR) was stocked with the same high density of tundra voles each year (2018-2021) to simulate consistently high herbivory pressure.

Plant community sampling

      Relative abundance was estimated in mid-late July each year (2008-2021 for the LTER site, and 2018, 2019, and 2021 for Team Vole) to species level, when possible, for all plant forms except for mosses and lichen which were lumped within each category. Other categories included litter (all species), bare ground (including frost boils, and standing water), and woody-standing dead (mainly deciduous shrub die off). Relative abundance was measured using standardized percent cover. At both the 06MAT and Team vole sites, each treatment (nutrient addition plots or herbivory fences) has a 8x1m long monitoring area. Along this area, eight $1m^2$ quadrats are aligned 0.2m in from the edge of the plots, and aerial percent cover is estimated for each species/group every year. To standardize values to 100% percent cover within quadrats, percent cover of individual species/group were divided by the sum of all percent cover values within a given quadrat. Species were then consolidated into growth forms (deciduous shrubs, evergreen shrubs, graminoid, *Eriophorum*, and forbs) (see Chapter 1 Methods).

Spectral reflectance

      Spectral reflectance at the LTER site was measured using a Unispec-DC (PP Systems). In each of the fertilization plots, there is an established 10m long monitoring area along the same side of the plot that plant cover is estimated in, however the locations of the scans do not overlap with the cover quadrats. Along this area, eight to ten spectra scans were taken, starting about 0.5m in from the edge of the plot. These measurements are done multiple times throughout the growing season beginning in June after the snow has melted, until mid-late August when the plants have senesced (ideally one to two times per week) for the years 2011, and 2014-2018.

At the Team Vole sites, spectral reflectance is measured just once during peak season (typically mid-July, for the summer of 2018-2021) using a RapidSCAN CS-45 (Holland Scientific). Within each plot, scans are taken directly above the 1m^2 quadrats where plant cover is estimated. The RapidSCAN footprint is about 0.8m x 0.1m, so eight scans are taken per 1m cover quadrat to roughly cover the full 1m area.

Equation 2: Formula for calculating normalized difference vegetative index NDVI. Where NIR is near-infrared light, and Red is red light.

$$NDVI = \frac{NIR - Red}{NIR + Red}$$

Greenness was calculated using the normalized difference vegetative index (NDVI) following similar methods as described in detail in Boelman et al., (2003, Equation 2). Red wavelengths ranged from 620-670 nm, and near-infrared (NIR) ranged from 841-876 nm. For the LTER site, the available dataset with NDVI values already calculated averaged NDVI across the ten scans per fertilization treatment plot, then across the three blocks (n = 3). The available dataset for Team Vole, however, contained NDVI values for each scan. Average NDVI values were then calculated by averaging first across the eight scans per 1m^2 quadrat, then across the eight quadrats per treatment.

NDVI and Betula regressions

To determine if NDVI can be used to predict *Betula* cover, regressions between NDVI and *Betula* cover were performed for the LTER and Team Vole sites separately. For the LTER site, four season time points were determined (initial, half, peak, and post-peak). The initial time point was the first measurement collected in a given season. This

typically occurred in early to mid-June, depending on when the snow fully melted off the plots. Peak green was defined as the date with the highest recorded NDVI value (typically mid to late July). Half is defined as the date that fell halfway between the initial and peak. And post-peak was defined as ~15 days after peak green occurred. If measurements ended prior to 15-days post-peak, then the final measurement of the season was used instead. Separate regressions were then run for each of these seasonal time periods to assess the relationship between average NDVI values (n = 3) and *Betula* cover across all years (2011, 2014-2018) and fertilization treatments (CT, F2, F5, F10). For the Team Vole sites, similar regressions were run across all herbivory treatments (CT, EX, PU, and PR) for each site separately, and only at peak season as it was the only available seasonal time point.

Results

LTER 06MAT

See Chapter 1 results for a summary of the LTER 06MAT plant community response to nutrient addition. Average NDVI across all fertilization treatments began low at the start of each growing season and then steadily increased until reaching peak NDVI values for a couple weeks after which values began to fall again (Figure 12). The first values each season differ across years mostly because of differences in when sampling began. There are other differences across years in terms of how the treatments responded relative to each other, the timing of greenup, and the timing of senescence (Figure 12).

Notably, in most years (except for 2011), NDVI values were lowest in the F10 treatment at the start of the season compared to all other treatments. Despite this, the F10

treatment, as well as the other fertilized treatments (F2 and F5), typically (except for 2015) had higher NDVI values by peak season compared to CT reflecting greater photosynthetic capacity of the vegetation. In almost all years, the F10 treatment had the highest NDVI values of the four fertilization treatments at peak season.

Regressions between *Betula* relative abundance and NDVI were evaluated separately for the four time points during the year. This relationship was significantly negative during the initial measurements (Figure 13, Table 9). This is likely driven by greater wood biomass from the increased *Betula* cover in these plots (Figure 5). Wood has a lower NDVI value than dead leaves and thus affects the overall NDVI values. At the other three time points in the season, there was no relationship between *Betula* cover and NDVI (Figure 13, Table 9). From 2011 to 2018 relative *Betula* abundance continued to increase in the F10 plots (Figure 5), but this shift was not reflected in the peak season NDVI values which were similar across those years.

Team Vole

No clear trends in herbivory treatment effects on plant community composition were detected. When comparing the relative cover averaged across sites (Figure 14), deciduous shrub cover appears higher in the enclosures compared to the other treatments. This trend, however, is likely not due to differences in herbivory pressure as the difference was apparent in 2018, the first year of the experiment, and deciduous shrubs in the tundra generally respond to changes in growing conditions at a slower rate. More likely, this trend was caused by naturally occurring variation in the tundra that was present when the treatments were first established. Furthermore, each of the three Team Vole sites (IM, PL, and ST) were intended to be replicates of each other, but when these

sites are compared (Figure 15), there is considerable variation among the three sites and among treatments in 2018.

There do not appear to be any consistent differences in NDVI among herbivory treatments when averaged across sites (Figure 16) or when sites are evaluated individually (Figure 17). Similarly to cover, there was substantial variation within and across treatments and sites. Looking just at 2021, year four of the experiment, there is a suggestion that the EX plots have slightly lower NDVI than the other three treatments (Fig. 16), but there was a great deal of variation, and when the sites are examined separately the role of ST in driving this pattern is clear.

At both IM and ST, significant positive regressions (p = <0.001) between *Betula* and NDVI at peak season were found (Figure 18, Table 10). These trends do not appear to be consistently driven by the same treatment effects. At IM the PR treatment values appear to drive this relationship, but at ST the EX and PU seem to be the main drivers. As described earlier, some of these treatment differences appear to have been present at the start of the experiment and may not be related to vole abundance or activity.

Discussion

NDVI is lowest in F10 treatments early in the growing season

At the initial time point of the growing season, a significant (p = 0.001) negative relationship between *Betula* and NDVI was found (Figure 13). Later in the growing season there were differences in NDVI among the fertilization treatments that were not correlated with *Betula* abundance. *Betula* cover in F2 and F5 treatments was not significantly different from the control (Figure 5, Table 2) and yet peak season NDVI

values were consistently higher than the control (except in 2015). Furthermore, while the F10 treatment has significantly higher *Betula* cover compared to all other treatments, the peak season NDVI values do not appear to be significantly different from the F2 and F5 treatment in most years (Figure 12). Similar nutrient addition studies have also found higher NDVI values in fertilized plots compared to unfertilized plots at peak season (Boelman et al., 2003, Boelman et al., 2005). Future work should therefore be focused on parsing out how much of the increase in NDVI is due to *Betula* abundance, compared with increases in productivity/greenness across all/other species.

NDVI was typically lowest in the F10 treatment early in the growing season (Figure 12). This trend is likely driven by the significantly higher deciduous shrub cover in F10 plots (Figure 5, and Table 2). Early in the growing season, deciduous shrubs have not produced leaves yet, and thus the plots are mostly dominated by tall woody branches. Between the woody branches themselves and the shadows they likely create, NDVI values would be driven down. This is further supported by the negative relationship between *Betula* and NDVI found only at the initial measurement of the growing season. These results suggest that NDVI values early in the growing season might be used to estimate woody shrub cover and could help with remote sensing efforts to understand the increase in shrub abundance occurring throughout the Arctic, but this requires additional study.

Herbivory treatment effects are not detectable after four years

No differences in community composition were detected among the herbivory treatments after four years. Despite the PU and PR treatments being stocked at high vole densities, four years was not enough time to see significant changes to the plant community using these metrics. In a long-term (22 years) herbivore exclusion experiment also conducted in the vicinity of Toolik Field Station, few significant effects on vegetation were found on the plant community other than increased moss and decreased shrub cover (Roy et al., 2020).

However, in a similar enclosure experiment with brown lemmings in coastal tundra, a reduction in NDVI in enclosures was detected within the same season lemmings were added (Plein et al., 2021). Their stocking density, however, was much higher (though for a short period of time, 1 vole / 25m^2 for 16hrs) compared to our stocking densities (1 vole / 100m^2). These results suggest that more time may be needed to see significant treatment effects.

NDVI alone is not a good predictor of Betula abundance

While several significant relationships between NDVI and *Betula* were found, these relationships are not consistent or strong enough on their own to predict *Betula* abundance. In the early season, a negative relationship between NDVI and *Betula* was observed in the 06MAT plots. By peak season, this relationship was no longer significant. At the Team Vole sites, however, two out of three sites had a significant positive relationship between *Betula* and NDVI at peak season. The inconsistency of these results suggests that NDVI alone may not be a good predictor of *Betula* abundance and that other variables may need to be accounted for to make these relationships stronger.

Another possibility is that there are confounding factors that are related to both NDVI and *Betula* cover that are making it seem as though there is a direct relationship between the two. For example, NDVI has been shown to be strongly correlated with above ground biomass (Boelman et al., 2003), and biomass and deciduous shrub abundance have both been found to increase under fertilization (Gough et al., 2012).

Future directions

Based on the results of this exploratory analysis, more work will be done on this topic in the future. NDVI data will be collected multiple times throughout the growing season in the Team Vole plots so that the patterns and timing of green up, and relationships between shrub cover and NDVI can be explored and compared to LTER sites. More recent years NDVI data will be processed for the LTER site, and more data (ex; biomass) may be used to look for relationships with NDVI. With these additional steps I hope to find and establish stronger trends amongst NDVI and changes to the plant community.

Conclusions

Nutrient addition can stimulate significant changes to moist acidic tussock tundra plant communities. The deciduous shrub, *Betula nana*, dominates in some fertilized treatments and leads to an overall loss of diversity. It is well established that the more diverse an ecosystem is, the more resilient it is to change (Peterson et al., 1998). Increased deciduous shrub abundance under fertilization leads to decreased diversity. This could negatively affect the overall resilience of MAT long-term. For example, the increase in standing dead (dominated mainly by dead *Betula*) in the F10 treatments

suggests that *Betula* is dying in significant quantities in these plots. Short term, a height advantage is beneficial to *Betula* as it can outcompete its neighbors for access to light. In the winter, however, it is beneficial to be shorter so that plants are protected and insulated by the snowpack. If *Betula* loses this protection and is exposed to harsh winter weather, it could die due to frost damage. This could then promote further loss of diversity and resilience.

Betula cover was only significantly greater in the highest nutrient addition plots which have far higher soil nutrient concentration than would naturally occur, even under climate change conditions. What is not taken up by plants or lost to run off is also left to accumulate in the soil over time, potentially creating even higher concentrations then what was originally intended to be applied. The more nutrients that are applied, the faster and more dramatic the shift in the plant community appears to be. These results suggest that while no significant changes have been observed in the F2 treatment to date, this may change over a longer time scale. While high-level nutrient addition is a useful tool for artificially 'speeding up' long term trends, these results should be accompanied by longer-term low-level nutrient addition studies for comparison. It is clear, however, that as the Arctic continues to warm, and soil nutrient concentrations subsequently rise, the plant community will become woodier in many locations. Depending on the scale and magnitude of these plant community composition shifts, they could potentially impact C cycling and budgets in the Arctic. Understanding how these changes may impact the C cycle in the Arctic is critical so that we can better predict how the Arctic will contribute to global C cycling and global warming.

A warming Arctic could have a net positive or net negative effect on tundra vole populations. Voles rely on a thick snowpack to remain insulated from harsh winter weather conditions. Greater woody shrub abundance could therefore benefit voles in the winter, as the taller canopy provided by the shrubs can trap snow and create a thicker snowpack. Voles may also initially experience a dietary benefit as increased soil nutrient availability contributes to greater forage quality. At the same time, however, as deciduous shrubs increase in abundance, voles' preferred forage species (*Eriophorum)* decreases. The results of this study demonstrate that *Eriophorum* productivity is not stimulated by herbivory and does not rapidly recover from herbivory events. Therefore, if greater forage quality promotes increased herbivory rates, it could further accelerate the decline of *Eriophorum*, and thus negatively affect vole populations over the long term. Compensatory growth has been documented amongst other graminoids and ecosystems however where the saliva of herbivores was found to significantly increase tiller number, and biomass, but did not affect tiller height (Liu et al., 2012). Future work on *Eriophorum* may benefit from incorporating herbivore saliva into simulated herbivory studies to investigate if there are any chemical or enzymatic feedbacks on productivity. The role and degree of impact that small mammals will have on arctic plant communities and the C cycle is complex but has the potential to be significant and should not be ignored.

While consistent, strong correlations between *Betula* and NDVI are lacking, NDVI was useful for picking up on fertilization treatment differences that seem beyond just a change in plant species composition. This study was exploratory, and more work needs to be done with NDVI on MAT communities to better understand seasonal trends in NDVI

in relation to species abundance and treatment responses. With the development of stronger relationships between NDVI and plant productivity or species abundance, remote sensing and NDVI could be a useful tool for monitoring the impact of climate change and small mammals on tundra plant communities.

In conclusion, as climate warming continues in the Arctic, many changes will occur in the plant and animal communities and will affect plant-herbivore interactions. The results here suggest that MAT plant communities will become shrub dominated and less diverse over time and that herbivory may contribute to these shifts. These changes are complex, require additional study, and could significantly alter tundra carbon cycling in the future.

Figure 1: Model of climate change driven nutrient addition impacts on interspecific competition and vole herbivory of Eriophorum. Red arrows indicate positive feedbacks, blue indicate negative feedbacks, and gray indicates that the effect can be positive or negative.
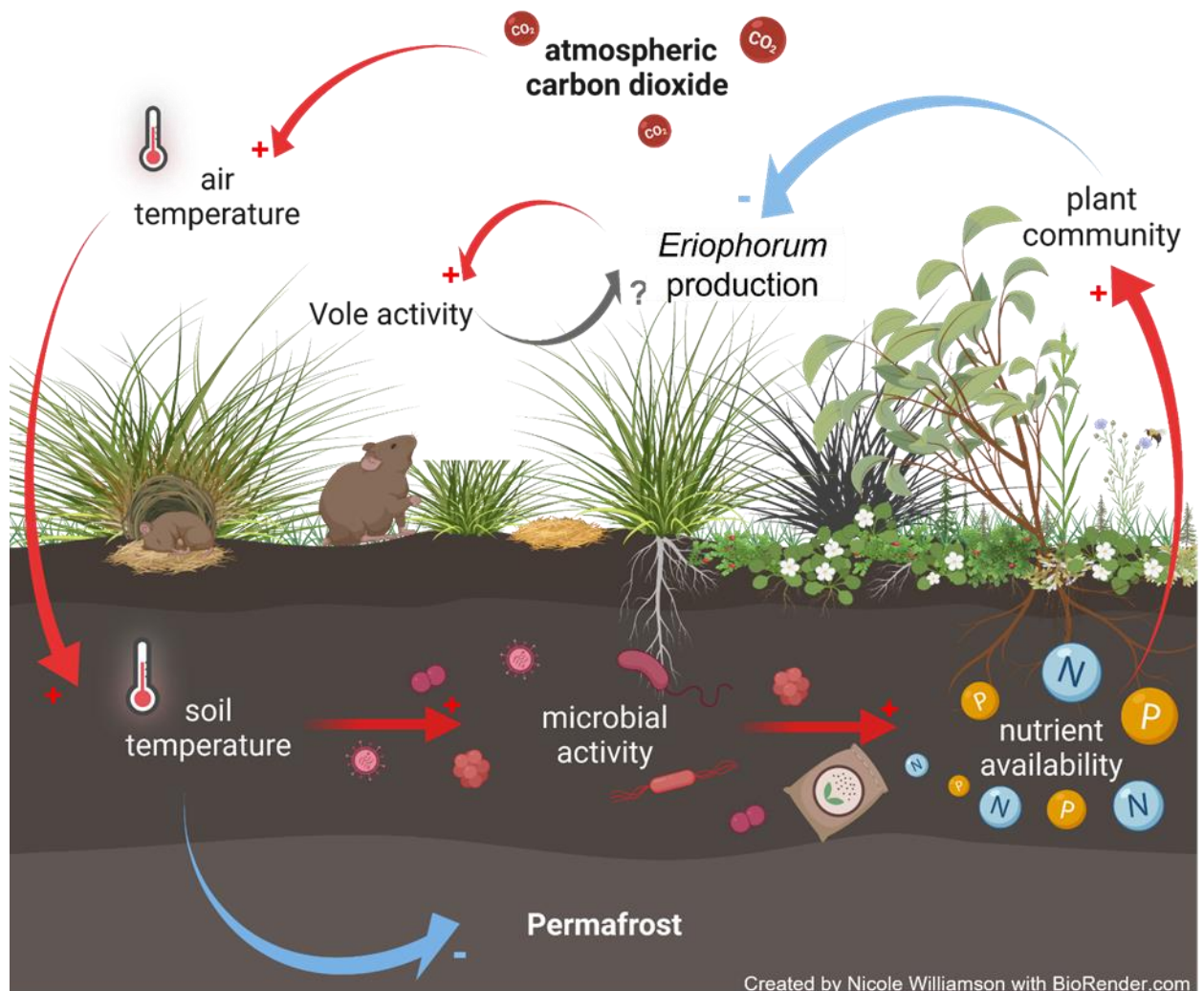
Figure 2: Tundra voles rely on Eriophorum for both food and shelter. 1) Voles consume the rhizomes of Eriophorum which severs and kills the leaves 2) voles burrow into the Eriophorum tussock mounds for shelter 3) voles eat the leaves off the top of Eriophorum tussocks 4) in the winter voles shelter within the subnivean zone and use chopped up Eriophorum leaves as bedding. They create tunnels through the snow to access food stores.
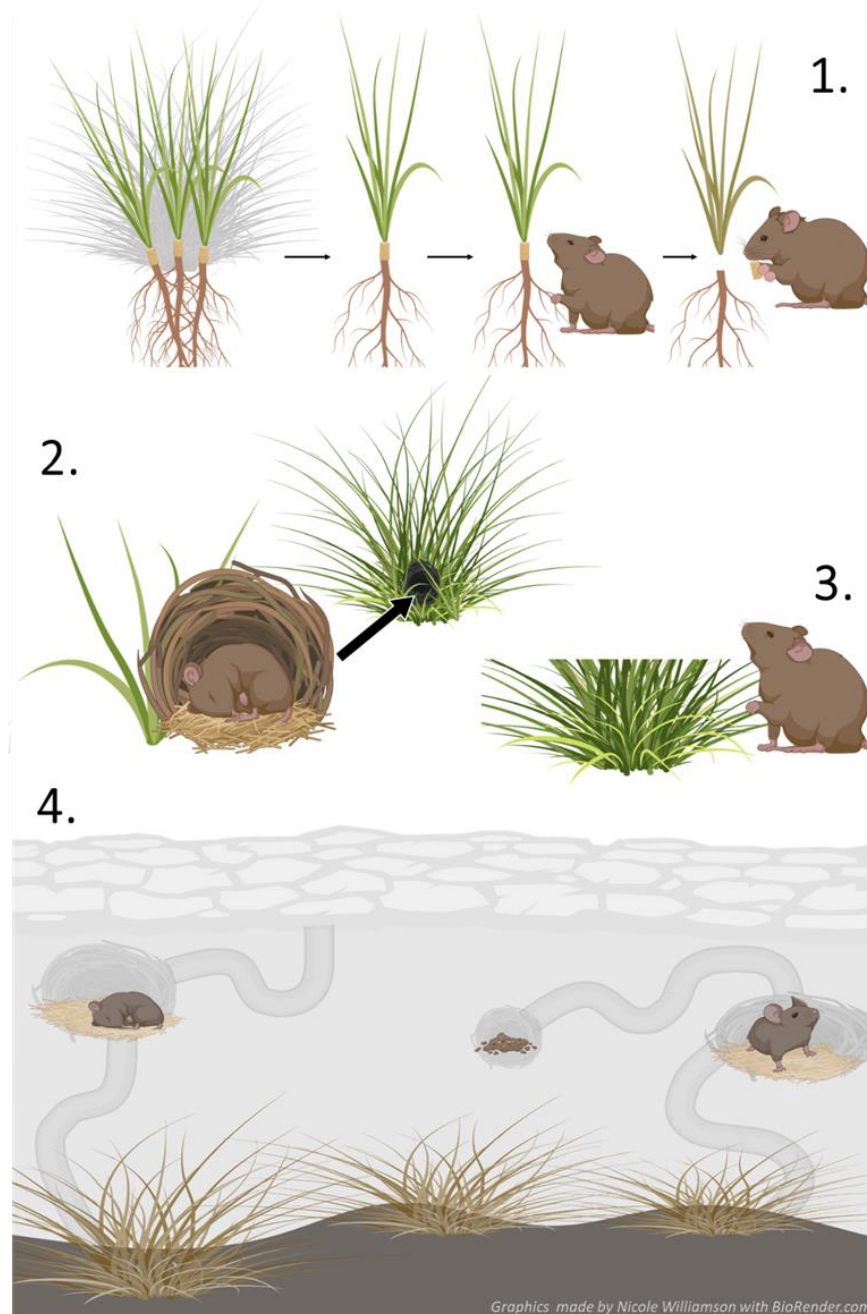
Figure 3: Study site location (Left) map of Alaska (Right) zoomed in view of Toolik Field Station location, and the moist acidic tussock tundra fertilization gradient experiment (06MAT, blocks 1-3).

Made by Nicole Williamson using Leaflet | © OpenStreetMap contributors, CC-BY-SA

Figure 4: Nutrient addition gradient study (06MAT) with simulated herbivory experimental design. Three blocks, each containing four 5x20m fertilization plots (CT, F2, F5, and F10). Each fertilization plot has two no-herbivory (NH), two pulse (PU), and two press (PR) individuals within them. This provides 6 replicates for each of the 12 possible combinations of fertilization and simulated herbivory (72 individuals total).
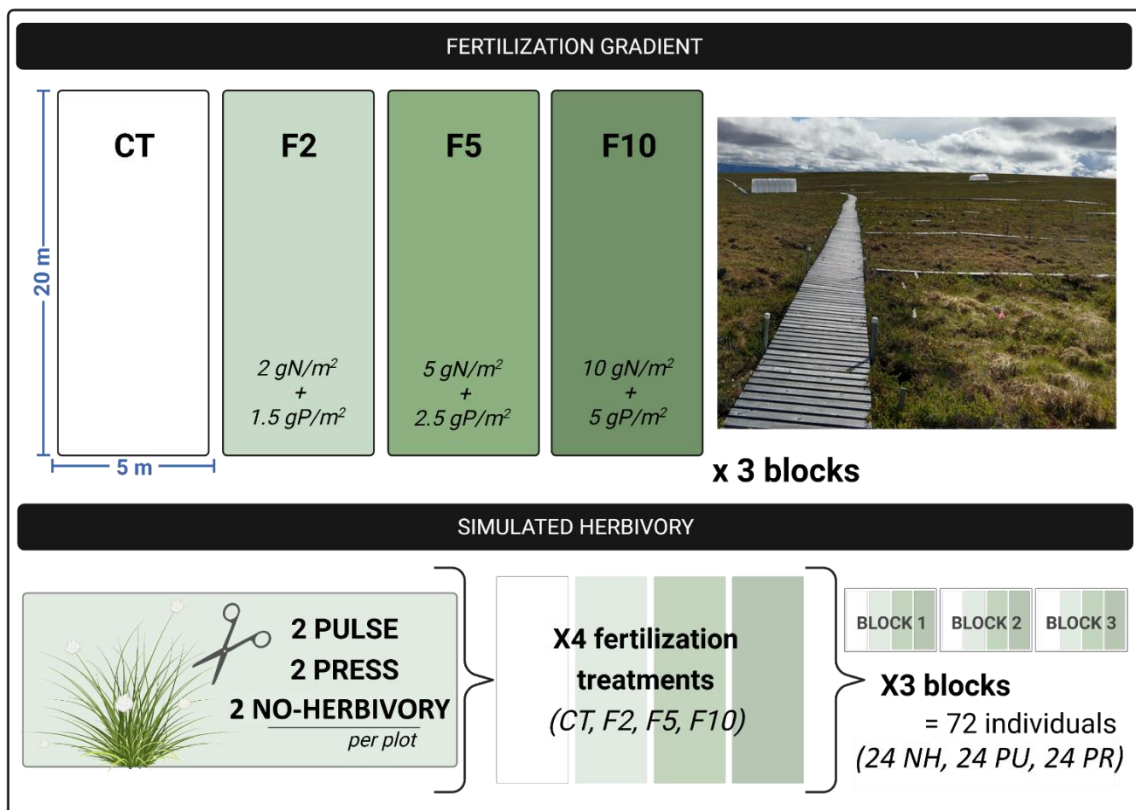
Table 1: List of species assigned to each growth forms. Mean relative cover by species and growth forms for CT fertilization plot across all years (2008-2021). Species with no data were not found in CT treatments but appeared in some higher nutrient addition treatments. Eriophorum is evaluated independently from the rest of the graminoids as it is the preferred forage for voles. n indicates the number of times the species was found within the CT treatment, out of a possible 306 quadrats.

	Mean ± SD	n
Deciduous shrubs	0.23 ± 0.09	282
Arctostaphylos alpina	0.04 ± 0.05	85
Betula nana	0.15 ± 0.08	280
Salix arctica	- ± -	-
Salix phlebophylla	- ± -	-
Salix pulchra	0.05 ± 0.04	190
Salix reticulata	0.00 ± 0.00	24
Vaccinium uliginosum	0.05 ± 0.05	214
Evergreen shrubs	0.25 ± 0.08	282
Andromeda polifolia	0.00 ± 0.00	32
Cassiope tetragona	0.04 ± 0.04	118
Dryas integrifolia	- ± -	-
Empetrum nigrum	0.03 ± 0.02	239
Ledum palustre	0.12 ± 0.07	280
Vaccinium vitis-idaea	0.09 ± 0.05	281
Graminoid	0.07 ± 0.06	270
Arctagrostis latifolia	0.01 ± na	1
Calamagrostis species	0.01 ± 0.01	5
Carex bigelowii	0.07 ± 0.05	254
Festuca species	- ± -	-
Eriophorum	0.15 ± 0.08	281
Eriophorum vaginatum	0.15 ± 0.08	281
Forbs	0.04 ± 0.04	278
Anthoxanthum species	- ± -	-
Arnica species	0.01 ± 0.00	2
Luzula species	- ± -	-
Minuartia species	- ± -	-
Pedicularis species	0.01 ± 0.01	153
Petasites species	0.02 ± 0.02	85
Polygonum bistorta	0.01 ± 0.01	241
Rubus chamaemorus	0.05 ± 0.04	116
Saussurea angustifolia	0.01 ± na	1
Stellaria species	- ± -	-
Tofieldia species	- ± -	-
Not identified to species		
Lichen	0.04 ± 0.04	268
Moss	0.11 ± 0.07	281
Litter	0.08 ± 0.05	279
Standing dead	0.02 ± 0.01	58
Bare ground	0.04 ± 0.04	95

Figure 5: Mean (n = 3) relative cover of growth forms/species among years (2008-2021) and fertilization treatments (see Table 2). Values were averaged across blocks. Relative cover was not measured in 2009 and F2 treatments were not sampled in 2010 and 2011.
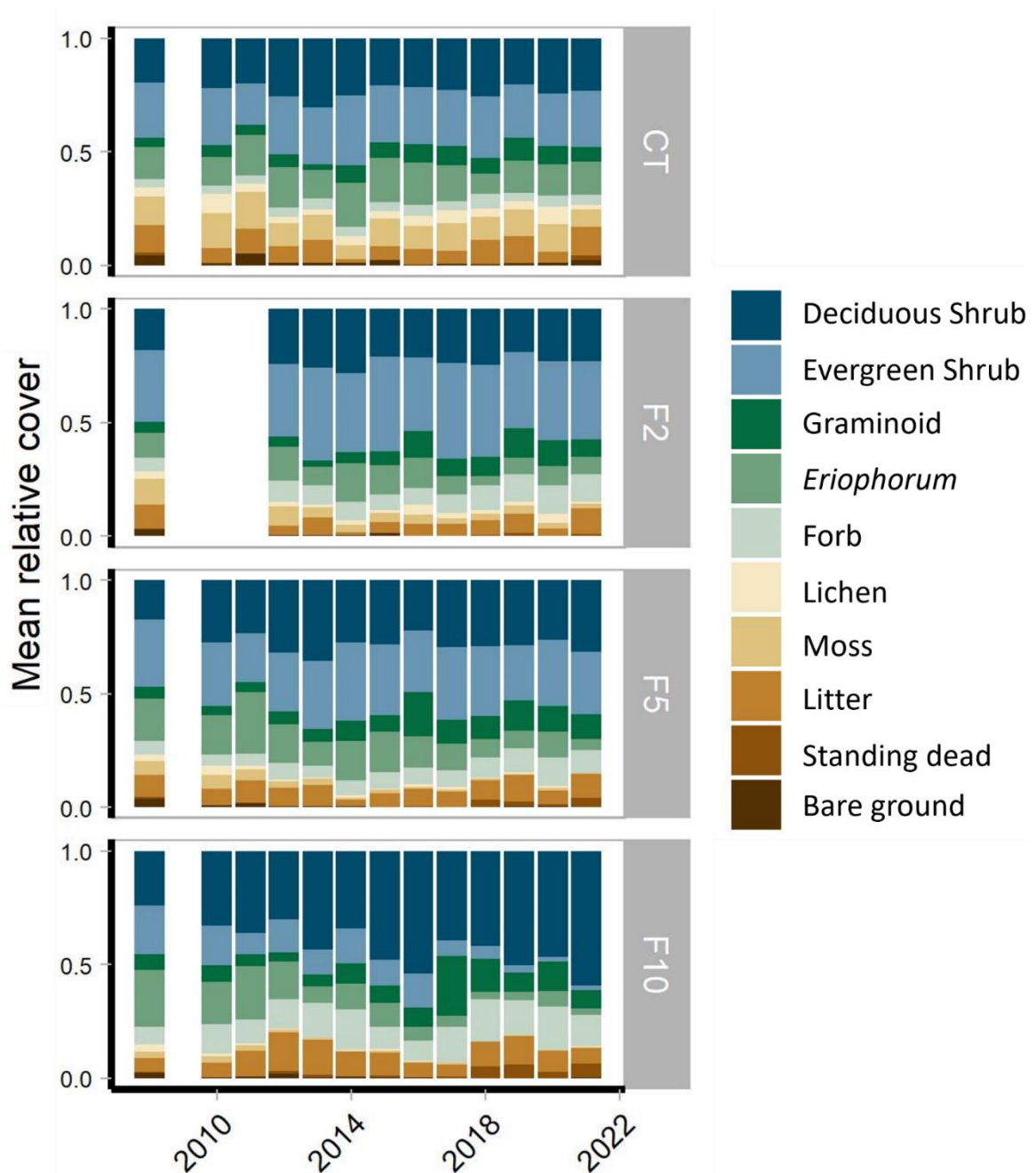
Table 2: Mean (± SD) (n = 3) relative percent cover among plant growth forms and fertilization treatments for 2008, 2015, and 2021. Shaded rows (for 2008 and 2021 only) indicate growth forms were significantly different across fertilization treatment (see Table 3).

		CT	F2	F5	F10
Deciduous shrubs					
	2008	0.19±0.05	0.18 ± 0.07	0.17 ± 0.06	0.24 ± 0.03
	2015	0.21±0.03	0.21 ± 0.02	0.28 ± 0.02	0.45 ± 0.08
	2021	0.23±0.03	0.23 ± 0.12	0.32 ± 0.06	0.59 ± 0.03
Evergreen shrubs					
	2008	0.24±0.02	0.32 ± 0.08	0.30 ± 0.02	0.22 ± 0.03
	2015	0.25±0.08	0.42 ± 0.12	0.31 ± 0.09	0.11 ± 0.03
	2021	0.25±0.05	0.34 ± 0.04	0.27 ± 0.12	0.02 ± 0.00
Graminoid					
	2008	0.04±0.01	0.05 ± 0.03	0.05 ± 0.01	0.07 ± 0.04
	2015	0.07±0.04	0.06 ± 0.04	0.07 ± 0.02	0.07 ± 0.04
	2021	0.07±0.02	0.08 ± 0.03	0.11 ± 0.05	0.08 ± 0.02
Eriophorum					
	2008	0.14±0.02	0.11 ± 0.06	0.19 ± 0.06	0.25 ± 0.05
	2015	0.19±0.06	0.13 ± 0.02	0.18 ± 0.01	0.10 ± 0.01
	2021	0.15±0.06	0.08 ± 0.06	0.05 ± 0.04	0.03 ± 0.03
Forb					
	2008	0.04±0.01	0.06 ± 0.03	0.06 ± 0.04	0.08 ± 0.03
	2015	0.04±0.04	0.07 ± 0.02	0.07 ± 0.06	0.09 ± 0.02
	2021	0.04±0.04	0.12 ± 0.07	0.10 ± 0.09	0.14 ± 0.09
Lichen					
	2008	0.04±0.01	0.03 ± 0.02	0.03 ± 0.00	0.03 ± 0.01
	2015	0.03±0.02	0.01 ± 0.01	0.01 ± 0.00	0.01 ± NA
	2021	0.02±0.02	0.01 ± 0.01	0.00 ± 0.00	0.00 ± 0.00
Moss					
	2008	0.12±0.04	0.11 ± 0.03	0.06 ± 0.01	0.03 ± 0.01
	2015	0.12±0.07	0.04 ± 0.02	0.02 ± 0.01	0.01 ± 0.00
	2021	0.08±0.03	0.02 ± 0.02	0.00 ± 0.00	0.00 ± 0.00
Litter					
	2008	0.12±0.03	0.10 ± 0.01	0.10 ± 0.03	0.06 ± 0.01
	2015	0.06±0.01	0.05 ± 0.02	0.06 ± 0.02	0.10 ± 0.06
	2021	0.12±0.05	0.11 ± 0.04	0.11 ± 0.02	0.07 ± 0.04
Standing dead					
	2008	0.01±0.01	0.01 ± 0	0.01 ± 0.01	0.00 ± 0.00
	2015	- ± -	- ± -	- ± -	0.01 ± 0.01
	2021	0.02±0.01	0.01 ± 0	0.04 ± 0.02	0.06 ± 0.05
Bare ground					
	2008	0.04±0.05	0.03 ± 0.01	0.04 ± 0.01	0.02 ± 0.01
	2015	0.02±0.01	0.01 ± NA	- ± -	0.00 ± NA
	2021	0.03±0.04	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00

Table 3: MANOVA table for mean living-plant growth forms cover for 2018 and 2021 (each year run independently). Shading indicates significant differences.

		DF	F	P
Deciduous shrubs				
	2008	3,8	0.92	0.48
	2021	3,8	17.5	<0.001
Evergreen shrubs				
	2008	3,8	3.62	0.06
	2021	3,8	12.2	<0.01
Graminoid				
	2008	3,8	0.64	0.61
	2021	3,8	1.03	0.43
Eriophorum				
	2008	3,8	4.87	0.03
	2021	3,8	3.46	0.07
Forb				
	2008	3,8	1.01	0.44
	2021	3,8	0.99	0.45
Lichen				
	2008	3,8	0.62	0.62
	2021	3,8	2.17	0.17
Moss				
	2008	3,8	7.87	0.01
	2021	3,8	14.5	<0.01

Table 4: Mean (± SD) species richness and Shannon diversity index (n = 3) per 1m2 by fertilization level for the year 2008 and 2021.

	CT			F2			F5			F10		
Richness												
2008	12	±	1	13	±	2	12	±	2	12	±	2
2021	12	±	1	11	±	2	8	±	1	5	±	1
Diversity												
2008	2.24	±	0.10	2.23	±	0.18	2.13	±	0.20	2.05	±	0.22
2021	1.98	±	0.13	1.76	±	0.08	1.18	±	0.24	0.63	±	0.21

Figure 6: Correlation between deciduous shrub and Eriophorum relative cover among fertilization treatments. Solid triangles indicate values from 2008, and solid circles indicate values from 2021. Each point represents the average for one block (n = 8) so that there are 3 points per treatment per year (2008-2021). Confidence interval around regression line is SE. See Table 5 for significance values.
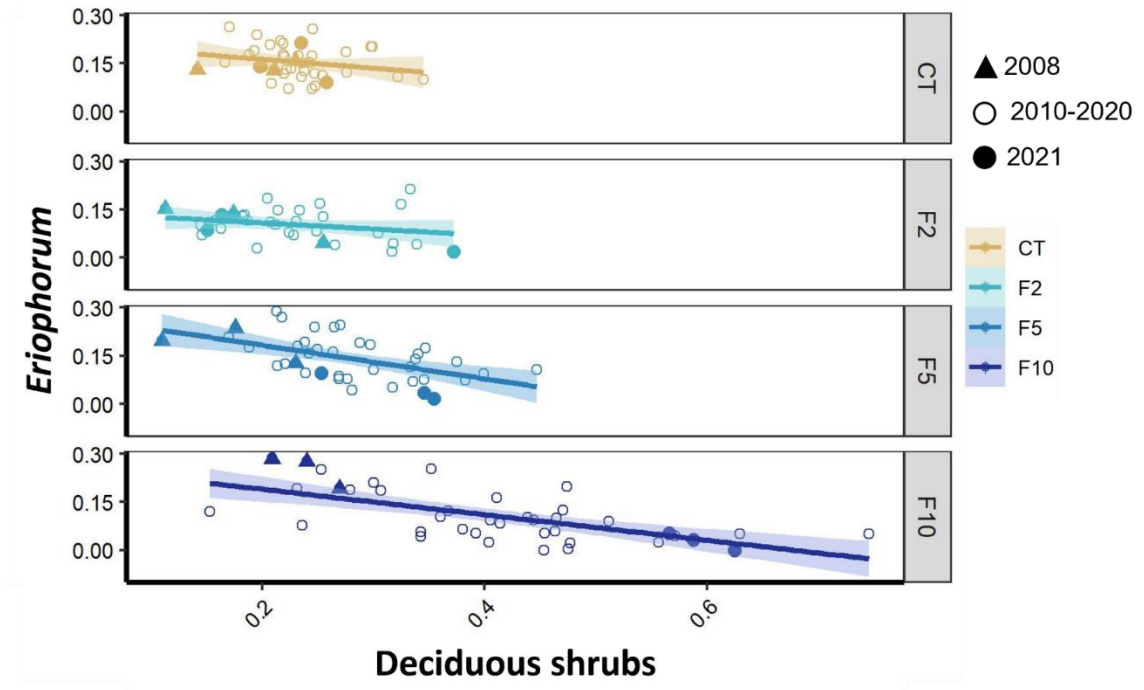
Table 5: Regression results between deciduous shrubs and Eriophorum relative cover among fertilization treatments (2008-2021). See Figure 6.

	P	Equation	R^2
CT	0.18	$y = 0.22 - 0.28x$	0.05
F2	0.16	$y = 0.15 - 0.19x$	0.065
F5	4.60E-04	$y = 0.29 - 0.52x$	0.29
F10	8.90E-06	$y = 0.27 - 0.4x$	0.42

Figure 7: Nonmetric multidimensional scaling (NMDS) ordination showing differences in plant growth forms cover measure in (A) 2008-2021 and (B) 2021 from four different fertilization treatments (CT, F2, F5, and F10).
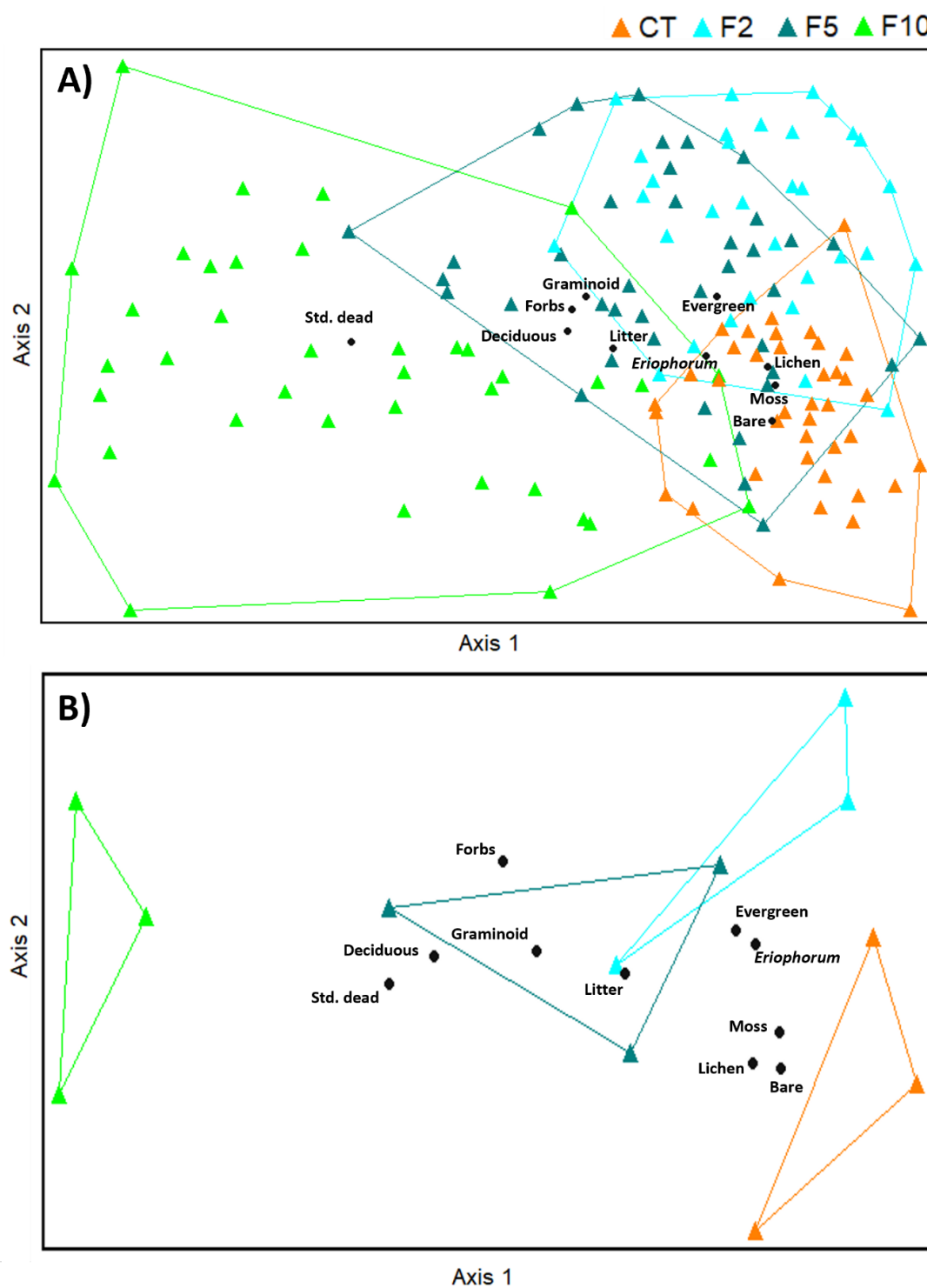
Figure 8: Mean (± SD, n = 3) Eriophorum tiller heights (cm) among simulated herbivory and fertilization treatments over four growing seasons (2018-2021). Vertical lines indicate the start of a new growing season. Note that tiller heights were only measured once in 2020 due to COVID-19 restrictions.

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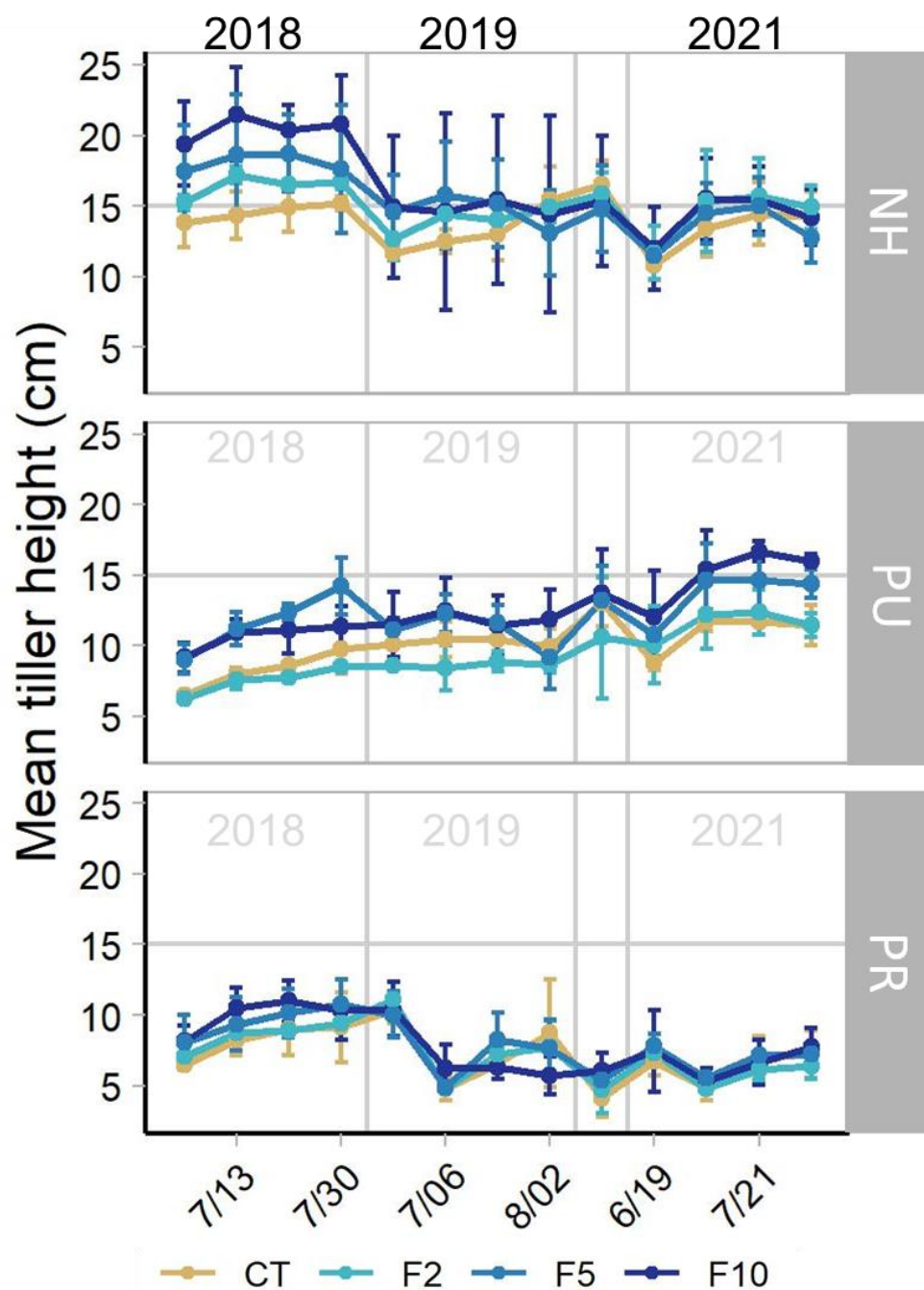
Figure 9: Final tiller heights (n = 3) among simulated herbivory and fertilization treatments for four growing seasons (2018-2021). X's indicate means, Tukeys letters indicate significant differences among the means caused by a significant interaction between herbivory and fertilization in 2021 (Table 7).
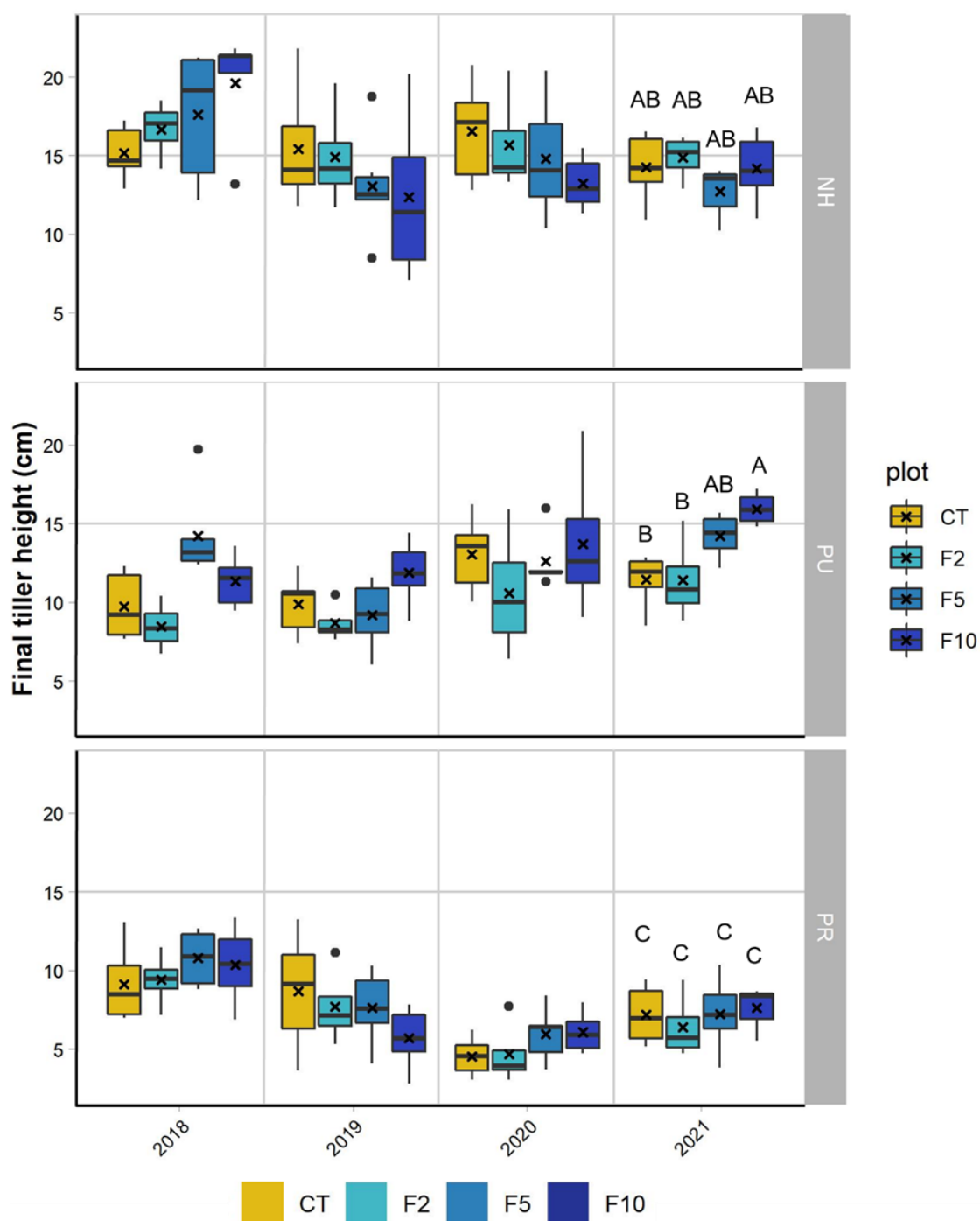
Table 6: Two-way ANOVA table for mean final tiller heights for 2018-2021 (each year run independently). Shading indicates significant differences (not including marginally significant differences).

		DF	SUM SQ	MEAN SQ	F	P
2018	*Simulated herbivory*	2	750.5	375.3	59.79	<0.01
	Fertilization	3	109.5	36.5	5.82	<0.01
	*Herbivory * Fertilization*	6	83.1	13.9	2.21	0.06
2019	*Simulated herbivory*	2	549.6	274.8	27.09	<0.01
	Fertilization	3	17.7	5.9	0.58	0.63
	*Herbivory * Fertilization*	6	60.8	10.1	0.99	0.44
2020	*Simulated herbivory*	2	1262.2	631.1	63.52	<0.01
	Fertilization	3	10.1	3.4	0.34	0.80
	*Herbivory * Fertilization*	6	31.1	5.2	0.52	0.79
2021	*Simulated herbivory*	2	597	298.5	90.56	<0.01
	Fertilization	3	29.5	9.8	2.98	0.04
	*Herbivory * Fertilization*	6	65.3	10.9	3.30	0.01

Table 7: Tukey's HSD p-values of the main effects of the 2-way ANOVA for mean final

tiller heights for 2018-2021

	Fertilization						Simulated herbivory		
	CT-F2	CT-F5	CT-F10	F2-F5	F2-F10	F5-F10	NH-PU	NH-PR	PU-PR
2018	0.84	0.01	0.01	0.13	0.14	1.00	<0.001	<0.001	0.26
2019	-	-	-	-	-	-	<0.001	<0.001	0.02
2020	-	-	-	-	-	-	0.01	<0.001	<0.001
2021	0.99	0.93	0.04	0.99	0.14	0.16	0.59	<0.001	<0.001

Figure 10: Study site location (Left) map of Alaska (Right) zoomed in view of Toolik field station location, 06MAT, and Team Vole site locations. Coordinates listed in Table 8.
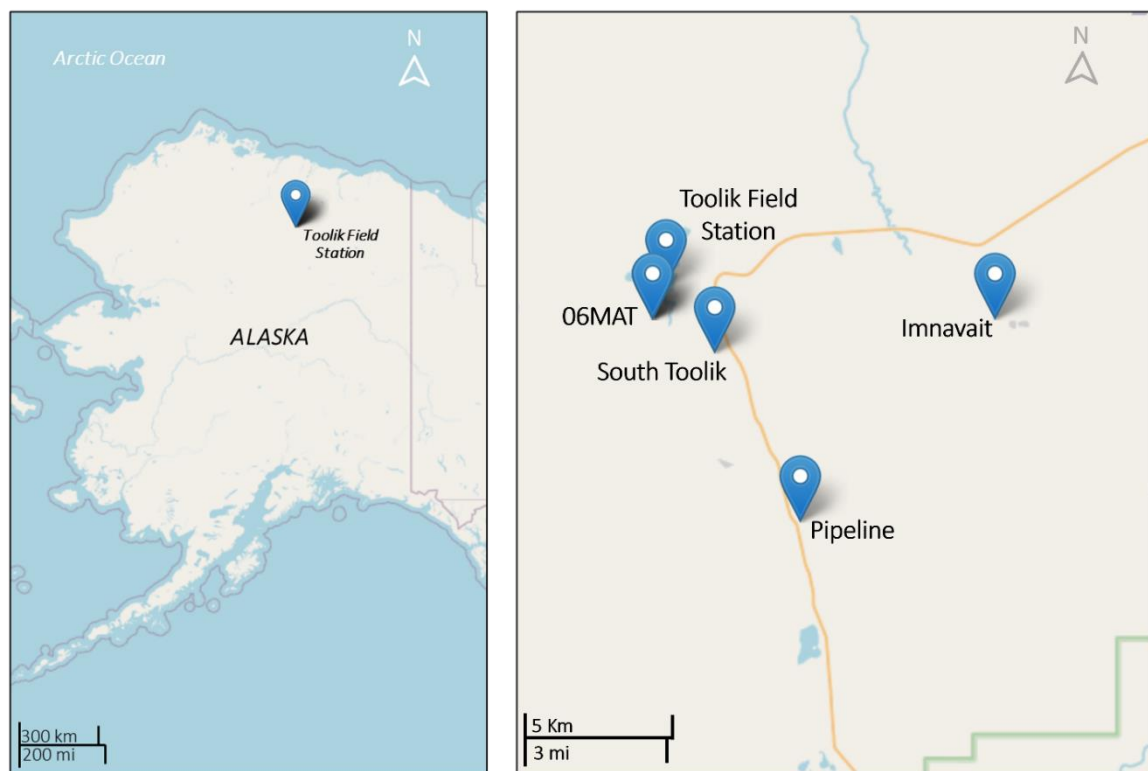
Made by Nicole Williamson using Leaflet | © OpenStreetMap contributors, CC-BY-SA

Table 8: Study site location coordinates.

	Latitude	Longitude
LTER 06MAT		
Block 1	*68.62*	*-149.61*
Block 2	*68.62*	*-149.61*
Block 3	*68.62*	*-149.61*
Team Vole sites		
Pipeline	*68.56*	*-149.49*
South Toolik	*68.61*	*-149.56*
Imnavait	*68.62*	*-149.33*

Figure 11: Example of the small-mammal herbivore manipulation experiment set up at one of three replicate Team Vole's sites on moist acidic tussock tundra.
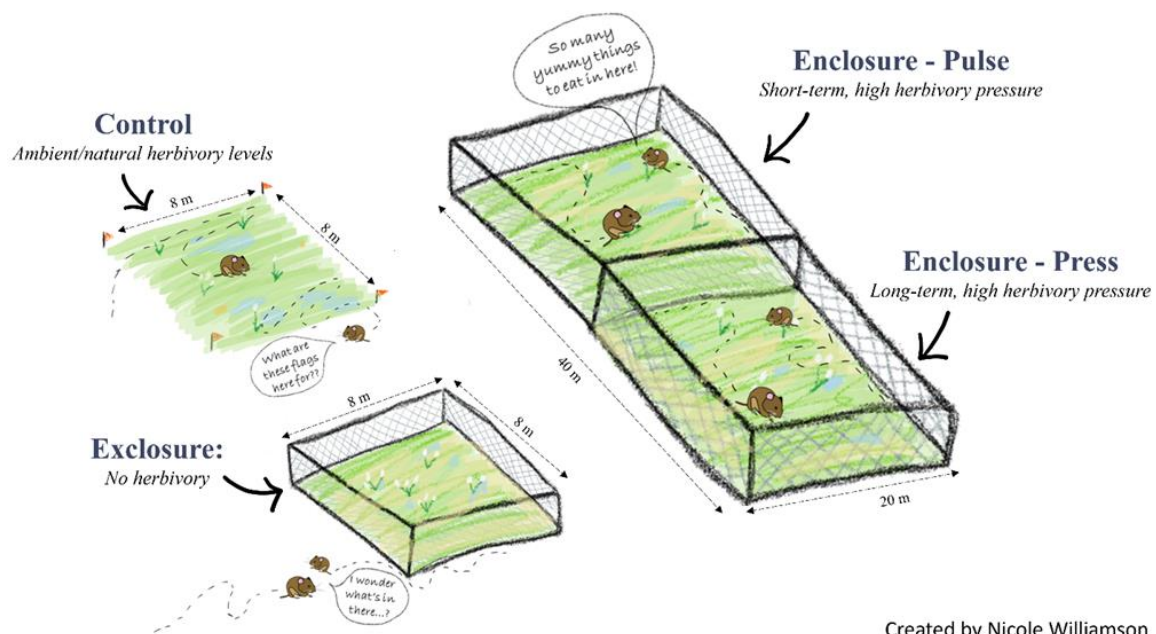
Figure 12: Mean (n = 3) NDVI values among fertilization treatments throughout the
growing seasons for the years 2011, and 2014-2018
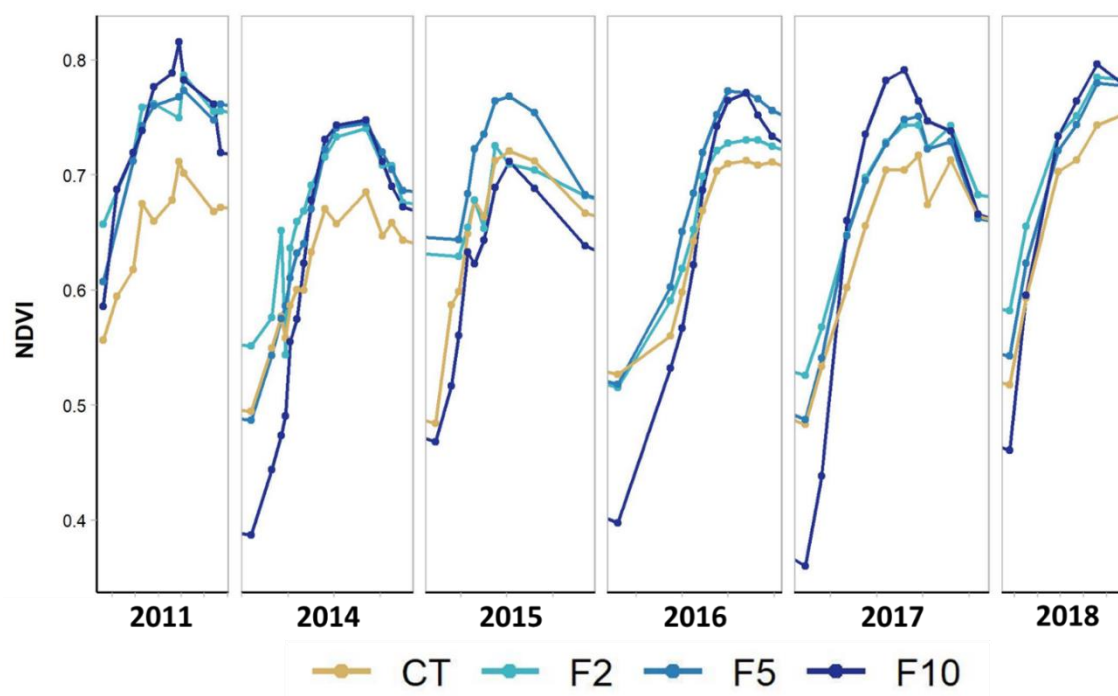
Figure 13: Correlations between Betual cover and NDVI at four different times in the growing season. Colors indicate fertilization treatment. Includes years 2011, 2014-2018. Each point represents the average NDVI of a treatment (n = 3).
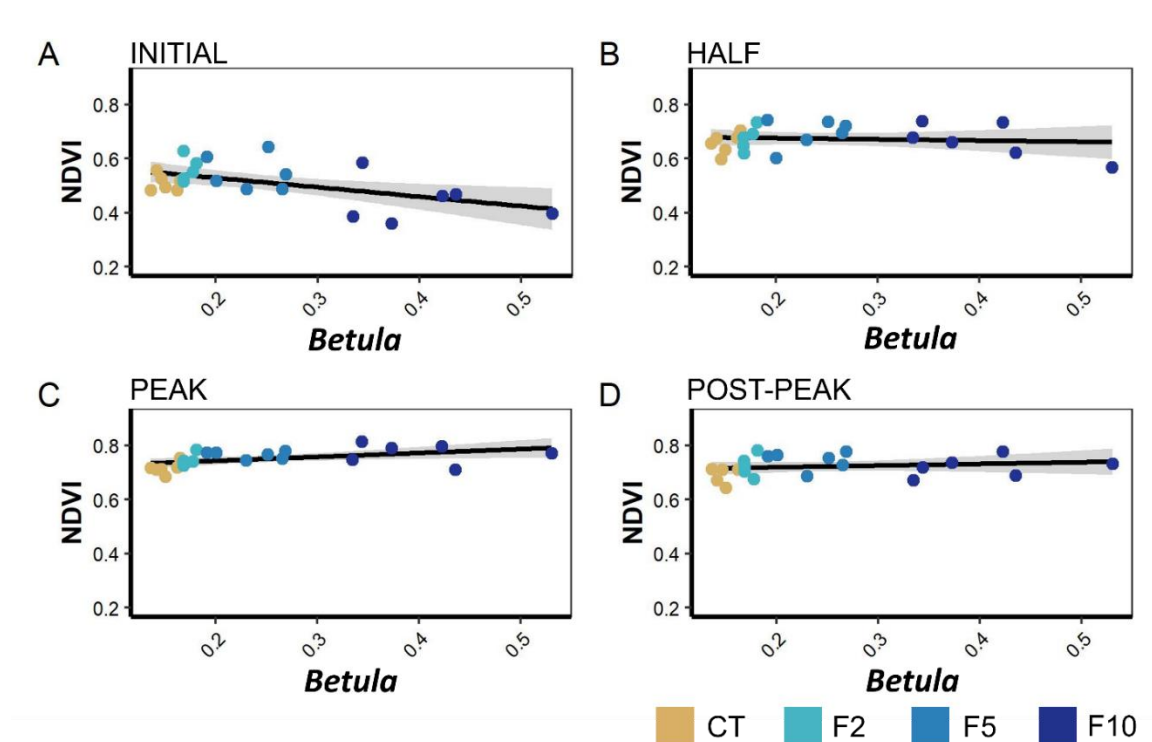
Table 9: Correlation results between Betula nana and NDVI at four different time points throughout the growing season.

Time	Species	P	Equation	R^2
Initial	*Betula*	0.0086	y = 0.6 - 0.35 x	0.29
Half	*Betula*	0.66	y = 0.68 - 0.044 x	0.0096
Peak	*Betula*	0.42	y = 0.71 + 0.14 x	0.24
Post	*Betula*	0.42	y = 0.71 + 0.062 x	0.032

Figure 14: Mean (n = 3) relative cover of growth forms/species among years and

herbivory treatments 2018-2021 averaged across three replicate sites (see Figure 15 for

sites presented separately). No data were collected from PU in 2018.
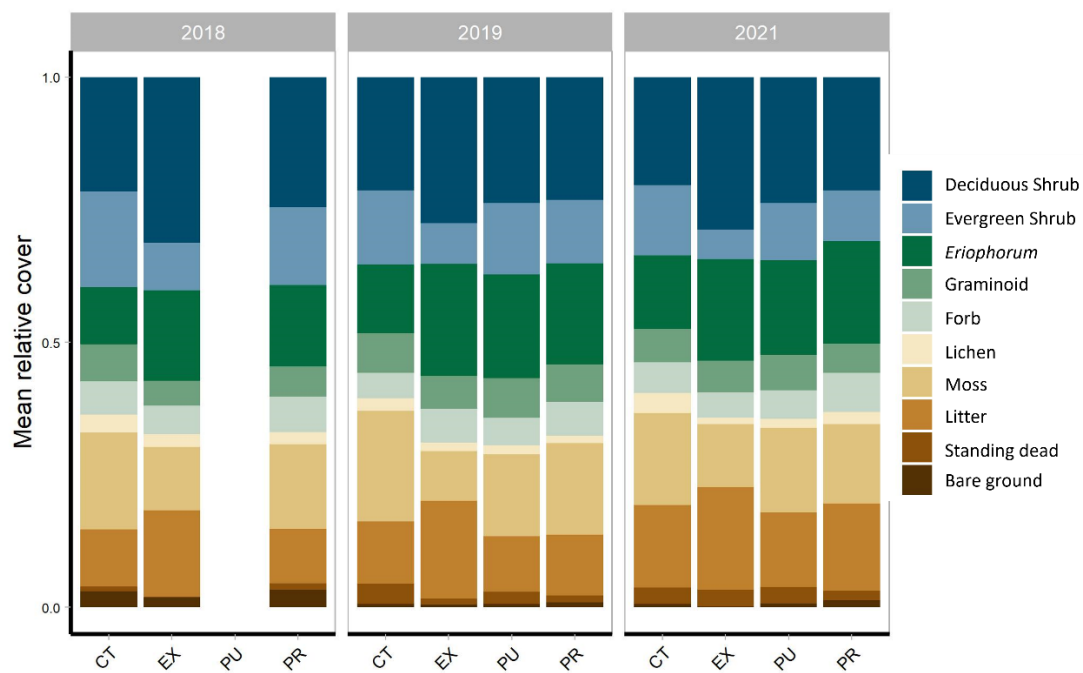
Figure 15: Mean (n = 8) relative cover of growth forms/species among years and herbivory treatments for each replicate site from 20018-2021. No data was collected from PU in 2018.
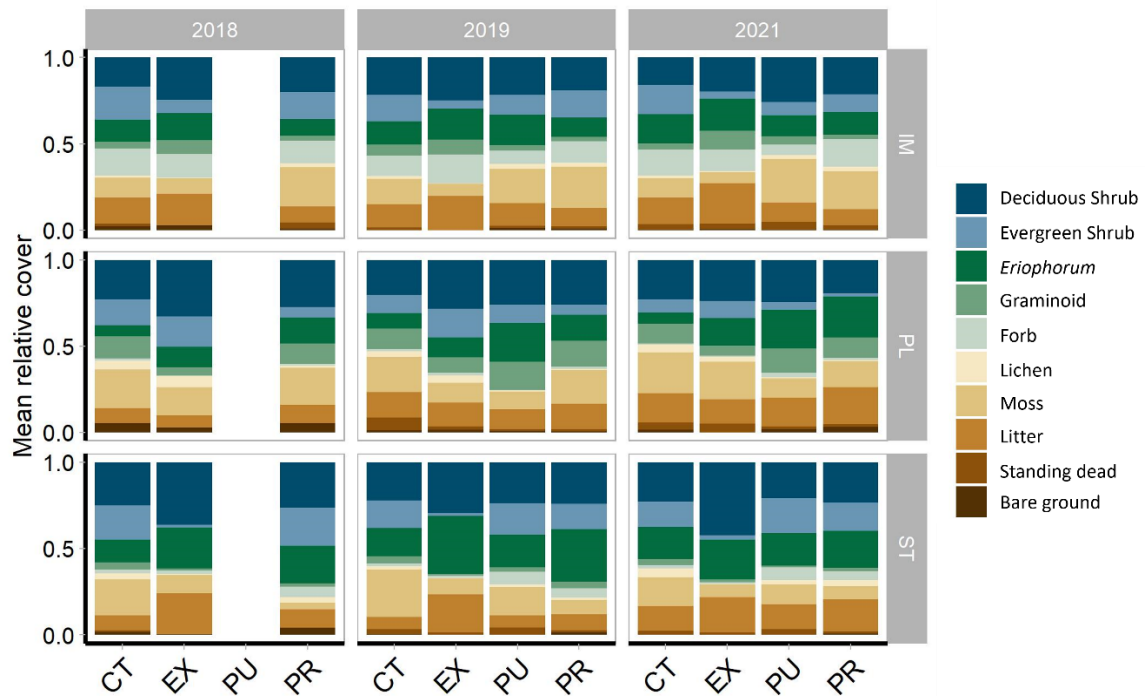
Figure 16: Team Vole site correlations between Betula cover and NDVI at peak season. Colors indicate herbivory treatment. Includes years 2018-2021. Each point represents an average NDVI value for a quadrat (n = 8).
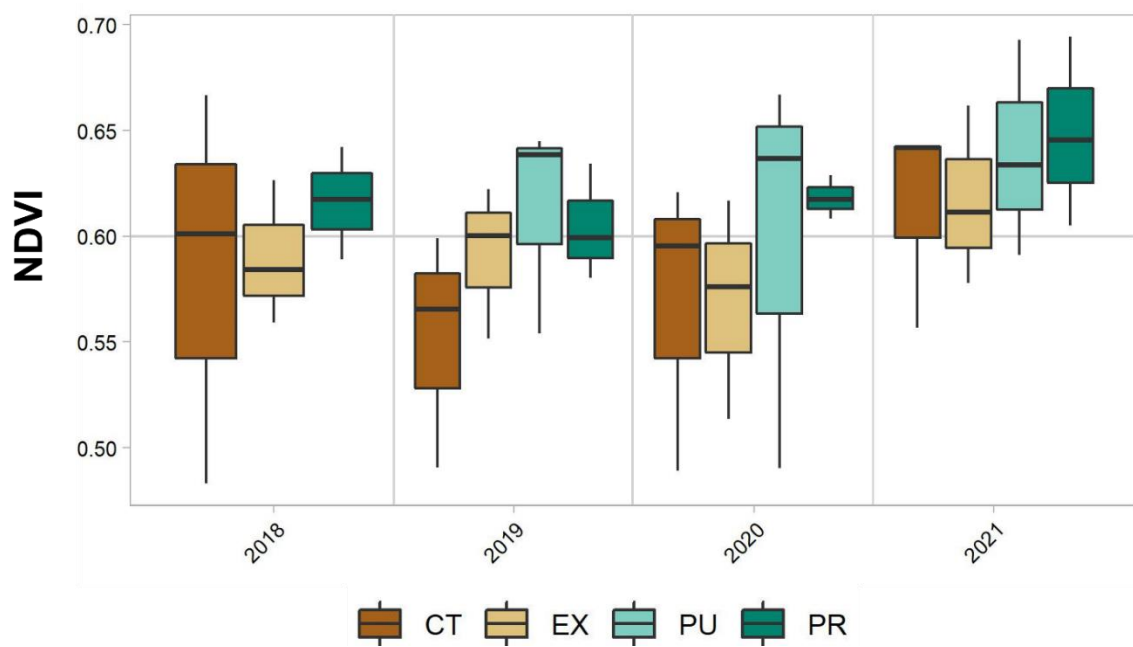
Figure 17: Mean (n = 8) NDVI values among herbivory treatments during peak season for the years 2018-2021. No data wascollected from PU in 2018.
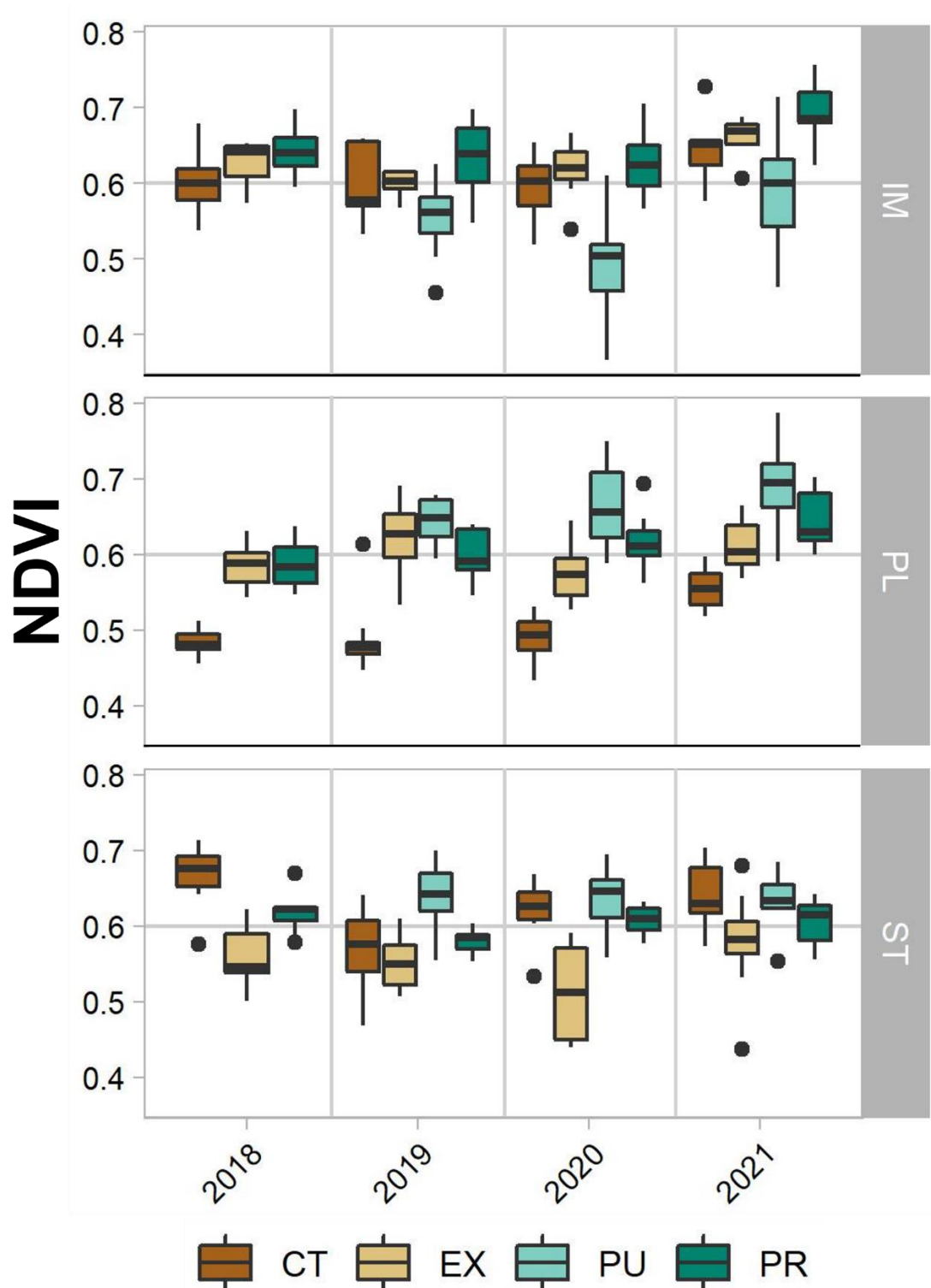
Figure 18: Team Vole site correlations between Betula cover and NDVI at peak season.

Colors indicate herbivory treatment. Includes years 2018-2021. Each point represents an

average NDVI value for a quadrat (n = 8).
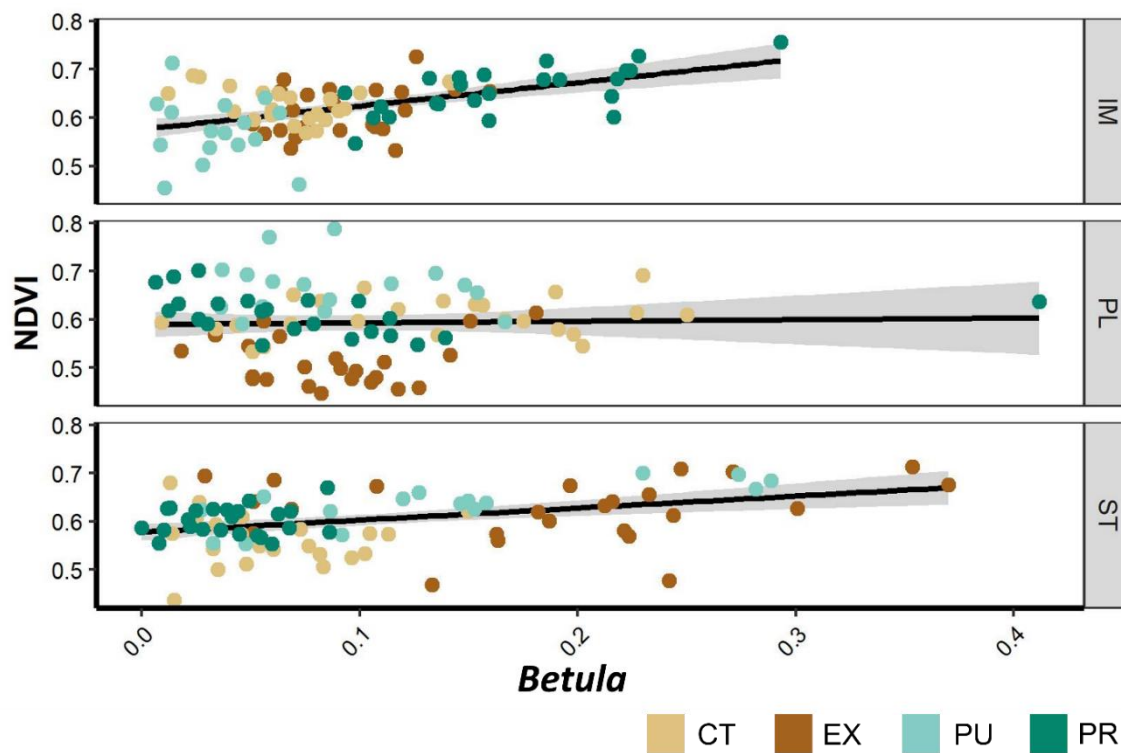
Table 10: Correlation results Betula and NDVI at each of the team vole locations.

Includes years 2018-2021.

Site	Species	P	Equation	R^2
IM	*Betula*	<0.001	$y = 0.58 + 0.48\ x$	0.26
PL	*Betula*	0.78	$y = 0.59 + 0.33\ x$	<0.001
ST	*Betula*	<0.001	$y = 0.58 + 0.25\ x$	0.16

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ACADEMIC BACKGROUND

M.S. Environmental Sciences (*Thesis Track*)   May 2022
Towson University, Towson, Maryland (3.89/4.00)

B.S. Environmental Science: Soils & Watershed Mgt   May 2019
Dual major: Ecogastronomy
University of New Hampshire, Durham, New Hampshire (3.64/4.00 GPA)
     Study Abroad: Ascoli Piceno, Italy   Fall 2017

RELEVANT COURSE WORK

Graduate:
Data Analysis and Interpretation for Biologists, Remote Sensing, Ecosystem Ecology, Global change Biology, Topics in Environmental Geology, Environmental Chemistry, Environmental Law and Regulation, and Professional Aspects of Biology.

Undergrad:
Ecology and Society in a Changing Arctic, GIS for Natural Resources, Fate and Transport in the Environment, Environmental Modeling, Soil Ecology, Aquatic Ecosystems, General Ecology, Studio Soils, Watershed and Water Quality Management, Environmental Biology, Intro to GIS, Intro to Environmental Science, Natural Resources & Environmental Policy, Geology and the Environment, Contemporary Conservation Issues, and Sustainable Agriculture.

Plus, general background classes in Chemistry, Biology, Physics, Calculus, and Statistics.

SCHOLARLY ACHIEVEMENT & PREVIOUS AWARDS

UNH Department of Natural Resources and the Environment, Outstanding student award in Environmental Sciences. (2019)

UNH Deans List- Highest Honors (Fall 2017 – Fall 2018), & High Honors (Fall 2016– Spring 2017, and Spring 2019)

Wolves and Moose of Isle Royal Student Scholarship (2017)
Lloyd W. Hawkensen Forestry Scholarship (2017)
Rockland Trust Scholarship (2016)

PUBLICATIONS

Steketee, J., Rocha, A., Gough, L., Griffin, K., Klupar, I., An, R., Williamson, N., and Rowe, R. Small herbivores with big impacts: tundra voles (*Microtus oeconomus*) alter post-fire ecosystem dynamics. Ecology. (*Accepted, 2021*).

Perryman, C., J. Wirsing, K. Bennett, O. Brennick, A. Perry, N. Williamson, J. Ernakovich. 2020Heavy metal in the Arctic: Characterizing the distribution of five metals in soil in the Alaskan Arctic. PLOS ONE. 10.1371/journal.pone.0233297

Aber, J.D., M.M. Smith, A.M. Leach, W.H. McDowell, M.D. Shattuck, N.A. Williamson, D.M. Hoffman and J.M. Davis. 2020. The Agroecosystem Project at the Organic Dairy Research Farm, University of New Hampshire: Summary of Results and Proposals for Applications. University of New Hampshire, Durham, NH, USA https://bit.ly/3qOi8B9

RESEARCH & WORK

<u>Graduate Research Assistant (master's thesis)</u>   Fall 2019 – Spring 2022
Towson University, Towson, MD

- Examined the effects of small mammals and nutrient addition on Arctic tundra plant community structure/productivity
- Investigated the relationship between spectral reflectance and plant species abundance
    - Worked in remote field conditions for 2-3 months at a time
    - Coordinated and collaborated with research teams from three universities to accomplish greater project goals
    - Supervised 3 field technicians in both remote field and laboratory settings
    - Conducted vegetation surveys and live-trapped small mammals
    - Collected and analyzed soil/plant samples, spectral reflectance, and gas flux measurements
    - Assisted in maintaining long-term ecological research (LTER) experiments at Toolik Field Station
    - Maintained data integrity and long-term data sets on publicly available databases for the Arctic-LTER network
    - Presented findings at professional and academic conferences (poster and oral presentations)

<u>Reproducible Practices for Arctic Research Using R</u>   Feb 14th-18th 2022
Remote class – NSF Arctic Data Center

- 5-day remote workshop (~30 hr) on best data management practices (data cleaning, analyzing, documenting, and preserving)
- Learned how to use R, Rmarkdown, and git/GitHub for data wrangling, analysis, visualization, and code versioning

<u>Graduate Teaching Assistant - Introductory Biology Lab</u>   Fall 2019–Spring 2020
Towson University, Towson, MD
- Instructed 2-3 labs (~20 students) a semester through hands on labs and activities and weekly lab reports
- Coached students through the design, data collection, and analysis of a semester long independent research project

<u>Heat Recovery Compost Research Assistant</u>   Fall 2015- Fall 2018
Fairchild Dairy Teaching and Research Center, Durham, NH

- Conducted a study on a biofilter for removing ammonia from the waste stream of an industrial scale composting facility
- Trained and oversaw new research assistants

<u>Wolves and Moose of Isle Royale Moose Watch Research Volunteer</u>
May 2016
Responsible for locating and collecting moose sheds and bones, while backpacking off trail on Isle Royal as part of the longest running population dynamic study.

PROFESSIONAL PRESENTATIONS

Williamson, N. 2022. Effects of Nutrient Eriophorum vaginatum response to simulated pulse and press vole herbivory under fertilization. ARC LTER Annual Meeting.
Williamson, N. 2021. Effects of Nutrient Addition on a Moist Acidic Tundra Plant Community. ARC LTER Annual Meeting.
Williamson, N., A. Leach, M. Smith, J. Aber, D. Winans. 2019. Increasing Farm Sustainability: Designing a Biofilter to mange Compost gas Exhaust. University of New Hampshire COLSA Undergraduate Research Conference.
Williamson, N., J Aber, A Leach. 2018. Designing a Biofilter for Ammonia Removal at a Commercial-Scale Compost Facility. University of New Hampshire COLSA Undergraduate Research Conference.

SCIENCE OUTREACH

<u>Family STEM Afternoon</u>   Jan. 11th 2020
Science outreach and education event for elementary school age children at the Millis Public Library in Millis MA sponsored by Pathways Wellness Center and in part by Towson University Biological Science department. Responsible for creating, organizing and executing this event. With the help of three other scientists we educated young kids interested in science through interactive experimental demonstrations.

Climate Change in the Arctic & how you can help   Jan. 8th 2020
Invited by an 8th grade science teacher to give a presentation for 8th grade students at
Benjamin Franklin Classical Charter Public School, Franklin MA. Introduced kids to the
topic of climate change, its impacts and steps the students can take to help.

ACADEMIC AFFILIATIONS

Phi Sigma: Biological Sciences Honor Society
Spring 2019
This honors society recognizes undergraduate students who excelled in the biological
sciences and who are involved in research. Phi Sigma members provide tutoring sessions
two days a week to other students taking introductory Biology courses.

Climate Reality Project at UNH: Club President   Fall 2015-
Summer 2017
Responsible for training volunteers and captains, organizing petitioning and phone
banking sessions, organizing campus events, planning campaigns, and setting club goals.

FAMILIAR PROGRAMS

R, ArcGIS, Stella, JMP, Excel, Image J, Audacity, Audition

INTERNATIONAL EXPERIENCE

UNH Study Abroad: Ascoli Piceno, Italy
Fall 2017
World Challenge Expedition: Ecuador & the Galapagos Islands
Summer 2013

REFERENCES

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