

Arctic Ground Squirrels as Ecosystem Engineers
of Projected Tundra Shrub Encroachment

BY

JENNIFER DALTON
B.A., University of Michigan, Ann Arbor, MI, 2000

THESIS

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Defense Committee:

Dr. Miquel A. Gonzalez-Meler, Chair and Advisor
Dr. Joel S. Brown
Dr. Christopher Whelan

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SUMMARY

Holarctic warming temperatures are leading to an expansive and rapid greening of the Arctic. Yet herbivores may play a role in mediating shrub expansion. The Arctic ground squirrel (*Urocitellus parryii*), is an omnivorous ecosystem engineer with Holarctic distribution, likely altering local plant communities and modifying edaphic properties in and around burrow systems. This thesis therefore investigates the role of Arctic ground squirrels in shaping local vegetation near Toolik Field Station on the North Slope of Alaska.

I quantified foraging intensity of the Arctic ground squirrel in experimental foraging patches along a heath-graminoid-shrub tundra gradient. Foraging intensity varied temporally, being highest in the afternoon and lowest overnight. During the morning, foraging intensity was inversely correlated with the normalized difference vegetation index (NDVI), a proxy for vegetation productivity. Foraging was additionally measured within landscapes of fear, confirming that vegetative and topographic obstructions of sightlines reduce foraging intensity. Our results suggest that Arctic ground squirrel foraging may impede or slow-down shrub expansion in areas of low predation risk, but not in areas of high risk.

I also examined the effects of AGS on local shrub productivity as regional patterns using known locations of Arctic ground burrows (N=37). I explored the relationship between Arctic ground squirrel habitat and patterns of shrub biomass, height, and NDVI using satellite imagery. Additionally, using elemental (C and N) and isotopic analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of both plant and soil samples taken within burrow systems and in adjacent undisturbed controls, I quantified the effect of Arctic ground squirrel nitrogen deposition on the collective, regional-scale promotion of local productivity. Via the satellite analysis, Arctic ground squirrels had a positive effect on NDVI compared to controls, also showing a fertilization effect in *Salix* spp. near burrows. The results suggest that Arctic ground squirrels are indeed engineering their environment, promoting the growth of preferred forage of many Arctic herbivores.

1. INTRODUCTION

1.1 Overview of abiotic and biotic controls of Arctic shrub expansion

1.1.1 Abiotic controls

Holarctic warming temperatures, evidenced by glacial and permafrost degradation (Lachenbruch et al. 1982; Lachenbruch and Marshall 1986), are leading to an expansive and rapid greening of the Arctic (Ju and Masek 2016). The shift in the structure and composition of tundra vegetation (Chapin et al. 1995; Serreze et al. 2000; Sturm et al. 2001) is attributed to a deepening of the active layer and accelerated decomposition of soil organic matter (SOM; Natali et al. 2011), releasing nutrients that aid in the transition of species composition and cover. Plant communities are shifting from tussock (*Eriophorum vaginatum*) to canopy-forming woody shrubs such as birch (*Betula* spp.) and willow (*Salix* spp.; Tape et al. 2006). In Arctic ecosystems that are naturally limited by low temperatures, short growing seasons and abundant permafrost (8.6% Earth land area), subtle alterations in decomposition, net mineralization, and increases in available soil nutrients lead to higher ecosystem net primary productivity (NPP; Chapin & Shaver 1996). As permafrost is thought to contain up to 50% of the total global terrestrial soil organic carbon (SOC), with 20-25% thought to be stored in the upper 30 cm, it is highly vulnerable to climate change (Blok et al. 2010). Subsequent release and accumulation of permafrost C in the atmosphere (CO₂ and CH₄) can lead to future warming and increases in NPP and plant cover changes.

Although this holistic tundra shift to higher NPP may mitigate expected increases in Arctic permafrost C losses, research suggests that shrub encroachment is not ubiquitous throughout the Arctic. Some shrub patches are rapidly expanding (infilling and increasing in extent) while others remain stable (Myers-Smith et al. 2011, Tape et al. 2012). This landscape heterogeneity is attributed to local variations in growing season temperature, precipitation, host soil characteristics, surficial geology and topography (Tape et al. 2012). Additionally, variations

in plant responses to experimental warming and nutrient additions highlight differences in species-specific physiological tolerances under novel climate change conditions (Bret-Harte et al. 2001; Heskell et al. 2013). These heterogeneous responses among plant species therefore make quantification of the expected feedback from Arctic C release uncertain (Pearson et al. 2013).

1.1.2 Biotic controls

While abiotic controls of Arctic shrub expansion are widely studied (Chapin et al. 1995; Lorant and Goetz 2012; Myers-Smith et al. 2015), less understood is how biotic factors may help drive changes in plant communities and ecosystem properties. The breadth of knowledge regarding the role of mammalian herbivory on Arctic ecosystem productivity in relation to climate change is lacking, despite being recognized as a major agent of change (Zimov et al. 1995). But in recent years, the number of publications have increased (Barrio et al. 2016), highlighting plant-herbivore and climate change controls over the structuring of Holarctic plant communities (Gough et al. 2007; Post and Pedersen 2008; Olofsson et al. 2009; Gough et al. 2012; Ravolainen et al. 2014; Kaarlejärvi et al. 2015). Much like the species-specific dominants found under abiotic-controlled climate change scenarios, exclosure studies of herbivores have highlighted clear competitive frontrunners. Selective foraging and palatability play a role in promoting these species-specific dominants. Deciduous shrub species vary in their concentrations of defense compounds, and those species higher in metabolites have a competitive advantage against herbivory, which plays a suspected role in the proliferation of shrubs higher in anti-herbivory compounds (Bryant et al. 2014).

Yet comparatively less information is available on the indirect effects of vertebrates on NPP, though this area of research is gaining attention. Arctic herbivores such as Arctic ground squirrels and microtine rodents, for example, can drastically alter geomorphic characteristics via their burrowing activities (Price 1971). They may also alleviate abiotic constraints to shrub expansion via substantially increasing soil nutrients through the deposition of urine and feces

(Mckendrick et al. 1980). Such activities can dramatically affect nutrient cycling (Olofsson et al. 2004a; Sjögersten et al. 2010) and, thus, plant productivity (Barthelemy et al. 2015; Gharajehdaghpour et al. 2016).

The fundamental dynamics of these trophic interactions can be divided into top-down and bottom-up controls. Top-down (consumer) versus bottom-up (resource) mechanisms controlling Arctic food chains are largely at odds. Proponents of bottom-up controls view the low productivity, low nutrient tundra as dominated by plant-herbivore interactions, with herbivore populations kept in check by low NPP. Yet recent research suggests that this will likely change due to increases in predation pressures as a result of warming (Legagneux et al. 2012; Legagneux et al. 2014), leading to top-down regulation.

To better understand the relative importance of these abiotic and biotic drivers in structuring future Arctic plant communities, this review will therefore examine the current state of knowledge of 1) Arctic trophic theory, herbivore selectivity, and plant functional group palatability 2) direct and indirect plant-herbivore interactions and ecosystem impacts and 4) overall anticipated changes in plant-herbivore interactions as a result of future climate change. Holistically, this review will highlight the broader implications for biodiversity, biogeochemical cycling, productivity and Arctic inputs to the global carbon cycle.

1.2 Arctic trophic framework

1.2.1 Trophic theory

A central goal of ecology over the last several decades has been to determine under what circumstances food webs are structured by the supply of nutrients and resources (bottom-up control) versus the actions of higher trophic levels on those below (top-down control). Hairston et al. (1960), in a landmark paper (now known the Green World Hypothesis), argued that in food webs with three trophic levels, top-down control of herbivores by carnivores allows plants to escape control from herbivores. Plants are therefore limited by competition for resources.

According to Hairston et al. (1960), the effect of herbivores on plant productivity is mediated by higher trophic levels. In food chains with three trophic levels, top-down control by carnivores causes cascading effects on plant productivity by reducing the abundance of herbivores. Conversely, in a bottom-up system plants are resource limited, mediating the transfer of nutrients to higher trophic levels and therefore restricting food chain length (Elton 1927; Lindeman 1942). Though it has been argued that not all plants are edible (Murdoch 1966; Ehrlich and Birch 1967), bottom-up controls have been refined to explain the role of secondary metabolites in regulating energy transfer. Consequently, climate-induced changes in a bottom-up system may favor resource-competitive dominants and plant community assemblages, shifting communities toward species less palatable to herbivores, such as tannin and terpene-rich woody shrubs (Jung et al. 1979; Oksanen 1992). Several studies have investigated the effect of trophic dynamics in the Arctic (Krebs et al. 2003; Post et al. 2009), analyzing the role of top-down (predation) and bottom-up (resource limited) drivers of plant productivity and the implications of climate change on trophic cycling (Ims and Fuglei 2005).

This exploration of top-down and bottom-up controls helped foster the ecosystem exploitation hypothesis (EEH; Oksanen 1990; Oksanen et al. 1981), which incorporates both bottom-up and top-down controls. EEH theory attempts to explain the development of food chains in relation to productivity, from which we can better understand observations of complex Arctic trophic interactions. The EEH highlights NPP as the dependent variable in regulating the number of community-level trophic levels, utilizing the idea that trophic dynamics change along a gradient of productivity (Fretwell 1977; Oksanen et al. 1981; Oksanen and Oksanen 2000). When productivity is low, only one trophic level can be supported. But with an increase in NPP, the additional biomass can support a higher number of trophic levels. Controls (bottom-up and top-down) are therefore fluid and vary along this environmental gradient. As increases in NPP driven by climate change are expected to support greater herbivore biomass and subsequent

trophic levels, this will increase the relative importance of herbivores in shaping Arctic plant communities (Gough et al. 2007).

1.2.2 Primary producers and defensive strategies

Plant species-specific defensive strategies play a role in the extent to which herbivores may shape plant communities. Plant defenses can be mechanical or chemical, constitutive (always present) or induced via herbivory. When consumed, plants can respond to herbivory via changes in the concentration of secondary metabolites to reduce palatability. Palatability can be variable and is linked to plant growth form, phenology, and the type and concentration of defensive compounds. Defenses induced via herbivory alter plant nutrient allocation, and instead of using C and N for growth, nutrients are allocated for defense (Bryant et al. 1983). In the nutrient-limited Arctic, secondary metabolites are often carbon-based (terpenes and phenols; Jung et al. 1979). Plants can also respond by increasing growth, also known as compensatory growth (McNaughton 1983; Paige and Whitham 1987). However tolerance to herbivory is contingent on seasonal availability of resources (nutrients), the plant part consumed, and species-specific physiological adaptations.

Arctic shrubs can either be evergreen and deciduous. The two groups vary in their responses to herbivory, defensive compound chemistry and concentrations. Evergreen ericoid shrubs such as *Vaccinium vitis-idaea* (cowberry) and *Rhododendron tomentosum* (Labrador tea) are typically well defended and are higher in constitutive plant defensive compounds (tannins) than deciduous shrubs. Their leaves are generally lower in nitrogen content (or concentration) and are generally avoided by herbivores except for more palatable plant parts such as flowers or fruits that are either free of or lower in defensive compounds (Batzli and Sobaski 1980).

Deciduous shrubs (*Betula* spp. and *Salix* spp.) differ in their use of constitutive and induced plant defenses. *Betula nana* (dwarf birch) is a deciduous shrub with Holarctic distribution, with three main subspecies that differ in plant secondary compound concentrations

(non-resinous *B. nana nana*, resinous subspecies *B. nana exilis*, and resinous subspecies *B. nana glandulosa*). The main secondary compound produced by the non-resin birches is condensed tannin, while the resin birches are densely covered in glandular trichomes that are rich in toxic dammarane triterpenes. These resin-rich subspecies are therefore less preferred and less prone to herbivory (Bryant et al. 1991). As a result, both subspecies have undergone expansion in recent years (Tremblay et al. 2012; Bryant et al. 2014).

By comparison, the fast-growing *Salix* spp. is less chemically defended. They are a preferred forage for large Arctic vertebrate herbivores, especially early in the growing season when rapidly growing leaves are high in nitrogen and low in structural materials, and exhibit strong compensatory growth in response to herbivory (Christie et al. 2014). Though growth can be inhibited by herbivores in heavily browsed areas at high densities (Danell et al. 1994; Ravolainen et al. 2014).

Plant toxins can reduce the nutritional quality of plants and have effects on reproductive success, subsequent population densities, and future browse intensity. In a study of snowshoe hare browsing on *Betula glandulosa*, moderate-severe browsing in the winter of the hare peak increased the toxicity of preferred plant parts. This caused mature woody plant parts to transition to the browsing-resistant juvenile form, forcing hares to eat more nutrient-deficient parts. This change therefore caused a lag in snowshoe hare population recovery following cyclic declines (DeAngelis et al. 2015).

However concentrations of defensive compounds are anticipated to decrease as a result of climate change. Fertilization experiments have confirmed the reduction of carbon-based defense compounds, in favor of utilizing excess C for increased growth (Ayres 1993). Phenotypic responses of plants to fertilization are considerable, representing an average of 38 percent increase in tissue nitrogen and 26 percent decrease in plant secondary metabolites. Shading has a larger effect on secondary metabolites (52 percent) but not foliar N (Ayres 1993). More recent research provides a caveat, highlighting the importance of metabolite type, and the effects of

fertilization and warming working in concert. Graglia et al. (2001) found that warming increased condensed tannins and decreased hydrolysable tannins in *B. nana* at Toolik, but not at the companion site in Abisko, Sweden. Fertilization and shading generally decreased concentrations (Graglia et al. 2001). Abiotic constraints (namely N:P) provide the rationale for these divergent findings (Kaarlejärvi et al. 2012). The response is therefore multidimensional.

To come full circle, the relative strength of the role of plant defenses in regulating expansion is hotly debated. Recent studies (Dahlgren et al. 2009, Aunapuu et al. 2008) indicate that predators, not plant defenses, prevent runaway consumption of vegetation by herbivores, vindicating HSS. Though the effects of predators may be scale dependent (Fauchald et al. 2017).

1.2.3 Primary consumers and selectivity

The body of vertebrate herbivory research encompasses three general categories: 1) small rodents, 2) large ungulates and 3) avian herbivores. Each group exhibits unique forage preferences, habitat use, and population dynamics (Table 1), therefore having distinctive impacts on local productivity. Studies typically center around one focal species, such as caribou (Bråthen et al. 2007; Post and Pedersen 2008; Olofsson et al. 2009; Post 2013; Kaarlejärvi et al. 2015) or microtine rodents (Batzli and Lesieutre 1991; Johnson et al. 2011), yet it is important to consider the effects of each group given their complementary effects on local vegetation (Ravolainen et al. 2014), in addition to their dichotomous effects that may help keep tundra communities at equilibrium.

Because of their small size and therefore restricted mobility, small herbivores such as Arctic ground squirrels and microtine rodents tend to prefer forage of smaller stature. Arctic ground squirrels are relatively omnivorous but exhibit preferences for herbaceous dicotyledons with high water content, avoiding evergreens and lichens. Forbs and graminoids are important forage for AGS, with forbs comprising roughly 20 to 75% of AGS diets (Batzli and Sobaski 1980, Gillis et al. 2005). Vole and lemming foraging drives inter-annual fluctuations in field-layer

vegetation biomass in the sub-Arctic Abisko region in northernmost Sweden (Olofsson et al. 2012), having the greatest effect on the abundance of dwarf shrubs (<0.3 m) and mosses (Olofsson et al. 2009). Though preferences vary somewhat spatially and by species, they mostly consume monocotyledons and dicotyledons (Batzli and Jung 1980).

Both small rodent groups exhibit some complementary habitat preferences. Arctic ground squirrels prefer dry heath with adequate drainage and rocky outcrops that provide good sightlines. They exhibit high perceived risk and extreme vigilance in continuous shrub habitat, preferring clear sightlines for foraging (Wheeler & Hik 2014, see Chapter 2). Their effects on plant productivity are therefore roughly constrained within burrow habitats, potentially exhibiting the greatest effect on plant competition at the shrub-tundra ecotone. Microtine rodents, namely tundra voles and singing voles, differ in preferred habitats. Tundra voles prefer low and wet habitats (meadows and watertracks) while singing voles prefer slopes and rocky flats, similar to Arctic ground squirrels.

Though activity patterns and population cycling differ amongst Arctic ground squirrels and microtines. Arctic ground squirrels are only active during the growing season and hibernate the remainder of the year (Buck and Barnes 1999). Active year-round, microtine rodent populations cycle with peaks every three to 6 years. Peak populations can reach densities up to 200 ha⁻¹, comprising approximately 67 percent of the small mammal biomass in the Arctic (Bliss et al. 1981). Their effects on local productivity are therefore intermittent.

Large vertebrate herbivores, such as caribou (*Rangifer tarandus*) and muskoxen (*Ovibos moschatus*), favor taller shrubs (>0.3 m) low in plant secondary metabolites (i.e. *Salix spp.*) and also reduce the abundance of lichens (Olofsson et al. 2009). Though, like microtine rodents, herbivory pressures are intermittent in migratory caribou populations. Caribou in North America are transient, migrating twice a year, with herds estimated upwards of 325,000 individuals. When present at high densities, caribou can homogenize the remaining standing crop of these preferred palatable plants, though the same effects are not seen in areas with lower herd densities (Bråthen

et al. 2007). But with herds in decline due to losses of lichens and the expansion of non-edible shrubs, their effects on local productivity may be diminishing (Fauchald et al. 2017).

Non-mammalian herbivores such as snow (greater and lesser; *Chen* spp.), barnacle (*Branta leucopsis*) and pink-footed geese (*Anser brachyrhynchus*) and ptarmigan (rock and willow; *Lagopus* spp.) are powerful agents of change in the Arctic. Geese predominate in wetland habitats and are quite selective, preferentially foraging on high nutrient items such as graminoids and forbs. They are powerful ecosystem engineers, altering nutrient cycling (Sjögersten et al. 2010) and enacting large-scale disturbances (Kerbes et al. 1990). Ptarmigan prefer subalpine, willow thickets and riparian areas and extensively browse on Arctic shrubs, namely feltleaf willow (*Salix alaxensis*). Though typically tolerant to sustained herbivory, studies have confirmed the effect of ptarmigan herbivory in inhibiting vertical growth and reproductions of feltleaf willow (Christie et al. 2014).

1.2.4 Secondary and tertiary consumers

The Arctic is home to several mammalian and avian predators. Mammalian predators include wolves (*Canis lupus*), coyote (*Canis latrans*) foxes (Arctic fox, *Vulpes lagopus*; red fox, *Vulpes vulpes*), grizzly bears (*Ursus arctos*), polar bears (*Ursus maritimus*), weasels (*Mustela* spp.), and wolverine (*Gulo gulo*). Avian predators encompass a variety of raptors, falcons, jaegers, owls, and ravens. Main diets are comprised of mostly small mammals, with some predator populations synchronous with small mammal population cycles (Arctic fox and lemming; Huryn and Hobbie 2012). In the low-productivity Arctic, predators are relatively transient and cover vast ranges (Oksanen et al. 1992), therefore predator pressure is intermittent and patchy.

Though recent Arctic research highlights the increasing role of predators in mediating plant-herbivore interactions (Legagneux et al. 2012). Governing the power of these interactions are higher trophic levels and population cycling, which are thought to be most influential on the

Arctic tundra (Ims and Fuglei 2005). These interactions fluctuate via short-term changes in climate (Forchhammer et al. 2005) but anticipated long-term changes in temperature are expected to cause an increase in the abundance of carnivores, initiating a switch from bottom-up to top-down regulation of herbivores in coming decades (Aunapuu et al. 2008; Legagneux et al. 2014). Though critics find current estimates of climate-induced changes in trophic interactions to be too simplistic, focusing only on the effect of a single climate change variable on an individual species (Rosenblatt and Schmitz 2014). The cumulative effect of multiple climate change variables on dynamic biotic relationships therefore needs further exploration.

1.3 Direct and indirect biotic controls on tundra NPP

1.3.1 Direct effects

Several studies have addressed the direct effects of vertebrate herbivory on direct and indirect feedbacks on aboveground biomass (Chapin et al. 1995) and plant community composition (Pajunen et al. 2012). Effects of herbivory have been assessed at small-scales via experimental manipulations such as manual clipping or exclosures of vertebrate herbivores (Post and Pedersen 2008; Zamin and Grogan 2013; Kaarlejärvi et al. 2015). Herbivory has also been studied at large scales via modeling and remote sensing (Bråthen et al. 2007; Newton et al. 2014; Rickbeil et al. 2015; Fauchald et al. 2017). Herbivory pressures vary, however, with variables such as herbivore selectivity, population density, grazing intensity (e.g., stationary versus migratory populations), and herbivore size in driving the strength of these interactions (Olofsson et al. 2004a; Ravolainen et al. 2014; Christie et al. 2015).

Direct consumption by large herbivores has been documented to keep warming-anticipated increases of shrub biomass in check. While warming experiments have commonly found an increase in the dominance of woody shrubs, grazing by muskoxen and caribou have been shown to significantly reduce total community biomass (Post and Pedersen 2008; Olofsson et al. 2009; Kaarlejärvi et al. 2015), altering plant community structure (Olofsson et al. 2004b)

and promoting greater species richness (Pajunen et al. 2012) at large scales (Bråthen et al. 2007). These studies demonstrate how Arctic herbivores may counteract anticipated warming temperatures and future greening.

Though large herbivores may keep graminoid-dominated ecosystems as a growing season carbon sink, this may have implications for the nearly 50% of global terrestrial soil organic carbon currently locked in Arctic permafrost. Comparatively, shrub-dominated systems represent a much stronger sink of atmospheric C (150 g C m^{-2} ; Valentini et al. 2000) than non-shrub-dominated systems like the tussock and wet sedge tundra (50 g C m^{-2} ; Loranty et al. 2011). Exclosures of large herbivores over just two consecutive growing seasons caused a nearly three-fold increase in net C uptake, indicating rapid sequestration (Cahoon et al. 2012). Removal of shrubs by consumption by large herbivores, or prevention of their expansion in the first place, will therefore limit the magnitude of the Arctic as a terrestrial C sink.

Yet small herbivores may counteract the effects of large herbivores via their opposing forage preferences and patterns, inadvertently promoting the amplification of shrubs via the removal of non-shrub competitors. While small herbivores may be dismissed for their diminutive size and relative contribution to shaping Arctic plant communities, their collective herbivory can effect large-scale changes in aboveground biomass, as seen in vole and lemming foraging observed from space (Olofsson et al. 2012). Their selective foraging may have an even more drastic effect on vegetation than transient feeding by caribou (Olofsson et al. 2004a). They have been documented to alter competitive interactions between plants. In an exclosure study by Gough et al. (2007, 2012), researchers found the biomass of *Betula nana exilis* to be greater outside exclosures, indicating that herbivores may stimulate the growth of deciduous shrubs via the removal from competition of more palatable, preferred species (*Eriophorum vaginatum*).

Yet the overall strength of these direct plant-herbivore interactions depends on herbivore density, temporal forage intensity (Augustine and McNaughton 1998) and complementary effects by both small and large herbivores (Olofsson et al. 2004a; Ravolainen et al. 2014). A review by

Augustine and McNaughton (1998) found that ungulate effects on plant communities exhibit an intermittent temporal pattern, closely linked to migration, leading to the increase of palatable species when not under selection by ungulate herbivores. A complementary study of both small and large herbivores on the mediation of *Salix* spp., confirming the dual impact of both reindeer and rodents in eliminating shrub recruits, similarly found that the extent of mediation was contingent on rodent population densities (Ravolainen et al. 2014). Therefore the degree of which herbivores can regulate future shrub expansion is conditional on herbivory intensity and the influence of higher trophic levels.

1.3.2 Indirect effects

Indirect feedbacks by Arctic herbivores on ecosystem productivity are gaining attention, with a wealth of information available in low-latitude systems providing a helpful foundation. To date, feedbacks have been documented via selective foraging and subsequent effects on leaf litter quality (Sirotnak and Huntly 2000; Kaarlejärvi et al. 2012), urine, fecal, and carcass deposition (Mckendrick et al. 1980; Danell et al. 1994), and via changes in biogeochemical and microbial soil variables through bioturbation (Price 1971; Wilske et al. 2015).

Selective herbivory and feedbacks on leaf litter quality – Vertebrate herbivores have been shown to alter plant chemistry and litter decomposition rates (Sirotnak and Huntly 2000; Olofsson and Oksanen 2002; Stark et al. 2007). In a litterbag experiment studying the effects of herbivory on litter decomposition rates, researchers found an improvement in litter quality via the selective herbivory of species with more-readily decomposing litter. Litter quality was additionally improved by defoliation, increasing N content and lowering its C/N ratio (Olofsson and Oksanen 2002). Although alternate studies have shown that selective feeding on plants with high nutrient content enables the dominance of plant with low nutritional quality, therefore low litter quality (Pastor 1993).

Unlike the low-quality litter of evergreen shrubs, which are high in lignans, secondary metabolites and slow to decompose, deciduous shrub dominance will increase litter inputs and quality and accelerate nutrient cycling (Chapin et al. 2012), producing more litter than other dominant tundra species. Higher nutrient quality will increase plant productivity and biomass, providing a positive feedback on future litter quality and nutrient cycling. Though deciduous litter is largely recalcitrant and might contribute to reductions in the mineralization rates (Cornelissen et al. 2007). Overall, the net effect will be largely temporal (Sirotnak and Huntly 2000). Researchers confirmed the effect of sustained herbivory as the mechanism for changes in litter quality. At vole population peaks, voles increase nitrogen mobility. Yet over longer periods, they found decreases in nitrogen mobilization caused by a reduction in plant litter quality via the selective foraging of plants higher in nitrogen.

Urine, fecal, and carcass deposition – Vertebrate mammals can influence nutrient cycling through direct fertilization via urine and fecal elimination (Mckendrick et al. 1980; Hik et al. 1991; Van Der Wal et al. 2004; Barthelemy et al. 2015) and via decaying carcasses of both herbivores (Danell et al. 2002) and carnivore prey items (Bump et al. 2009b; Gharajehdaghpour et al. 2016). Through analysis of soils cores, studies have confirmed the heterogeneous creation of nutrient-rich patches via the deposition of urine, feces and decaying carcasses. McKendrick et al. (1980) found nitrogen and phosphorous deposition to be greater near Arctic ground squirrel burrow entrances than in nearby, undisturbed plots. Clark et al. (2011) found that Hispid cotton rats deposited $3.7 \text{ kg N ha}^{-1} \text{ year}^{-1}$, comparable to the annual nitrogen deposition of large herbivores occupying the same system (Clark et al. 2011). Though the relative contribution of feces to nutrient fluxes is contingent on the timing of degradation, which is based on the size of the herbivore. Vole fecal decomposition and assimilation into soils is estimated to take a few days (Pastor et al. 1996), whereas larger herbivores take longer.

This type of fertilization (through urine and feces) has been shown to transfer between animals and their preferred forage species (Sjögersten et al. 2010), having profound effects on net

aboveground primary production thanks to a variety of herbivores, including snow geese (Hik et al. 1991), reindeer (Barthelemy et al. 2015), and predators such as Arctic fox (Bruun et al. 2005; Gharajehdaghpour et al. 2016). These fertilization effects may last up to three years (Bump et al. 2009a) in tundra ecosystems (Van Der Wal et al. 2004).

Edaphic properties, bioturbation and microbial stimulation – With expanding shrubs benefitting from higher soil temperatures with low moisture (Tape et al. 2012), vertebrate herbivores may be key to priming soils. The main physical characteristic of Arctic ground squirrel habitat is coarse soil, which has lower water-holding capacity, providing adequate drainage for burrowing and denning (Walker et al. 2010). Coarse soils are also warmer because solar radiation penetrates deeper into their active layer. Burrows often exhibit greater thaw depth and higher temperatures (Walker et al. 2010). Edaphic properties found in and around ground squirrel burrows are thanks in part to their impressive geomorphic effects. Price et al. (1971) estimated that squirrels excavate approximately 145 kgs of material per acre. This excavation and bioturbation can contribute to soil formation (see earlier) and potentially to alterations in biogeochemistry, and ecosystem function. While the direct effects of herbivores on soil variables (SOC and N turnover) have not yet been confirmed, it is estimated that the effects are contingent on fluctuations in populations (voles; Wilske et al. 2015)

Cascading further, warmer soils stimulate microbial respiration and N mineralization. Insulation and warming of soils both deepens the active layer, exposing new SOM to decomposition by microbes therefore increasing respiration (Nowinski et al. 2010). Secondly, warming stimulates microbial enzyme kinetics, also increasing respiration (German et al. 2012). Through the aeration and warming of soils by burrowing animals (Walker et al. 2010), herbivory of vegetative insulation against thermal warming (Van der Wal et al. 2001) and changes in leaf litter abundance and quality (Peschel et al. 2015), herbivores may indirectly stimulate microbial decomposition. Thus indirect top-down effects of herbivores on soil microbial communities may foster higher rates of nutrient mineralization and losses of C to the atmosphere.

1.4 Implications of global change

1.4.1 Plant functional group plasticity under simulated climate change scenarios

Sustained low pan-Arctic temperatures and short growing seasons provide little opportunity for plant decomposition and chemical weathering, causing limited soil nutrient availability. Controlled nitrogen and phosphorus additions increased vascular plant biomass production, confirming nutrient limitation in the Arctic inhibits plant growth (Chapin et al. 1995; Bret-Harte et al. 2001). Warming experiments confirm species-specific advantages to anticipated surges in Arctic temperatures.

Simulated warming experiments confirm that climate change will produce competitive dominants. A meta-analysis of 61 Arctic experimental warming studies showed that deciduous shrubs are more responsive to warming than evergreen, with an increase in low-growing and deciduous shrubs (Elmendorf et al. 2012). Fertilization studies have similarly confirmed the competitive advantage of deciduous shrubs, specifically of *Betula* spp. over other woody shrub species in response to nitrogen additions representative of future climate change scenarios. Chapin et al. (1995) found that a 9-year fertilization experiment reduced species diversity 30-50%, resulting in the strong dominance of *Betula nana*. Bret-Harte et al. (2001) investigated growth rates and resource allocation of three co-dominant Arctic shrubs (*Betula nana exilis*, *Salix pulchra*, and *Ledum palustre*) in response to long-term nitrogen and phosphorous fertilization and warming treatments. They found that fertilization increased *Betula* ramet biomass significantly more than *Salix* or *Ledum*. *Salix* and *Ledum* total community biomass decreased during the treatment. Similarly, *Betula glandulosa* responds positively to both warming and nutrient additions. Though few experiments have been conducted in the dry heath (Gough et al. 2002; Graglia et al. 1997; Grellman 2002).

Soil nutrient heterogeneity is common in nutrient-poor ecosystems, causing variations in plant foraging mechanisms, ultimately leading to competitive advantages among plants able to exploit nutrient-rich patches (Robinson et al. 1999). But little is known about the allocation of

root biomass to nutrient-rich microsites amongst Arctic shrub species. To date, resource partitioning and resource-based niches explains much of the plant species diversity within the Arctic tundra. Dominant species utilize more abundant forms of nitrogen (organic and inorganic forms of N) whereas less productive species utilize less abundant forms (nitrate). Although evergreen (*Ledum palustre*) and deciduous (*Betula nana*) shrubs both utilize the same form of nitrogen (ammonium), their co-dominance is explained by differences in the timing and depth of uptake, with *Betula* spp. accessing deeper forms and later (McKane et al. 2002). While current loads of atmospheric N deposition in nitrogen the Arctic is low (<2-3 kg N ha⁻¹yr⁻¹; (Bobbink et al. 2010)), global climate models project the largest impact in biomes that are nutrient-limited, namely boreal, Arctic and alpine regions by the end of the century (Sala 2000), thus amplifying the proliferation of these competitive dominants.

Overall, the growth of less preferred and less palatable species will be detrimental to important herbivores such as larger mammals (caribou and muskoxen) and the willow ptarmigan that rely on species shrub species such as *Salix* spp. or understory vegetation such as lichen. As mentioned earlier, caribou herds are in decline due to losses of lichens and the expansion of non-edible shrubs. Their effects on local productivity are therefore diminishing (Fauchald et al. 2017). This may have important ramifications on ecosystem processes, as noted earlier (Section 1.3.1).

1.4.2 Changes in trophic interactions

The low productivity Arctic tundra is a bitrophic-level food web, composed of primary producers and herbivores, with transient carnivores. In line with the EEH, as long-term changes in temperature are expected to cause an increase in NPP, the additional biomass generated can support a higher number of trophic levels or pass NPP to resource-limited herbivores (Oksanen 1992). This resultant increase in the abundance of Arctic predators will likely cause a switch from bottom-up to top-down regulation of herbivores in coming decades, likely having the greatest effect on small herbivores (Aunapuu et al. 2008; Legagneux et al. 2014).

Increases in predator pressure can have both direct and indirect effects on Arctic herbivore populations, having cascading effects on ecosystem processes. Studies have confirmed the negative effects of the predator pressure on the population structure and reproductive success of Arctic ground squirrels (Hubbs and Boonstra 1997; Wheeler and Hik 2014a) and microtine rodents (Batzli and Jung 1980), classically having subsequent cyclical feedbacks on predator populations (Elton 1924; Ims et al. 2013). Increases in aboveground biomass compound the effects of predation, Arctic ground squirrels have become locally extirpated when dense cover prevents predator detection in Yukon boreal forest (Donker and Krebs 2012). In areas with the highest perceived risk, energetically profitable items will be favored over plants high in secondary metabolites, thus leading to increases in woody vegetation high in antibrowsing defenses (Bryant et al. 2014).

Though the effects of predation are thought to be less pronounced in small mammal populations that are active year-round. With expected increases in winter precipitation (Serreze et al. 2000), small mammals may benefit from added cover and insulation, leading to greater population densities. But any pulses in reproductive success can be offset by shortened Arctic winters and increases in the frequency and duration of winter warming events (Graham et al. 2017). Winters shortened by just a few days dramatically lower survival rates of voles, for example (Aars and Ims 2002).

These amplified changes in herbivore biomass will likely be detrimental to specialist predators that cannot exploit a range of prey items. Decreases in specialist predator populations have already been documented in Fennoscandia (Arctic fox and snowy owl), suspected as an indirect result of climate change (Ims and Fuglei 2005). Changes will also alter predation pressures by means of prey switching (Werner et al. 2016).

1.5 Conclusions

1.5.1 Future considerations

In concert, climate change is suspected to drastically alter aboveground biomass, herbivore densities and predation pressures, causing subsequent effects on ecosystem processes. Though four common themes arise within the body of plant-herbivore research that highlight particular knowledge gaps. Future research should focus on 1) the effects of intermittent temporal patterns associated with herbivore population migration/cycling on plant community dynamics 2) the effects of climate change and herbivory pressure on the rate of expansion of shrubs high in plant secondary metabolites 3) the effects of climate change and dual herbivory pressure (both large and small herbivores (Ravolainen et al. 2014)) across a broader range of habitat types (dry heath) and 4) an analysis of local impacts (direct and indirect) at broader scales via the use of satellite imagery.

The use of satellite imagery is gaining traction in Arctic research, with advances in technology and the accessibility of data. Repeat photography (Sturm et al. 2001; Tape et al. 2006; Tape et al. 2012) and seasonal fluctuations in Normalized Difference Vegetative Index (NDVI; Tape et al. 2012, Pettorelli et al. 2005) have been used to monitor Arctic shrub amplification and advancement, while only a few studies have analyzed the regional effects plant-herbivore interactions (Forchhammer et al. 2005; Bråthen et al. 2007). Though new collaborative programs are incorporating airborne and satellite imagery to enable widespread monitoring, such as with the Arctic-Boreal Vulnerability Experiment (ABoVE; <https://above.nasa.gov>).

Collaborative roadmaps and protocols are also in the works. Protocols for assessing the spread of vegetation have been suggested by the Alaska Geobotany Center to help promote the consistency of surveying, archiving and classifying tundra plot data (Walker et al. 2016; <http://www.geobotany.uaf.edu>). Cooperative efforts for monitoring and reporting plant-herbivore interactions are also gaining traction (Barrio et al. 2016), with the formation of groups such as The Herbivory Network (<http://herbivory.biology.ualberta.ca>). Yet collaborations between both disciplines (vegetation and herbivory) are encouraged to improve the conceptualization of critical

top-down and bottom-up controls on key ecosystem processes. Such collaborations are necessary for best informing global climate models.

1.5.2 Scope of thesis

Based on the framework developed above, my thesis investigates the role of Arctic ground squirrels in shaping tundra vegetation (studied near Toolik Field Station on the North Slope of Alaska). Arctic ground squirrels are ecosystem engineers with Holarctic distribution, likely altering local plant communities (Barker and DeRocher 2010) and modifying edaphic properties in and around burrow systems (Batzli and Sobaski 1980; Price 1971). In Chapter 2, I analyze the foraging behaviors of the Arctic ground squirrel using giving-up densities (GUDs) in experimental food patches to estimate foraging intensity along a tundra-shrub gradient and their potential effect on local shrub expansion. In Chapter 3, examine the local effects of AGS as regional patterns using known locations of Arctic ground burrows (N=37). I explore the relationship between Arctic ground squirrel habitat selection and patterns in shrub biomass, height, and NDVI. Additionally, using total organic N and isotopic analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of both plant and soil samples taken within burrow systems and in adjacent undisturbed controls, I quantify the effect of Arctic ground squirrel nitrogen deposition on the collective, regional-scale promotion of local productivity.

1.6 References

- Aars J, Ims RA. 2002. Intrinsic and climatic determinants of population demography: the winter dynamics of tundra voles. *Ecology* 83:3449. doi: 10.2307/3072093
- Augustine DJ, McNaughton SJ (1998) Ungulate effects on the functional species composition of plant communities: Herbivore selectivity and plant tolerance. *J Wildl Manage* 62:1165. doi: 10.2307/3801981
- Aunapuu M, Dahlgren J, Oksanen T, et al (2008) Spatial patterns and dynamic responses of arctic food webs corroborate the exploitation ecosystems hypothesis (EEH). *Am Nat* 171:249–262. doi: 10.1086/524951
- Ayres MP (1993) Plant defense, herbivory, and climate change. *Biot Interact Glob Chang* 75:75–94. doi: 10.1016/S0169-5347(97)01078-1
- Barrio IC, Hik DS, Jónsdóttir IS, et al (2016) Herbivory Network: An international, collaborative effort to study herbivory in Arctic and alpine ecosystems. *Polar Sci* 10:297–302. doi: 10.1016/j.polar.2016.03.001
- Barthelemy H, Stark S, Olofsson J (2015) Strong responses of subarctic plant communities to long-term reindeer feces manipulation. *Ecosystems* 18:740–751. doi: 10.1007/s10021-015-9856-y
- Batzli GO, Jung H-JG (1980) Nutritional ecology of microtine rodents: Resource utilization near Atkasook, Alaska. *Arct Alp Res* 12:483. doi: 10.2307/1550496
- Batzli GO, Lesieutre C (1991) The influence of high quality food on habitat use by Arctic microtine rodents. *Oikos* 60:299. doi: 10.2307/3545071
- Batzli GO, Sobaski ST (1980) Distribution, abundance, and foraging patterns of ground squirrels near Atkasook, Alaska. *Arct Alp Res* 12:501–510.
- Bliss LC, Heal OW, Moore JJ, Programme IB (1981) *Tundra ecosystems: A comparative analysis*. CUP Archive.
- Blok D, Heijmans MMPD, Schaepman-Strub G, et al (2010) Shrub expansion may reduce summer permafrost thaw in Siberian tundra. *Glob Chang Biol* 16:1296–1305. doi: 10.1111/j.1365-2486.2009.02110.x
- Bobbink R, Hicks K, Galloway J, et al (2010) Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecol Appl* 20:30–59. doi: 10.1890/08-1140.1
- Bråthen KA, Ims RA, Yoccoz NG, et al (2007) Induced shift in ecosystem productivity? Extensive scale effects of abundant large herbivores. *Ecosystems* 10:773–789. doi: 10.1007/s10021-007-9058-3
- Bret-Harte MS, Shaver GR, Zoerner JP, et al (2001) Developmental plasticity allows *betula nana* to dominate tundra subjected to an altered environment. *Ecology* 82:18–32. doi: 10.1890/0012-9658(2001)082[0018:DPABNT]2.0.CO;2

- Bruun HH, Österdahl S, Moen J, Angerbjörn A (2005) Distinct patterns in alpine vegetation around dens of the Arctic fox. *Ecography* 28:81–87. doi: 10.1111/j.0906-7590.2005.04033.x
- Bryant JP, Chapin, F Stuart I, Klein DR (1983) Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* 40:357–368. doi: 10.2307/3544308
- Bryant JP, Joly K, Chapin FS, et al (2014) Can antibrowsing defense regulate the spread of woody vegetation in arctic tundra? *Ecography (Cop)* 37:204–211. doi: 10.1111/j.1600-0587.2013.00436.x
- Bryant JP, Provenza FD, Pastor J, et al (1991) Interactions between woody plants and browsing mammals mediated by secondary metabolites. *Annu Rev Ecol Syst* 22:431–446. doi: 10.1146/annurev.es.22.110191.002243
- Buck CL, Barnes BM (1999) Annual Cycle of Body Composition and Hibernation in Free-living Arctic Ground Squirrels. *J Mammal* 80:p430. doi: 10.2307/1383291
- Bump JK, Peterson RO, Vucetich JA (2009a) Wolves modulate soil nutrient heterogeneity and foliar nitrogen by configuring the distribution of ungulate carcasses. *Ecology* 90:3159–3167. doi: 10.1890/09-0292.1
- Bump JK, Webster CR, Vucetich JA, et al (2009b) Ungulate carcasses perforate ecological filters and create biogeochemical hotspots in forest herbaceous layers allowing trees a competitive advantage. *Ecosystems* 12:996–1007. doi: 10.1007/s10021-009-9274-0
- Cahoon SMP, Sullivan PF, Post E, Welker JM (2012) Large herbivores limit CO₂ uptake and suppress carbon cycle responses to warming in West Greenland. *Glob Chang Biol* 18:469–479. doi: 10.1111/j.1365-2486.2011.02528.x
- Chapin FS, Jefferies RL, Reynolds JF, et al (2012) Arctic ecosystems in a changing climate: An ecophysiological perspective. Academic Press
- Chapin FS, Shaver GR (1996) Physiological and growth responses of arctic plants to a field experiment simulating climatic change. *Ecology* 77:822–840. doi: 10.2307/2265504
- Chapin FS, Shaver GR, Giblin AE, et al (1995) Responses of Arctic tundra to experimental and observed changes in climate. *Ecology* 76:694–711. doi: 10.2307/1939337
- Christie KS, Bryant JP, Gough L, et al (2015) The role of vertebrate herbivores in regulating shrub expansion in the Arctic: A synthesis. *Bioscience* 65:1123–1133. doi: 10.1093/biosci/biv137
- Christie KS, Ruess RW, Lindberg MS, Mulder CP (2014) Herbivores influence the growth, reproduction, and morphology of a widespread arctic willow. *PLoS One* 9:e101716. doi:10.1371/journal.pone.0101716. doi: 10.1371/journal.pone.0101716
- Clark JE, Hellgren EC, Parsons JL, et al (2011) Nitrogen outputs from fecal and urine deposition implications for nitrogen cycling of small mammals. *Ecology* 144:447–455.
- Cornelissen JHC, Van Bodegom PM, Aerts R, et al (2007) Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. *Ecol Lett*

10:619–627. doi: 10.1111/j.1461-0248.2007.01051.x

- Danell K, Bergström R, Edenius L (1994) Effects of large mammalian browsers on architecture, biomass, and nutrients of woody plants. *Source J Mammal* 75:833–844. doi: 10.2307/1382465
- Danell K, Berteaux D, Bråthen KA (2002) Effect of muskox carcasses on nitrogen concentration in tundra vegetation. *Arctic* 55:389–392. doi: 10.14430/arctic723
- DeAngelis DL, Bryant JP, Liu R, et al (2015) A plant toxin mediated mechanism for the lag in snowshoe hare population recovery following cyclic declines. *Oikos* n/a-n/a. doi: 10.1111/oik.01671
- Donker SA, Krebs CJ (2012) Evidence for sourcesink dynamics in a regional population of arctic ground squirrels (*Urocitellus parryii plesius*). *Wildl Res* 39:163–170. doi: 10.1071/WR11167
- Ehrlich PR, Birch LC (1967) The “Balance of Nature” and “Population Control.” *Am Nat* 101:97–107. doi: 10.1086/282477
- Elmendorf SC, Henry GHR, Hollister RD, et al (2012) Global assessment of experimental climate warming on tundra vegetation: Heterogeneity over space and time. *Ecol Lett* 15:164–175. doi: 10.1111/j.1461-0248.2011.01716.x
- Elton C (1927) *Animal Ecology*. *Anim Ecol* 207. doi: 10.1098/rstb.2010.0107
- Elton CS (1924) Periodic fluctuations in the numbers of animals: Their causes and effects. *Br J Exp Biol* 2:119–163.
- Fauchald P, Park T, Tømmervik H, et al (2017) Arctic greening from warming promotes declines in caribou populations. *Sci. Adv.* 3:65–69.
- Forchhammer MC, Post E, Berg TBG, et al (2005) Local-scale and short-term herbivore-plant spatial dynamics reflect influences of large-scale climate. *Ecology* 86:2644–2651. doi: 10.1890/04-1281
- Fretwell SD (1977) The regulation of plant communities by the food chains exploiting them. *Perspect Biol Med* 20:169–185. doi: 10.1353/pbm.1977.0087
- German DP, Marcelo KRB, Stone MM, Allison SD (2012) The Michaelis-Menten kinetics of soil extracellular enzymes in response to temperature: a cross-latitudinal study. *Glob Chang Biol* 18:1468–1479. doi: 10.1111/j.1365-2486.2011.02615.x
- Gharajehdaghypour T, Roth JD, Fafard PM, Markham JH (2016) Arctic foxes as ecosystem engineers: increased soil nutrients lead to increased plant productivity on fox dens. *Sci Rep* 6:24020. doi: 10.1038/srep24020
- Gough L, Moore JC, Shaver GR, et al (2012) Above- and belowground responses of arctic tundra ecosystems to altered soil nutrients and mammalian herbivory. *Ecology* 93:1683–1694. doi: 10.1890/11-1631.1
- Gough L, Ramsey EA, Johnson DR (2007) Plant-herbivore interactions in Alaskan arctic tundra

change with soil nutrient availability. *Oikos* 116:407–418. doi: 10.1111/j.0030-1299.2007.15449.x

- Gough L, Wookey PA, Shaver GR (2002) Dry heath Arctic tundra responses to long-term nutrient and light manipulation. *Arctic, Antarct Alp Res* 34:211–218.
- Graglia E, Julkunen-Tiitto R, Shaver GR, et al (2001) Environmental control and intersite variations of phenolics in *Betula nana* in tundra ecosystems. *New Phytol* 151:227–236. doi: 10.1046/j.1469-8137.2001.00149.x
- Graham RM, Cohen L, Petty AA, et al (2017) Increasing frequency and duration of Arctic winter warming events. *Geophys Res Lett* 44:6974–6983. doi: 10.1002/2017GL073395
- Heskel M, Greaves H, Kornfeld A, et al (2013) Differential physiological responses to environmental change promote woody shrub expansion. *Ecol Evol* 3:1149–1162. doi: 10.1002/ece3.525
- Hik DS, Sadul HA, Jefferies RL (1991) Effects of the timing of multiple grazings by geese on net above-ground primary production of swards of *Puccinellia phryganodes*. *J Ecol* 79:715–730.
- Hubbs H, Boonstra R (1997) Population limitation in Arctic ground squirrels: Effects of food and predation. *J Anim Ecol* 66:527–541.
- Huryn AD, Hobbie JE (2012) *Land of extremes: A natural history of the North Slope of Arctic Alaska*. University of Alaska Press.
- Ims RA, Fuglei E (2005) Trophic interaction cycles in tundra ecosystems and the impact of climate change. *Bioscience* 55:311. doi: 10.1641/0006-3568(2005)055[0311:TICITE]2.0.CO;2
- Ims RA, Henden J-A, Thingnes A V, Killengreen ST (2013) Indirect food web interactions mediated by predator-rodent dynamics: relative roles of lemmings and voles. *Biol Lett* 9:20130802. doi: 10.1098/rsbl.2013.0802
- Johnson DR, Lara MJ, Shaver GR, et al (2011) Exclusion of brown lemmings reduces vascular plant cover and biomass in Arctic coastal tundra: resampling of a 50 + year herbivore exclosure experiment near Barrow, Alaska. *Environ Res Lett* 6:45507. doi: 10.1088/1748-9326/6/4/045507
- Ju J, Masek JG (2016) The vegetation greenness trend in Canada and US Alaska from 1984-2012 Landsat data. *Remote Sens Environ* 176:1–16. doi: 10.1016/j.rse.2016.01.001
- Jung HJG, Batzli GO, Seigler DS (1979) Patterns in the phytochemistry of arctic plants. *Biochem Syst Ecol* 7:203–209.
- Kaarlejärvi E, Baxter R, Hofgaard A, et al (2012) Effects of warming on shrub abundance and chemistry drive ecosystem-level changes in a forest–tundra ecotone. *Ecosystems* 15:1219–1233. doi: 10.1007/s10021-012-9580-9
- Kaarlejärvi E, Hoset KS, Olofsson J (2015) Mammalian herbivores confer resilience of Arctic shrub-dominated ecosystems to changing climate. *Glob Chang Biol* 21:3379–88. doi:

10.1111/gcb.12970

- Kerbes RH, Kotanen PM, Jefferies RL (1990) Destruction of wetland habitats by Lesser Snow Geese: a keystone species on the West Coast of Hudson Bay. *J Appl Ecol* 27:242–258. doi: 10.2307/2403582
- Krebs CJ, Danell K, Angerbjörn A, et al (2003) Terrestrial trophic dynamics in the Canadian Arctic. *Can J Zool* 81:827–843. doi: 10.1139/z03-061
- Lachenbruch AH, Marshall BV (1986) Changing climate: geothermal evidence from permafrost in the alaskan arctic. *Science* 234:689–696. doi: 10.1126/science.234.4777.689
- Lachenbruch AH, Sass JH, Marshall BV, Moses TH (1982) Permafrost, heat flow, and the geothermal regime at Prudhoe Bay, Alaska. *J Geophys Res* 87:9301. doi: 10.1029/JB087iB11p09301
- Legagneux P, Gauthier G, Berteaux D, et al (2012) Disentangling trophic relationships in a High Arctic tundra ecosystem through food web modeling. *Ecology* 93:1707–1716. doi: 10.1890/11-1973.1
- Legagneux P, Gauthier G, Lecomte N, et al (2014) Arctic ecosystem structure and functioning shaped by climate and herbivore body size. *Nat Clim Chang* E2168:1–5. doi: 10.1038/NCLIMATE2168
- Lindeman RL (1942) The trophic dynamics aspect of ecology. *Ecology* 23:399–418. doi: 10.1017/CBO9781107415324.004
- Loranty MM, Goetz SJ (2012) Shrub expansion and climate feedbacks in Arctic tundra. *Environ Res Lett* 7:11005. doi: 10.1088/1748-9326/7/1/011005
- Loranty MM, Goetz SJ, Rastetter EB, et al (2011) Scaling an Instantaneous Model of Tundra NEE to the Arctic Landscape. *Ecosystems* 14:76–93. doi: 10.1007/s10021-010-9396-4
- McKane RB, Johnson LC, Shaver GR, et al (2002) Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature* 415:68–71. doi: 10.1038/415068a
- Mckendrick JD, Batzli GO, Everett KR, et al (1980) Some effects of mammalian herbivores and fertilization on tundra soils and vegetation. *Arct Alp Res Arct and Alpine Res* 12:565–578. doi: 10.2307/1550501
- Mcaughton SJ (1983) Compensatory plant growth as a response to herbivory. *OIKOS* 40:329–336.
- Murdoch WW (1966) “Community Structure, Population Control, and Competition” A Critique. *Am Nat* 100:219–226. doi: 10.2307/2459479
- Myers-Smith IH, Elmendorf SC, Beck PSA, et al (2015) Climate sensitivity of shrub growth across the tundra biome. *Nat Clim Chang* 5:887–891. doi: 10.1038/nclimate2697
- Myers-Smith IH, Forbes BC, Wilmking M, et al (2011) Shrub expansion in tundra ecosystems:

dynamics, impacts and research priorities. *Environ Res Lett* 6:45509. doi: 10.1088/1748-9326/6/4/045509

Natali SM, Schuur E a. G, Trucco C, et al (2011) Effects of experimental warming of air, soil and permafrost on carbon balance in Alaskan tundra. *Glob Chang Biol* 17:1394–1407. doi: 10.1111/j.1365-2486.2010.02303.x

Newton EJ, Pond BA, Brown GS, et al (2014) Remote sensing reveals long-term effects of caribou on tundra vegetation. *Polar Biol* 37:715–725. doi: 10.1007/s00300-014-1472-3

Nowinski NS, Taneva L, Trumbore SE, Welker JM (2010) Decomposition of old organic matter as a result of deeper active layers in a snow depth manipulation experiment. *Oecologia* 163:785–92. doi: 10.1007/s00442-009-1556-x

Oksanen L (1992) Evolution of exploitation ecosystems I. Predation, foraging ecology and population dynamics in herbivores. *Evol Ecol* 6:15–33. doi: 10.1007/BF02285331

Oksanen L (1990) Predation, herbivory, and plant strategies along gradients of primary productivity. *Perspect. plant Compet.* pp 445–474

Oksanen L, Fretwell SD, Arruda J, Niemela P (1981) Exploitation Ecosystems in Gradients of Primary Productivity. *Am Nat* 118:240–261. doi: 10.1086/283817

Oksanen L, Oksanen T (2000) The logic and realism of the hypothesis of exploitation ecosystems. *Am Nat* 155:703–723. doi: 10.1086/303354

Oksanen T, Oksanen L, Norberg M (1992) Habitat use of small mustelids in north Fennoscandiantundra: a test of the hypothesis of patchy exploitation ecosystems. *Ecography* 152:237–244.

Olofsson J, Hulme PE, Oksanen L, Suominen O (2004a) Importance of large and small mammalian herbivores for the plant community structure in the forest tundra ecotone. *Oikos* 106:324–334. doi: 10.1111/j.0030-1299.2004.13224.x

Olofsson J, Oksanen L (2002) Role of litter decomposition for the increased primary production in areas heavily grazed by reindeer: a litterbag experiment. *Oikos* 96:507–515. doi: 10.1034/j.1600-0706.2002.960312.x

Olofsson J, Oksanen L, Callaghan T, et al (2009) Herbivores inhibit climate-driven shrub expansion on the tundra. *Glob Chang Biol* 15:2681–2693. doi: 10.1111/j.1365-2486.2009.01935.x

Olofsson J, Stark S, Oksanen L (2004b) Reindeer influence on ecosystem processes in the tundra. *Oikos* 105:386–396. doi: 10.1111/j.0030-1299.2004.13048.x

Olofsson J, Tømmervik H, Callaghan T V. (2012) Vole and lemming activity observed from space. *Nat Clim Chang* 2:880–883. doi: 10.1038/nclimate1537

Paige KN, Whitham TG (1987) Overcompensation in response to mammalian herbivory: The advantage of being eaten. *Am Nat* 129:407. doi: 10.1086/284645

Pajunen A, Virtanen R, Roininen H (2012) Browsing-mediated shrub canopy changes drive

- composition and species richness in forest-tundra ecosystems. *Oikos* 121:1544–1552. doi: 10.1111/j.1600-0706.2011.20115.x
- Pastor J, Dewey B, Christian DP (1996) Carbon and nutrient mineralization and fungal spore composition of fecal pellets from voles in Minnesota. *Ecography* 19:52–61. doi: 10.1111/J.1600-0587.1996.Tb00154.X
- Pearson RG, Phillips SJ, Loranty MM, et al (2013) Shifts in Arctic vegetation and associated feedbacks under climate change. *Nat Clim Chang* 3:673–677. doi: 10.1038/nclimate1858
- Peschel AR, Zak DR, Cline LC, Freedman Z (2015) Elk, sagebrush, and saprotrophs: Indirect top-down control on microbial community composition and function. *Ecology* 96:2383–2393. doi: 10.1890/15-0164.1
- Pettorelli N, Vik JO, Mysterud A, et al (2005) Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends Ecol Evol* 20:503–510. doi: 10.1016/j.tree.2005.05.011
- Post E (2013) Erosion of community diversity and stability by herbivore removal under warming. *Proceedings Biol Sci* 280:20122722. doi: 10.1098/rspb.2012.2722
- Post E, Forchhammer MC, Bret-Harte MS, et al (2009) Ecological dynamics across the Arctic associated with recent climate change. *Science* (80). 325-328
- Post E, Pedersen C (2008) Opposing plant community responses to warming with and without herbivores. *Proc Natl Acad Sci U S A* 105:12353–12358. doi: 10.1073/pnas.0802421105
- Price LW (1971) Geomorphic effect of the Arctic ground squirrel in an alpine environment. *Source Geogr Ann Ser A, Phys Geogr* 53:100–106.
- Ravolainen VT, Bråthen KA, Yoccoz NG, et al (2014) Complementary impacts of small rodents and semi-domesticated ungulates limit tall shrub expansion in the tundra. *J Appl Ecol* 51:234–241. doi: 10.1111/1365-2664.12180
- Rickbeil GJM, Coops NC, Adamczewski J (2015) The grazing impacts of four barren ground caribou herds (*Rangifer tarandus groenlandicus*) on their summer ranges: An application of archived remotely sensed vegetation productivity data. *Remote Sens Environ* 164:314–323. doi: 10.1016/j.rse.2015.04.006
- Robinson D, Hodge a., Griffiths BS, Fitter a. H (1999) Plant root proliferation in nitrogen-rich patches confers competitive advantage. *Proc R Soc B Biol Sci* 266:431. doi: 10.1098/rspb.1999.0656
- Rosenblatt AE, Schmitz OJ (2014) Interactive effects of multiple climate change variables on trophic interactions: a meta-analysis. *Clim Chang Responses* 1:8. doi: 10.1186/s40665-014-0008-y
- Sala OE (2000) Global biodiversity scenarios for the year 2100. *Science* 287:1770–1774. doi: 10.1126/science.287.5459.1770
- Serreze MC, Walsh JE, Chapin FS, et al (2000) Observational evidence of recent change in the

northern high-latitude environment. *Clim Change* 46:159–207. doi: 10.1023/a:1005504031923

- Sirotnak JM, Huntly NJ (2000) Direct and indirect effects of herbivores on nitrogen dynamics: Voles in riparian areas. *Ecology* 81:78–87. doi: 10.1890/0012-9658(2000)081[0078:DAIEOH]2.0.CO;2
- Sjögersten S, Kuijper DPJ, van der Wal R, et al (2010) Nitrogen transfer between herbivores and their forage species. *Polar Biol* 33:1195–1203. doi: 10.1007/s00300-010-0809-9
- Stark S, Julkunen-Tiitto R, Kumpula J (2007) Ecological role of reindeer summer browsing in the mountain birch (*Betula pubescens* ssp. *czerepanovii*) forests: Effects on plant defense, litter decomposition, and soil nutrient cycling. *Oecologia* 151:486–498. doi: 10.1007/s00442-006-0593-y
- Sturm M, Racine C, Tape K (2001) Climate change. Increasing shrub abundance in the Arctic. *Nature* 411:546–547. doi: 10.1038/35079180
- Tape K, Sturm M, Racine C (2006) The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Glob Chang Biol* 12:686–702. doi: 10.1111/j.1365-2486.2006.01128.x
- Tape KD, Hallinger M, Welker JM, Ruess RW (2012) Landscape heterogeneity of shrub expansion in Arctic Alaska. *Ecosystems* 15:711–724. doi: 10.1007/s10021-012-9540-4
- Tremblay B, Lévesque E, Boudreau S (2012) Recent expansion of erect shrubs in the Low Arctic: evidence from Eastern Nunavik. *Environ Res Lett* 7:35501. doi: 10.1088/1748-9326/7/3/035501
- Valentini R, Matteucci G, Dolman a J, et al (2000) Respiration as the main determinant of carbon balance in European forests. *Nature* 404:861–865. doi: 10.1038/35009084
- Van Der Wal R, Bardgett RD, Harrison KA, Stien A (2004) Vertebrate herbivores and ecosystem control: Cascading effects of faeces on tundra ecosystems. *Ecography* 27:242–252. doi: 10.1111/j.0906-7590.2004.03688.x
- Van der Wal R, Van Lieshout SMJ, Loonen MJJE (2001) Herbivore impact on moss depth, soil temperature and arctic plant growth. *Polar Biol* 24:29–32. doi: 10.1007/s003000000170
- Walker DA, Daniëls FJA, Alsos I, et al (2016) Circumpolar Arctic vegetation: a hierarchic review and roadmap toward an internationally consistent approach to survey, archive and classify tundra plot data. *Environ Res Lett*. doi: 10.1088/1748-9326/11/5/055005
- Walker MD, Walker DA, Auerbach NA (2010) Plant communities of a tussock tundra landscape in the Brooks Range Foothills, Alaska. *J Veg Sci* 5:843–866. doi: 10.2307/3236198
- Werner JR, Gillis EA, Boonstra R, Krebs CJ (2016) You can hide but you can't run: apparent competition, predator responses and the decline of Arctic ground squirrels in boreal forests of the southwest Yukon. *PeerJ* 4:e2303. doi: 10.7717/peerj.2303
- Wheeler HC, Hik DS (2014a) Influence of shrub canopies on growth rate and pre-hibernation mass of juvenile Arctic ground squirrels. *Wildlife Biol* 20:253–258. doi: 10.2981/wlb.00038

- Wheeler HC, Hik DS (2014b) Giving-up densities and foraging behaviour indicate possible effects of shrub encroachment on arctic ground squirrels. *Anim Behav* 95:1–8. doi: 10.1016/j.anbehav.2014.06.005
- Wilske B, Eccard JA, Zistl-Schlingmann M, et al (2015) Effects of short term bioturbation by common voles on biogeochemical soil variables. *PLoS One* 10:e0126011. doi: 10.1371/journal.pone.0126011
- Zamin TJ, Grogan P (2013) Caribou exclusion during a population low increases deciduous and evergreen shrub species biomass and nitrogen pools in low Arctic tundra. *J Ecol* 101:671–683. doi: 10.1111/1365-2745.12082
- Zimov SA, Chuprynin VI, Oreshko AP, et al (1995) Steppe-tundra transition: A herbivore-driven biome shift at the end of the Pleistocene. *Am Nat* 146:765–794. doi: 10.1086/285824

Table 1.1. Key Arctic herbivores and life histories. ¹Batzli and Sobaski 1980, ²Batzli and Jung 1980, ³Huryn and Hobbie 2012, ⁴Olofsson et al. 2009.

Common name	Scientific name	Location	Habitat	Population dynamics	Preferred forage
Arctic ground squirrel	<i>Spermophilus parryi</i>	Holarctic	Dry, rocky slopes	Stable	Monocots and herbaceous dicots ¹
Tundra vole	<i>Microtus oeconomus</i>	Holarctic	Low-lying wet habitats and riparian areas	Cyclical	Monocots ²
Singing voles	<i>Microtus miurus</i>	Alaska and Canada	Dry, rocky slopes	Cyclical	Monocots and dicots ³
Brown lemming	<i>Lemmus sibericus</i>	Alaska and Canada	Low-lying wet habitats	Cyclical	Monocots and mosses ²
Collared lemming	<i>Dicrostonyx groenlandicus</i>	Alaska, Canada and Greenland	Upland tundra and meadows	Cyclical	Dicots (<i>Salix</i> spp.) ²
Caribou/reindeer	<i>Rangifer tarandus</i>	Holarctic	Transitory	Some subherds in decline	Dicots (<i>Salix</i> spp.) and lichens ⁴
Muskox	<i>Ovibos moschatus</i>	Alaska, Canada and Greenland	Transitory	Stable	Monocots and dicots (<i>Salix</i> spp.) ³
Goose (greater and lesser snow goose, barnacle, pink-footed)	<i>Chen</i> spp. <i>Branta leucopsis</i> <i>Anser brachyrhynchus</i>	Variable	Migratory, generalized mostly riparian areas	Stable	Monocots ³
Ptarmigan (rock and willow)	<i>Lagopus</i> spp.	Holarctic	Subalpine and willow thickets	Stable	Dicots (<i>Salix</i> spp.) ³

2. PATCH USE IN THE ARCTIC GROUND SQUIRREL: IMPLICATIONS FOR PROJECTED SHRUB ENROACHMENT

2.1 Introduction

Warming temperatures in the Arctic degrade permafrost (Lachenbruch et al. 1982; Lachenbruch and Marshall 1986), increase winter precipitation (Serreze et al. 2000), and promote disturbances such as fire (Mack et al. 2011). Degrading permafrost stimulates mineralization of soil organic matter (Natali et al. 2011; Blanc-Betes et al. 2016) releasing nutrients that favor shrubs over mosses and graminoids (Bret-Harte et al. 2001; Sturm et al. 2005; Heskel et al. 2013). Rapid shrub encroachment by birch (*Betula* spp.) and willow (*Salix* spp.; Tape et al. 2006; Elmendorf et al. 2011) increase plant stature and biomass, and northward range expansions (Myers-Smith et al. 2011). Shifts in tundra vegetation (Sturm et al. 2001) modify soil biodiversity (Ricketts et al. 2016), biogeochemical cycling (Chapin et al. 1995), and ecosystem productivity (Schuur et al. 2009). Recent and projected increases in shrub cover can alter the energy and carbon balance of the tundra, as permafrost soils store about half of the total terrestrial carbon reservoir, leading to both positive and negative climate feedbacks at regional and global scales (Euskirchen et al. 2006; Blok et al. 2010; Mishra et al. 2013; Blanc-Betes et al. 2016). Many studies have investigated abiotic factors driving changes in tundra plant communities. How biotic factors may drive tundra plant community changes and biogeochemical fluxes represent a key knowledge gap in ecosystem-climate feedbacks (Schmitz et al. 2014).

Theory suggests herbivores may accelerate or impede vegetation change (Hairston et al. 1960; Slobodkin et al. 1967; Bale et al. 2002). The response of shrubs to increased concentration of CO₂, temperature or snow cover may be influenced by top-down effects of herbivores (e.g., Oksanen et al. 1981). According to the exploitation ecosystem hypothesis (Oksanen et al. 1981, 1990), the Arctic tundra may be a 'two-link ecosystem' composed of primary producers and herbivores (with transient carnivores). Resource-limited herbivores intensely crop vegetation. Increasing primary productivity (NPP) produces increased herbivore biomass. Aboveground

biomass remains relatively unchanged and the higher productivity simply gets passed up the food-chain to the herbivores (Oksanen 1992; Fraser 1998). Herbivory retards vegetation changes or diverts changes towards species less palatable to the herbivore. Conversely, if the tundra is primarily a three-trophic level system, increasing productivity results in increased aboveground biomass. Predators control the herbivores, and plant biomass increases and favors competitive dominants (Hairston et al. 1960; Slobodkin et al. 1967; Oksanen 1990). The inability of herbivores to control the vegetation may accelerate the succession of tundra shrub expansion (Jung et al. 1979; Oksanen 1992).

The expansion of Arctic shrubs has long been recognized (Tape et al. 2006; Blok et al. 2010). The northward advancement of shrubs is attributed to climate (temperature, precipitation) and edaphic factors (nutrient availability, moisture, thaw depth) promoting a patchy distribution of shrubs across the landscape (Tape et al. 2006; Ackerman et al. 2017). A paucity of information about mechanisms generating the landscape-scale patterns of shrub distribution and expansion in the Arctic makes incorporating shrub effects into the climate system difficult. Recent research implicates Arctic herbivores in mediating vegetation structure and change in the Arctic (Myers-Smith et al. 2011; Christie et al. 2015; Myers-Smith et al. 2015; Kaarlejärvi et al. 2015). Caribou foraging promotes taller shrubs (>0.3 m) by reducing the abundance of lichens (Olofsson et al. 2009). Vole and lemming foraging drives inter-annual fluctuations in vegetation biomass in northernmost Sweden (Olofsson et al. 2012), with their greatest impact on the abundance of dwarf shrubs (<0.3 m) and mosses (Olofsson et al. 2009); changes seen in satellite images as reductions in NDVI. Exclosure studies at Toolik Lake, Alaska, found that vole foraging, by preferentially cropping the graminoid *Eriophorum vaginatum*, enhanced the growth of *Betula nana* via competitive release (Gough et al. 2007; Gough et al. 2012). Furthermore, dominant shrubs may experience less herbivory because of high levels of defensive compounds (Bryant et al. 2014). Herbivores may thus alter the function and structure of Arctic plant communities (Brashares et al. 2010), leading to the inhibition or amplification of shrub encroachment.

The Arctic ground squirrel (*Urocitellus parryii plesius*) provides an excellent candidate for investigating conditions by which herbivores may accelerate or impede Arctic greening. With a pan-Arctic distribution and in the tundra (occupying an area of more than 2 million km² in Siberia and the Alaska and Yukon territories), the Arctic ground squirrel exhibits high local abundances, stable populations, and great energy demands during the short growing season. Arctic ground squirrels prefer open sight lines in continuous shrub habitat with high predation risk (Wheeler and Hik 2014). Arctic ground squirrels can become locally extirpated when dense cover prevented predator detection in Yukon boreal forest (Donker and Krebs 2012). As ecosystem engineers (Barker and Derocher 2010), Arctic ground squirrels are prodigious burrowers, altering soil turnover, water infiltration and topography (Price 1971). They browse woody vegetation, including birch and willow and graze a wide diversity of grasses and forbs (Batzli and Sobaski 1980; Mckendrick et al. 1980). In addition to climatic factors, could Arctic ground squirrels simultaneously be suppressors of and victims of shrub encroachment (Wheeler et al. 2015)?

The answer may involve predation risk. Herbivores crop vegetation more thoroughly in areas of low than high predation risk (Huntly 1987). For example, Ogden et al. (1973) noted “grazing halos” centered on spots where sea urchins feel most safe from predatory fish. The intensity with which an herbivore crops vegetation can be measured as giving-up densities (GUDs) in experimental food patches (Brown 1988; Brown and Kotler 2004). The GUDs of mule deer (Altendorf et al. 2001) and Nubian ibex (Hochman and Kotler 2006), herbivores that favor sightlines, increase with distance from forest or shrub cover. Similarly, Arctic ground squirrels may crop all vegetation including woody plants more thoroughly where they have good sightlines and feel safe. Conversely, Arctic ground squirrels may browse less intensively where sightlines are obstructed by topography or existing vegetation. There may be a level of predation risk below which the Arctic ground squirrel inhibits shrub encroachment and above which it facilitates encroachment.

We measured the foraging intensity of Arctic ground squirrels in experimental food patches along tundra vegetation gradients. Intense foraging along the gradient regardless of vegetation type indicates top-down control. Superficial foraging across the gradient indicates bottom-up control. Alternatively, Arctic ground squirrel foraging intensity may vary in response to sightlines, existing shrub standing biomass as measured by NDVI across the gradient. The ecosystem-level effects of herbivores, including the Arctic ground squirrel, may be spatially heterogeneous. Herbivores may exert top-down control on vegetation composition and structure where they feel safe and forage vegetation thoroughly. Conversely, they may exert no effects on vegetation composition and structure where they are fearful and thus forage superficially.

2.2 Materials and Methods

2.2.1 Study site

The study was conducted in late July and early August 2014 at the Toolik Field Station, in the foothills of the Brooks Range on Alaska's North Slope (68°38'N, 149°36'W elevation 760 m a.s.l.). The study site consisted predominantly of gradients of dry heath tundra to moist tussock tundra ecotones. Briefly, vegetation consists of non-tussock forming sedges and grasses, tussock-forming graminoids (*Eriophorum vaginatum*), intermixed with low stature and canopy-forming willow and birch species (*Salix pulchra*, *S. alaxensis*, *Betula nana*). Topographical strata range from elevated granite substrate to low-lying floodplain. The study was restricted to a roughly 500 m² area west of the NSF ITEX dry heath fence on at least 4 identified independent colonies. All Arctic ground squirrel burrows within the study area were identified and mapped via GPS (Trimble Inc., Sunnyvale, CA).

Arctic ground squirrels are widespread semi-fossorial rodents inhabiting Arctic tundra, alpine meadow and boreal forest, preferring sloped terrain with adequate drainage, permafrost depth up to 1 m and sparse vegetation for burrowing. As an obligate hibernator, they are active only 3-5 months of the year, emerging as early as April and remaining active as late as

September. Arctic ground squirrels are opportunistic foragers with a broad diet consisting of plants, fungi, invertebrates, or small vertebrates. Squirrel home ranges vary between 60-230 m² (Carl 1971; Barker and Derocher 2010) yet the majority of foraging typically occurs within 30 m from burrows (Batzli and Sobaski 1980). Diet preference has been documented via caching behavior, stomach contents (Gillis et al. 2005; Zazula et al. 2006) and palatability trials, showing a preference for forbs and deciduous shrubs (*Salix* spp.) with high water content. Forbs and grasses account for 20-75 percent of their overall diet (Batzli and Sobaski 1980). Preferred burrowing habitat includes open and elevated areas with little to no vegetation (Karels and Boonstra 1999; Barker and Derocher 2010). Because foraging intensity varies during the growing season, the experiments were carried out during the post-breeding season in late July and early August, when individuals must gain weight and accumulate an overwinter cache to survive during the long hibernation.

2.2.2 Canopy spectral imaging (NDVI) and shrub biomass and height

We quantified vegetation greenness along six study transects set up to study Arctic ground squirrel foraging (see below) with a dual channel portable spectroradiometer (Unispec-DC, PP Systems International, Inc., Amesbury, MA) that simultaneously measures plot radiance and sky irradiance. The resulting normalized difference vegetation index (NDVI; a proxy of vegetation greenness) of the 1 m² foraging area (foraging tray excluded during measurement) was measured using average reflectance in the red and near infrared spectral regions as described by Anderson-Smith (2013). To determine the relationship between NDVI and plant biomass, we quantified aboveground vegetation biomass (g m⁻²), vegetation height (cm), and NDVI within 20, 70 cm² quadrats located randomly along a gradient of high to low shrub heights. Average vegetation height was determined by summing the maximum height of each shrub within each quadrat and dividing by the number of shrubs. Aboveground shrub biomass was destructively harvested within each quadrat and oven-dried until constant dry weight. We then regressed the

\log_{10} of plant biomass against NDVI (14 plots) and the \log_{10} of vegetation height against the \log_{10} of aboveground shrub biomass (12 plots). In the remainder of the paper, we use NDVI as a proxy for vegetation standing crop (biomass and height).

2.2.3 Foraging along gradients of vegetation density and height

This experiment was a nested block design with six transects of 5 foraging stations each. Transects were ~ 30 m long to assure that all five foraging stations were accessible to the same squirrel or group of squirrels. Transects were > 50 m apart and encompassed at least four clearly identifiable independent colonies. Each transect was situated so that the first station (station 1) was no more than 2-3 m from an active burrow. Within each transect, the five stations traversed a microhabitat gradient beginning in sparsely vegetated dry heath tundra (stations 1 and 2), moist acidic tundra (stations 3 and 4), and culminating in densely shrub-covered tundra (emulating predicted future shrub encroachment scenarios; station 5). Stations with similar numbers are therefore placed on similar cover type within each transect regardless of distance among stations. Stations were between 5 and 8 m apart. A motion-sensitive camera trap deployed at stations 1 and 3 of each transect (for a total of 12 cameras) monitored foraging activity and foragers' identities. Each camera trap was set to take three photographs in succession upon triggering to ensure the animal was photographed. Animals in only one of the triplet photographs were counted to avoid counting the same individual multiple times. After evidence of vole foraging within transect 6 during run 4, the camera was moved from station 3 to station 5 to confirm their activity. Evidence of vole foraging was also noted at station 5 of transect 5, but the camera was not moved. No evidence of vole foraging appeared in the other transects. The photo frames were analyzed for all visitors, which included other herbivores and predators.

2.2.4 Landscape of fear (LOF)

To determine whether predation risk varies little or strongly within the home range of a squirrel, and to relate the squirrels' fear of predation to sightlines and/or vegetation cover, in 2014

we established a 4×4 grid of food patches (16 trays total) with 10 m spacing between patches within an established colony. The entire grid was in dry heath habitat with heterogeneous topography of small rises and depressions, although topography generally rose from the NE corner toward the SW corner. Data were collected 5 times over a 4-day period. Additionally, photos were taken at each foraging station in each of the four cardinal directions at a height of approximately 17 cm to simulate the sightline of a vigilant squirrel. Photos were additionally taken from overhead to document evidence of vertical obstruction. Each photo was given a value for vegetation (0 = 0-33% lateral obstruction, 1 = 34-66% lateral obstruction, and 2 = 67-100% lateral obstruction), slope (0 = none, 1 = partial, and 2 = total), and overhead obstruction (0 = none, 1 = some). Scores were assessed and assigned by four independent observers. Using GPS, we recorded the latitude and longitude of all foraging stations and mapped all the burrow entrances on and within 10 m of the grid, noting that squirrels tended to reside on the NW corner and along the northern margin of the grid.

The LOF was repeated in 2015 utilizing three blocks, 3×3 grids of food patches (27 feeding patches total). Each feeding patch was placed 10 m apart with each block more than 150 m from one another to ensure no or little overlap in use by squirrels. Each site was chosen to be similar to the 2014 LOF with a heterogeneous landscape of rolling topography and variable vegetation. GUDs were collected twice a day (0500-1300, 1300-2100) over a 2.5-day period for a total of 5 runs. Logistical constraints prohibited the collection of photos to analyze local obstructions as was done in 2014. Therefore, each station was scored on a scale of 1-3 with respect to vegetation cover (3 representing high vegetation and obstructed sightlines), and 1-3 with respect to whether the food patch was elevated or within a depression (3 representing high elevation and unobstructed sightlines).

2.2.5 Experimental food patch

Over a period of 10 days in late July 2014 we optimized the foraging patch tray design, which consisted of circular plastic trays (36 cm diameter/5 cm deep) filled with 1.5 L pea gravel, with small drain holes. We used 20 raw peanut halves and 20 raisins per tray, with two whole peanuts placed on top to serve as initial bait. To raise the difficulty of the patches, we inserted a plastic mesh disc (5 cm mesh) that rested on and covered the gravel. To keep the mesh in place, we attached a 2×2 grid of heavy gauge wire placed 9 cm apart through holes drilled in the upper lip of the trays. GUDs were measured by counting the number of remaining peanuts and raisins in the tray after a feeding period. Though novel to the squirrels, we intentionally used peanuts and raisins. They represent both hard and soft food textures that are present in the tundra. In addition, these foods are particulate, providing uniform and repeatable quality, resistant to the weather, readily recognized as food to the squirrels, and the two together allowed for higher resolution of foraging behavior (see Bedoya-Perez et al. 2013; Kotler et al. 2016). Being preferred, peanuts were sometimes foraged to zero, and, being less preferred, raisins at times were skipped even as peanuts were consumed.

In 2015, during pre-bait trials using the 2014 foraging tray design, squirrels totally depleted the patches. Therefore, the level of difficulty was further increased by inserting a second plastic mesh disc and 10 roughly 5 cm rocks per tray.

2.2.6 Giving-up density (GUD)

We measured foraging intensity (the GUD) in the experimental foraging patches in three equal-length time periods (0500-1300, 1300-2100 and 2100-0500) over the 24 h daily cycle. The food patches must produce diminishing returns for the squirrels as they harvest the resources. Consequently, the forager's harvest rate declines as the patch is depleted, and eventually it abandons the patch when its harvest rate no longer exceeds the sum of its metabolic, predation and missed opportunity costs of foraging. The food remaining in the patch after the foraging round constitutes the GUD. Because of persistent damp, drizzle and rain during our study, we

used pea-sized gravel as substrate. During each round of data collection, gravel was poured from the trays into a larger plastic saucer, the remaining peanut halves and raisins were removed and counted, and the trays were refilled with a fresh aliquot of 20 peanut halves, 20 raisins, and two indicator peanuts.

2.2.7 Growing degree days

To account for differences in weather in the growing seasons of 2014 and 2015 (Partain et al. 2016), we calculated growing degree days for both years. We used the maximum and minimum temperatures reported for each day beginning with the average date of the recorded snow free dates for all monitored dry heath plots to mark the start the growing season until the peak green date for each of 2014 and 2015. We used 0°C as the base temperature (Pop et al. 2000). Temperature and snow free dates came from the Toolik Lake Field Station Environmental Data Center (https://toolik.alaska.edu/edc/abiotic_monitoring/index.php).

2.3 Results

2.3.1 Canopy spectral imaging (NDVI) and shrub biomass and height

Mean NDVI along the six transects was 0.702 ± 0.035 (0.479 – 0.865). With linear regression, we found positive relationships between NDVI and plant biomass (g m^{-2}): $\log_{10}(\text{biomass}) = 5.79 \times \text{NDVI} - 1.74$ ($P < 0.001$, $R^2 = 0.715$; Fig. 2.1a), and between plant biomass (g m^{-2}) and plant height (cm): $\log_{10}(\text{plant height}) = 0.466 \times \text{Biomass} + 0.449$ ($P = 0.002$, $R^2 = 0.613$; Fig. 2.1b).

2.3.2 Foraging along gradients of vegetation density and height

To examine differences in foraging intensity within and among transects, we tested for differences among GUDs with a partially-hierarchical ANOVA with time-period (0500-1300; 1300-2100; 2100-0500) and transect (6) as group variables, 8-hour runs (12) nested within time periods, stations (30) nested within transects, and the interaction effect between time periods and

transect. We summed the total remaining peanuts and raisins (the GUD) and then square root transformed that sum to achieve assumptions of normality. The overall model provided a good fit to the data (multiple $R^2=0.755$). GUDs differed significantly with time-period, with the lowest GUDs occurring during the 1300-2100 period and, the highest during the 2100-0500 period ($F_{2,9}=12.01$, $P=0.003$; Fig. 2.2a). GUDs did not differ significantly among transects ($F_{5,24}=2.25$, $P>0.08$) indicating similar patterns of foraging intensity across the different squirrel home ranges. A significant interaction between time-period and transect reflected a tendency for squirrels to skip some transects altogether during different time periods ($F_{10,309}=10.87$, $P<0.001$). As random effects, GUDs varied significantly with both stations within transects and runs within time periods ($F_{24,309}=2.60$, $P<0.001$ and $F_{9,309}=22.81$, $P<0.001$, respectively).

To investigate a potential relationship between foraging intensity and vegetation density, we regressed mean total GUDs of a station ($n=30$) against the station's NDVI score at each station. We ran a separate regression for each foraging period (Fig. 2.2b). GUDs varied positively with NDVI during the morning period ($F_{1,28}=17.01$; $P<0.001$; $R^2=0.378$), but showed no relationship during the afternoon ($F_{1,28}=0.349$; $P=0.559$) when foraging intensity was consistently high (low GUD), nor during the overnight period ($F_{1,28}=0.6329$; $P=0.433$) when foraging intensity was consistently low (high GUD; Fig. 2.3).

We examined the potential role of weather (temperature, precipitation and humidity) on foraging intensity using an ANCOVA with mean GUD for a run as the dependent variable, time-period as a grouping variable, and temperature, precipitation, and relative humidity during the run as covariates. GUDs exhibited no relationship with air temperature ($F_{1,66}=0.29$, $P=0.588$), precipitation ($F_{1,66}=0.04$, $P=0.842$), or relative humidity ($F_{1,66}=0.29$, $P=0.587$).

2.3.3 Photographs

The twelve motion-triggered cameras (placed at stations 1 and 3 of the six transects) photographed a total of 811 images with animals present at experimental food patches. Species

photographed included Arctic ground squirrel (83%), vole (7.3%), raven (5.2%), fox (3.2%), and sparrow (1.3%; see Table 2.1). Foxes were photographed predominantly during the overnight period. Voles were photographed only at station 5 of transect 6, yet accounted for 7.3% of all photographs. Voles were photographed most frequently during the morning period (87%). Visits to foraging trays (indexed by photographs) were dominated by squirrels the morning (79%) and afternoon (93%), the periods of lowest GUDs. Squirrels were photographed significantly more frequently at station 1 than station 3 (Welch's T-test, $t_{7,13} = 2.62$, $P=0.034$; Fig. 2.3a), and squirrels were photographed most frequently during the morning and afternoon periods, and least overnight (Fig. 2.3b).

2.3.4 Landscape of fear

In 2014, we tested for differences in GUDs (square root of total GUD) across the 4×4 grid with a two-way ANOVA. GUDs varied significantly with both run and station ($F_{4,60}=17.614$; $P<0.001$ and $F_{15,60}=3.235$; $P=0.001$ respectively; Fig. 2.4 and Fig. 2.5). To determine effects of topography and vegetation across the LOF grid, we regressed (multiple regression) the mean GUD of a station against its vegetation score, sightline score, and their interaction. The interaction term was not significant ($t = 0.59$, $P>0.5$). We then ran the multiple regression omitting the interaction term. GUDs increased with vegetation cover ($t = 2.86$, $P=0.013$), and decreased non-significantly with sightline obstruction ($t = -1.7$, $P=0.11$). The relationship was Mean GUD at a station = $7.1 - 1.15 \times \text{Sightline} + 1.18 \times \text{Vegetation}$.

In 2015, we tested for differences in GUDs within and among the three 3×3 grids. In a partially hierarchical ANOVA, we considered site and run (5, 8-hour foraging periods over 2.5 days) as group variables (including their interaction effect), and station nested within site. The dependent variable was the square-root of total GUD. The overall model provided a moderate fit to the data (multiple $R^2=0.562$). GUDs differed significantly among the sites ($F_{2,24}=10.88$, $P<0.001$; Fig. 2.5). GUDs did not differ with run period ($F_{4,24}=1.43$, $P=0.228$), though there was a

significant interaction of run and site ($F_{8,96}=5.28$, $P<0.001$). Finally, GUDs varied significantly across stations nested with sites ($F_{24,96}=1.64$, $P=0.047$; Fig. 2.5b-c). To explore how the variability of vegetation and topography across stations nested within site may have affected GUDs, we conducted an ANCOVA with site as a grouping variable and vegetation and sightline as covariates (having first found no significant interaction of site with either vegetation or with sightline). GUDs varied significantly among the three sites ($F_{2,47}=5.35$, $P=0.008$) and with sightlines ($F_{2,47}=4.78$, $P=0.013$) but not with vegetation ($F_{2,47}=0.33$, $P>0.7$)

2.3.5 Growing degree days

The beginning of the 2015 growing season was warmer and earlier by 14 days than in 2014 (Figure 2.6). Growing degree days rose faster in 2015 than 2014 (two sample Kolmogorov-Smirnov test, $P = 0.069$; Anderson-Darling test, $P = 0.04$).

2.4 Discussion

Arctic ground squirrel foraging intensity varied spatially. Close to tall and dense shrubs (high NDVI) and in topographic depressions, Arctic ground squirrel foraging was cursory or superficial (high GUDs; Fig. 2.2b, 2.5a). In areas of sparse vegetation (low NDVI) and topographic ridges and mounds, foraging was intense and foraging patches were depleted more thoroughly (low GUDs) (Figs. 2.2b and 2.4b). These results suggest that Arctic ground squirrel does have ecosystem-level effects on tundra vegetation composition and structure, but such effects will be spatially heterogeneous.

In addition to spatial variability, Arctic ground squirrel foraging intensity varied by time of day (Fig. 2.2b). In the morning period, foraging intensity varied inversely with NDVI, with low GUDs associated with sparse vegetation (low NDVI), and high GUDs associated with tall and dense vegetation (high NDVI; see Fig. 2.1). We hypothesize that the sensitivity of Arctic ground squirrel foraging intensity to vegetation mass and height during the morning bout (Fig. 2.2b) reflects carryover predation effects from the overnight period, when red foxes are most

active (Table 2.1). During the morning, therefore, Arctic ground squirrels forage intensely in areas of low risk – areas in which low NDVI affords good sightlines for predator detection. Foraging in early to late afternoon, when light levels are high, red foxes are inactive, and thermoregulatory costs are minimal (Williams et al. 2014) was uniformly intense. Foraging during the overnight period, when red foxes are most active (Table 2.1), was uniformly light (high GUDs).

Together, the spatial and temporal variation in foraging intensity suggest that Arctic ground squirrels may impact the rate at which climate change induced shrub expansion occurs in Arctic tundra (Barker and Derocher 2010). Low NDVI or topographic crest areas coincide with low perceived predation risk, and Arctic ground squirrel forage crops vegetation to low stature, as expected from theory (Hairston et al. 1960; Oksanen 1990). High NDVI or topographical depressions present high predation risk, causing low foraging intensity with minimal effects on vegetation. In high predation risk areas, abiotic climate forcing factors would induce the most important changes in tundra vegetation, including shrub encroachment.

The effects of predation risk were scale dependent. Over two years we examined 1) station to station variation in risk (5 – 8 m spacing of trays along transects), 2) variation in risk as an LOF within an area of c. 0.1 ha (4 x 4 grid of patches with 10 m spacing in 2014) and 3) differences in perceived risk among sites (three LOF sites of 2015, separated by roughly 0.15 km). We found significant effects at all three scales. At the scale of a station, predation risk is composite of predator visitation rates, sightlines, topography, and NDVI. At the site scale, variation in presence and visitation rates of predators, in combination with variation in sightlines, vegetation, escape routes and burrows, promotes landscape-scale variation in squirrel foraging intensity. Consequently, the impacts of squirrel foraging on ecosystem functioning should also manifest at multiple spatial scales.

Weather and growing conditions varied markedly between 2014 and 2015. The growing season of 2015 was warmer and drier across Alaska, with over 2.06 million hectares (5.1 million

acres) burned in wildfires (Partain et al. 2016). The inconsistent results of vegetation and sightline effects between the 2014 and the 2015 LOFs may reflect these different growing conditions, or they could indicate that the vegetation was shorter and/or less dense in the three 2015 LOF sites than in the 2014 LOF site (irrespective of weather effects). In both years, sightlines were important determinants of fear, but in 2014 sightline obstruction was caused primarily by vegetation, whereas in 2015 sightline obstruction resulted primarily from topographic heterogeneity, which may act in concert with vegetation height. A comparative analysis of NDVI from 2014 and 2015 provided by the AON-ITEX Mobile Instrumented Sensor Platform (MISP), evaluating NDVI along a 50 m heath-graminoid-shrub tundra gradient, revealed a significant reduction in NDVI within the heath plant community in 2015 (Oberbauer and May, unpublished data). The increased temperatures and growing degree days in 2015 might lead to the expectation of increased NDVI in 2015 when compared to 2014. That the opposite occurred suggests, speculatively, that Arctic ground squirrels were exerting stronger top-down effects (extra plant growth consumed by herbivores) in the heath in 2015 than in 2014, as expected under the Exploitation Ecosystem Hypothesis in a “two-link” system (Oksanen et al. 1981; Oksanen 1992).

In areas of high intensity squirrel foraging, reduction or elimination of more favored plant species, such as grasses, sedges and forbs (Batzli and Sobaski 1980), may release shrub species from competition (Gough et al. 2007; Gough et al. 2012; Bryant et al. 2014) and affect the amount and quality of litter inputs, affecting ecosystem dynamics (Chapin et al. 2012). Continued warming and expansion of woody shrubs likely increases accessible forms of nitrogen, causing increased greening, height and productivity further (Weintraub and Schimel 2005; Salmon et al. 2016). Overall, these effects provide positive feedbacks on future shrub expansion as taller vegetation continues to minimize Arctic ground squirrel foraging intensity.

Many studies have shown that herbivores affect ecosystem processes, like plant succession and standing crop (Batzli and Pitelka 1970; Howe and Brown 1999) nutrient cycling (Mckendrick et al. 1980; Sirotnak and Huntly 2000; Olofsson et al. 2004), and productivity

(Batzli and Pitelka 1970; Olofsson et al. 2004; Bråthen et al. 2007). Potential ecosystem impacts of Arctic ground squirrels will likely vary spatially owing to the differential intensity of their foraging in response to predation risk. Climate forcing may enhance productivity of vegetation and reduce the impact of Arctic ground squirrels on shrub expansion and deserves further attention. Based on the results presented here, we contend that landscape patterns and drivers of shrub encroachment across the Arctic can be partly explained by foraging by Arctic ground squirrels in addition to climate and soil factors. Both biotic and abiotic effects may impact the changing carbon and energy balance of Arctic regions and the climate system.

2.5 Conclusions

We found that foraging intensity of Arctic ground squirrels both impacts and is impacted by existing vegetation as mediated by predation risk. How biotic interactions, such as these, determine ecosystem productivity and ecosystem responses to climate change is gaining attention. Recent research suggests that intrinsic biotic ecosystem properties such as biomass and species interactions may govern net primary productivity as much as extrinsic forcing by climate change (Michaletz et al. 2014; Flower and Gonzalez-Meler 2015). Factors such as species composition and resource availability may help explain the disagreement between observed and modeled ecosystem responses to elevated CO₂ (Nowak et al. 2004). Processes such as grazing, invasions and trophic cascades affect ecosystem properties at magnitudes similar to or larger than abiotic disturbances (Mckendrick et al. 1980; Flower et al. 2013; Moore et al. 2013). This is particularly true in ecosystems exhibiting relatively low productivity, such as the Arctic tundra (Mckendrick et al. 1980; Wahren et al. 2005). Consumer-driven interactions may drive changes in composition, structure, and even productivity of Arctic ecosystems in ways not predicted or well represented by current climate models. Our approach revealed that these impacts, generated by individual foragers at the scale of the patch, scale up to landscape through their collective behaviors. Together with results from elsewhere in Alaska (Wheeler et al. 2015) and in the

Yukon (Donker and Krebs 2012; Wheeler and Hik 2014), ecosystem impacts of consumers like the Arctic ground squirrel may be extrapolated to the entire Arctic system (Voosen 2017). Therefore, consumer driven ecosystem effects need to be incorporated into models to understand the impact of tundra vegetation change on the climate system.

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2.7 References

- Ackerman D, Griffin D, Hobbie SE, Finlay JC (2017) Arctic shrub growth trajectories differ across soil moisture levels. *Glob Chang Biol*. doi: 10.1111/gcb.13677
- Altendorf KB, Laundre JW, Lopez Gonzalez CA, Brown JS (2001) Assessing effects of predation risk on foraging behavior of mule deer. *J Mammal* 82:430–439. doi: 10.1644/1545-1542(2001)082<0430:aeopro>2.0.co;2
- Anderson-Smith M (2013) Remotely-sensed spectral data linked to increasing shrub abundance and greater growing season carbon uptake in Alaska Arctic Tundra. MSc. Thesis, Department of Biological Sciences, University of Alaska Anchorage, USA.
- Bale JS, Masters GJ, Hodkinson ID, Awmack C, Bezemer TM, Brown VK, Butterfield J, Buse A, Coulson JC, Farrar J, Good JEG, Harrington R, Hartley S, Jones TH, Lindroth RL, Press MC, Symmioudis I, Watt AD, Whittaker JB (2002) Herbivory in global climate change research: Direct effects of rising temperature on insect herbivores. *Glob Chang Biol* 8:1–16. doi: 10.1046/j.1365-2486.2002.00451.x
- Barker OE, Derocher AE (2010) Habitat selection by arctic ground squirrels (*Spermophilus parryii*). *J Mammal* 91:1251–1260. doi: 10.1644/10-MAMM-A-030.1
- Batzli GO, Pitelka FA (1970) Influence of meadow mouse populations on California grassland. *Ecology* 51:1027–1039. doi: 10.2307/1933629
- Batzli GO, Sobaski ST (1980) Distribution, abundance, and foraging patterns of ground squirrels near Atkasook, Alaska. *Arct Alp Res* 12:501–510.
- Bedoya-Perez MA, Carthey AJR, Mella VSA, McArthur C, Banks PB (2013) A practical guide to avoid giving up on giving-up densities. *Behav Ecol Sociobiol* 67:1541–1553. doi: 10.1007/s00265-013-1609-3
- Blanc-Betes E, Welker JM, Sturchio NC, Chanton JP, Gonzalez-Meler MA (2016) Winter precipitation and snow accumulation drive the methane sink or source strength of Arctic tussock tundra. *Glob Chang Biol* 22:2818–2833. doi: 10.1111/gcb.13242
- Blok D, Heijmans MMPD, Schaepman-Strub G, Kononov AV, Maximov TC, Berendse F (2010) Shrub expansion may reduce summer permafrost thaw in Siberian tundra. *Glob Chang Biol* 16:1296–1305. doi: 10.1111/j.1365-2486.2009.02110.x
- Brashares JS, Prugh PR, Stoner CJ, Epps CW (2010) Trophic cascades: Predators, prey, and the changing dynamics of nature. In: Terborgh J, Estes JA (eds) *Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature*. Island Press, Washington, DC, pp 221–240
- Bråthen KA, Ims RA, Yoccoz NG, Fauchald P, Tveraa T, Hausner VH (2007) Induced shift in ecosystem productivity? Extensive scale effects of abundant large herbivores. *Ecosystems* 10:773–789. doi: 10.1007/s10021-007-9058-3
- Bret-Harte MS, Shaver GR, Zoerner JP, Johnstone JF, Wagner JL, Chavez AS, Gunkelman IV RF, Lippert SC, Laundre JA (2001) Developmental plasticity allows *betula nana* to dominate tundra subjected to an altered environment. *Ecology* 82:18–32. doi: 10.1890/0012-

9658(2001)082[0018:DPABNT]2.0.CO;2

- Brown JS (1988) Patch use as an indicator of habitat preference, predation risk, and competition. *Behav Ecol Sociobiol* 22:37–47. doi: 10.1007/BF00395696
- Brown JS, Kotler BP (2004) Hazardous duty pay and the foraging cost of predation. *Ecol Lett* 7:999–1014. doi: 10.1111/j.1461-0248.2004.00661.x
- Bryant JP, Joly K, Chapin FS, DeAngelis DL, Kielland K (2014) Can antibrowsing defense regulate the spread of woody vegetation in arctic tundra? *Ecography* 37:204–211. doi: 10.1111/j.1600-0587.2013.00436.x
- Carl EA (1971) Population control in arctic ground squirrels. *Ecology* 52:395. doi: 10.2307/1937623
- Chapin FS, Jefferies RL, Reynolds JF, Shaver GR, Svoboda J, Chu EW (2012) Arctic ecosystems in a changing climate: An ecophysiological perspective. Academic Press, San Diego, CA
- Chapin FS, Shaver GR, Giblin AE, Nadelhoffer KJ, Laundre JA (1995) Responses of Arctic tundra to experimental and observed changes in climate. *Ecology* 76:694–711. doi: 10.2307/1939337
- Christie KS, Bryant JP, Gough L, Ravolainen VT, Ruess RW, Tape KD (2015) The role of vertebrate herbivores in regulating shrub expansion in the Arctic: A synthesis. *Bioscience* 65:1123–1133. doi: 10.1093/biosci/biv137
- Donker SA, Krebs CJ (2012) Evidence for sourcesink dynamics in a regional population of arctic ground squirrels (*Urocitellus parryii plesius*). *Wildl Res* 39:163–170. doi: 10.1071/WR11167
- Elmendorf SC, Henry GHR, Hollister RD, Björk RG, Bjorkman AD, Callaghan TV, Collier LS, Cooper EJ, Cornelissen JHC, Day TA, Fosaa AM, Gould WA, Grétarsdóttir J, Harte J, Hermanutz L, Hik DS, Hofgaard A, Jarrad F, Jónsdóttir IS, Keuper F, Klanderud K, Klein JA, Koh S, Kudo G, Lang SI, Loewen V, May JL, Mercado J, Michelsen A, Molau U, Myers-Smith IH, Oberbauer SF, Pieper S, Post E, Rixen C, Robinson CH, Schmidt NM, Shaver GR, Stenström A, Tolvanen A, Totland O, Troxler T, Wahren CH, Webber PJ, Welker JM, Wookey PA (2011) Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecol Lett*. doi: 10.1111/j.1461-0248.2011.01716.x
- Environmental Data Center Team. 2017. Meteorological monitoring program at Toolik, Alaska. Toolik Field Station, Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775. http://toolik.alaska.edu/edc/abiotic_monitoring/data_query.php
- Euskirchen ES, McGuire AD, Kicklighter DW, Zhuang Q, Clein JS, Dargavill RJ, Dye DG, Kimball JS, McDonald KC, Melillo JM, Romanovsky VE, Smith NV (2006) Importance of recent shifts in soil thermal dynamics on growing season length, productivity, and carbon sequestration in terrestrial high-latitude ecosystems. *Glob Chang Biol* 12:731–750. doi: 10.1111/j.1365-2486.2006.01113.x
- Flower CE, Gonzalez-Meler MA (2015) Responses of temperate forest productivity to insect and

pathogen disturbances. *Annu Rev Plant Biol* 66:547–569. doi: 10.1146/annurev-arplant-043014-115540

- Flower CE, Knight KS, Gonzalez-Meler MA (2013) Impacts of the emerald ash borer (*Agrilus planipennis fairmaire*) induced ash (*Fraxinus* spp.) mortality on forest carbon cycling and successional dynamics in the eastern United States. *Biol Invasions* 15:931–944. doi: 10.1007/s10530-012-0341-7
- Fraser LH (1998) Top-down vs bottom-up control influenced by productivity in a North Derbyshire, UK, Dale. *Oikos* 81:99–108. doi: 10.2307/3546472
- Gillis EA, Morrison SF, Zazula GD, Hik DS (2005) Evidence for selective caching by Arctic ground squirrels living in alpine meadows in the Yukon. *Arctic* 58:354–360.
- Gough L, Moore JC, Shaver GR, Simpson RT, Johnson DR (2012) Above- and belowground responses of arctic tundra ecosystems to altered soil nutrients and mammalian herbivory. *Ecology* 93:1683–1694. doi: 10.1890/11-1631.1
- Gough L, Ramsey EA, Johnson DR (2007) Plant-herbivore interactions in Alaskan arctic tundra change with soil nutrient availability. *Oikos* 116:407–418. doi: 10.1111/j.0030-1299.2007.15449.x
- Hairston NG, Smith FE, Slobodkin LB (1960) Community structure, population control, and competition. *Am Nat* 94:421. doi: 10.1086/282146
- Heskel M, Greaves H, Kornfeld A, Gough L, Atkin OK, Turnbull MH, Shaver GR, Griffin KL (2013) Differential physiological responses to environmental change promote woody shrub expansion. *Ecol Evol* 3:1149–1162. doi: 10.1002/ece3.525
- Hochman V, Kotler BP (2006) Patch use, apprehension, and vigilance behavior of Nubian Ibex under perceived risk of predation. *Behav Ecol* 18:368–374. doi: 10.1093/beheco/arl087
- Howe HF, Brown JS (1999) Effects of birds and rodents on synthetic tallgrass communities. *Ecology* 80:1776–1781. doi: 10.2307/176568
- Huntly NJ (1987) Influence of refuging consumers (pikas: *Ochotona princeps*) on subalpine meadow vegetation. *Ecology* 68:274–283. doi:10.2307/1939258
- Jung HJG, Batzli GO, Seigler DS (1979) Patterns in the phytochemistry of arctic plants. *Biochem Syst Ecol* 7:203–209.
- Kaarlejärvi E, Hoset KS, Olofsson J (2015) Mammalian herbivores confer resilience of Arctic shrub-dominated ecosystems to changing climate. *Glob Chang Biol* 21:3379–88. doi: 10.1111/gcb.12970
- Karels TJ, Boonstra R (1999) The impact of predation on burrow use by arctic ground squirrels in the boreal forest. *Proc Biol Sci* 266:2117–2123. doi: 10.1098/rspb.1999.0896
- Kotler BP, Morris DW, Brown JS (2016) Direct behavioral indicators as a conservation and management tool. In: Berger-Tal O, Saltz D (eds) *Conserv. Behav. Appl. Behav. Ecol. to Wildl. Conserv. Manag.* Cambridge University Press, Cambridge, pp 307–351

- Lachenbruch AH, Marshall BV (1986) Changing climate: geothermal evidence from permafrost in the alaskan arctic. *Science* 234:689–696. doi: 10.1126/science.234.4777.689
- Lachenbruch AH, Sass JH, Marshall BV, Moses TH (1982) Permafrost, heat flow, and the geothermal regime at Prudhoe Bay, Alaska. *J Geophys Res* 87:9301. doi: 10.1029/JB087iB11p09301
- Mack MC, Bret-Harte MS, Hollingsworth TN, Jandt RR, Schuur EAG, Shaver GR, Verbyla DL (2011) Carbon loss from an unprecedented Arctic tundra wildfire. *Nature* 475:489–492. doi: 10.1038/nature10283
- Mckendrick JD, Batzli GO, Everett KR, Swanson JC (1980) Some effects of mammalian herbivores and fertilization on tundra soils and vegetation. *Arct Alp Res Arct and Alpine Res* 12:565–578. doi: 10.2307/1550501
- Michaletz ST, Cheng D, Kerkhoff AJ, Enquist BJ (2014) Convergence of terrestrial plant production across global climate gradients. *Nature* 512:39–43. doi: 10.1038/nature13470
- Mishra U, Jastrow JD, Matamala R, Hugelius G, Koven CD, Harden JW, Ping CL, Michaelson GJ, Fan Z, Miller RM, McGuire AD, Tarnocai C, Kuhry P, Riley WJ, Schaefer K, Schuur EAG, Jorgenson MT, Hinzman LD (2013) Empirical estimates to reduce modeling uncertainties of soil organic carbon in permafrost regions: a review of recent progress and remaining challenges. *Environ Res Lett* 8:35020. doi: 10.1088/1748-9326/8/3/035020
- Moore DJP, Trahan NA, Wilkes P, Quaife T, Stephens BB, Elder K, Desai AR, Negron J, Monson RK (2013) Persistent reduced ecosystem respiration after insect disturbance in high elevation forests. *Ecol Lett* 16:731–737. doi: 10.1111/ele.12097
- Myers-Smith IH, Elmendorf SC, Beck PSA, Wilmking M, Hallinger M, Blok D, Tape KD, Rayback SA, Macias-Fauria M, Forbes BC, Speed JDM, Boulanger, Lapointe N, Rixen C, Lévesque E, Schmidt NM, Baittinger C, Trant, AJ, Hermanutz L, Collier LS, Dawes MA, Lantz TC, Weijers S, Jørgensen RH, Buchwal A, Buras A, Naito AT, Ravolainen VT, Schaepman-Strub G, Wheeler JA, Wipf S, Guay KC, Hik DS, Vellend M (2015) Climate sensitivity of shrub growth across the tundra biome. *Nat Clim Chang* 5:887–891. doi: 10.1038/nclimate2697
- Myers-Smith IH, Forbes BC, Wilmking M, Hallinger M, Lantz T, Blok D, Tape KD, Macias-Fauria M, Sass-Klaassen U, Lévesque E, Boudreau S, Ropars P, Hermanutz L, Trant A, Collier LS, Weijers S, Rozema J, Rayback SA, Schmidt NM, Schaepman-Strub G, Wipf S, Rixen C, Ménard CB, Venn S, Goetz S, Andreu-Hayles L, Elmendorf S, Ravolainen VT, Welker J, Grogan P, Epstein HE, Hik DS (2011) Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environ Res Lett* 6:45509. doi: 10.1088/1748-9326/6/4/045509
- Natali SM, Schuur EAG, Trucco C, Trucco C, Hicks Pries CE, Crummer KG, Baron Lopez AF (2011) Effects of experimental warming of air, soil and permafrost on carbon balance in Alaskan tundra. *Glob Chang Biol* 17:1394–1407. doi: 10.1111/j.1365-2486.2010.02303.x
- Nowak RS, Ellsworth DS, Smith SD (2004) Functional responses of plants to elevated atmospheric CO₂— do photosynthetic and productivity data from FACE experiments support

early predictions? *New Phytol* 162:253–280.

- Ogden JC, Brown RA, Salesky N (1973) Grazing by the echinoid *diadema antillarum philippi*: Formation of halos around West Indian patch reefs. *Science* 182:715–717. doi: 10.1126/science.182.4113.715
- Oksanen L (1992) Evolution of exploitation ecosystems I. Predation, foraging ecology and population dynamics in herbivores. *Evol Ecol* 6:15–33. doi: 10.1007/BF02285331
- Oksanen L (1990) Predation, herbivory, and plant strategies along gradients of primary productivity. In: Grace J, Tilman D (eds) *Perspectives on Plant Competition*. Academic Press, New York, pp 445–474
- Oksanen L, Fretwell SD, Arruda J, Niemela P (1981) Exploitation ecosystems in gradients of primary productivity. *Am Nat* 118:240. doi: 10.1086/283817
- Olofsson J, Oksanen L, Callaghan T, Hulme PE, Oksanen T, Suominen O (2009) Herbivores inhibit climate-driven shrub expansion on the tundra. *Glob Chang Biol* 15:2681–2693. doi: 10.1111/j.1365-2486.2009.01935.x
- Olofsson J, Stark S, Oksanen L (2004) Reindeer influence on ecosystem processes in the tundra. *Oikos* 105:386–396. doi: 10.1111/j.0030-1299.2004.13048.x
- Olofsson J, Tømmervik H, Callaghan TV (2012) Vole and lemming activity observed from space. *Nat Clim Chang* 2:880–883. doi: 10.1038/nclimate1537
- Partain JL, Alden S, Bhatt US, Bieniek PA, Brettschneider BR, Lader RT, Olsson PQ, Rupp TS, Strader H, Thoman RL, Walsh JE, York AD, Ziel RH (2016) An assessment of the role of anthropogenic climate change in the Alaska fire season of 2015. *Bull Am Meteorol Soc* 97:S14–S18. doi: 10.1175/BAMS-D-16-0149.1
- Pop EW, Oberbauer SF, Starr G (2000) Predicting vegetative bud break in two arctic deciduous shrub species, *Salix pulchra* and *Betula nana*. *Oecologia* 124:176–184. doi: 10.1007/s004420050005
- Price LW (1971) Geomorphic effect of the Arctic ground squirrel in an alpine environment. *Geogr Ann Ser A, Phys Geogr* 53:100–106.
- Ricketts MP, Poretsky RS, Welker JM, Gonzalez-Meler MA (2016) Soil bacterial community and functional shifts in response to altered snowpack in moist acidic tundra of northern Alaska. *Soil* 2:459–474. doi: 10.5194/soil-2-459-2016
- Salmon VG, Soucy P, Mauritz M, Celis G, Natali SM, Mack MC, Schuur EAG (2016) Nitrogen availability increases in a tundra ecosystem during five years of experimental permafrost thaw. *Glob Chang Biol* 22:1927–1941. doi: 10.1111/gcb.13204
- Schmitz OJ, Raymond PA, Estes JA, Kurz WA, Holtgrieve GW, Ritchie ME, Schindler DE, Spivak AC, Wilson RW, Bradford MA, Christensen V, Deegan L, Smetacek V, Vanni MJ, Wilmers CC (2014) Animating the carbon cycle. *Ecosystems* 17:344–359. doi: 10.1007/s10021-013-9715-7

- Schuur EAG, Vogel JG, Crummer KG, Lee H, Sickman JO, Osterkamp TE (2009) The effect of permafrost thaw on old carbon release and net carbon exchange from tundra. *Nature* 459:556–559. doi: 10.1038/nature08031
- Serreze MC, Walsh JE, Chapin FS, Osterkamp T, Dyrugerov M, Romanovsky V, Oechel WC, Morison J, Zhang T, Barry RG (2000) Observational evidence of recent change in the northern high-latitude environment. *Clim Change* 46:159–207. doi: 10.1023/a:1005504031923
- Sirotnak JM, Huntly NJ (2000) Direct and indirect effects of herbivores on nitrogen dynamics: Voles in riparian areas. *Ecology* 81:78–87. doi: 10.1890/0012-9658(2000)081[0078:DAIEOH]2.0.CO;2
- Slobodkin LB, Smith FE, Hairston NG (1967) Regulation in terrestrial ecosystems, and the implied balance of nature. *Am Nat* 101:109. doi: 10.1086/282478
- Sturm M, Racine C, Tape KD (2001) Climate change: Increasing shrub abundance in the Arctic. *Nature* 411:546–547. doi: 10.1038/35079180
- Sturm M, Schimel J, Michaelson G, Welker JM, Oberbauer SF, Liston GE, Fahnestock J, Romanovsky VE (2005) Winter biological processes could help convert Arctic tundra to shrubland. *Bioscience* 55:17. doi: 10.1641/0006-3568(2005)055[0017:WBPCHC]2.0.CO;2
- Tape KD, Sturm M, Racine C (2006) The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Glob Chang Biol* 12:686–702. doi: 10.1111/j.1365-2486.2006.01128.x
- Voosen P (2017) NASA armada targets thaw in Arctic soil. *Science* 356:12–13
- Wahren CHA, Walker MD, Bret-Harte MS (2005) Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. *Glob Chang Biol* 11:537–552. doi: 10.1111/j.1365-2486.2005.00927.x
- Weintraub MN, Schimel JP (2005) Nitrogen cycling and the spread of shrubs control changes in the carbon balance of Arctic tundra ecosystems. *Bioscience* 55:408. doi: 10.1641/0006-3568(2005)055[0408:NCATSO]2.0.CO;2
- Wheeler HC, Chipperfield JD, Roland C, Svenning JC (2015) How will the greening of the Arctic affect an important prey species and disturbance agent? Vegetation effects on arctic ground squirrels. *Oecologia* 178:915–929. doi: 10.1007/s00442-015-3240-7
- Wheeler HC, Hik DS (2014) Giving-up densities and foraging behaviour indicate possible effects of shrub encroachment on arctic ground squirrels. *Anim Behav* 95:1–8. doi: 10.1016/j.anbehav.2014.06.005
- Williams CT, Wilsterman K, Kelley AD, Breton AR, Stark H, Humphries MM, McAdam AG, Barnes BM, Boutin S, Buck CL (2014) Light loggers reveal weather-driven changes in the daily activity patterns of arboreal and semifossorial rodents. *J Mammology* 95:1230–1239. doi: 10.1644/14-MAMM-A-062
- Zazula GD, Mathewes RW, Harestad AS (2006) Cache selection by arctic ground squirrels inhabiting Boreal-steppe meadows of southwest Yukon territory, Canada. *Arctic, Antarct*

Alp Res 38:631–638. doi: 10.1657/1523-0430(2006)38[631:CSBAGS]2.0.CO;2

Table 2.1. Number and proportion of photographs of different animals present at experimental food patches contingent upon time of day.

	Morning (number)	Morning (%)	Afternoon (number)	Afternoon (%)	Overnight (number)	Overnight (%)	Total (%)
Fox	5	1.2	3	0.8	18	43.9	3.2
Raven	25	6.0	17	4.8	0	0.0	5.2
Sparrow	7	1.7	3	0.8	1	2.4	1.3
Squirrel	328	78.8	329	92.9	16	39.0	83
Vole	51	12.3	2	0.6	6	14.6	7.3
Total	416		354		41		

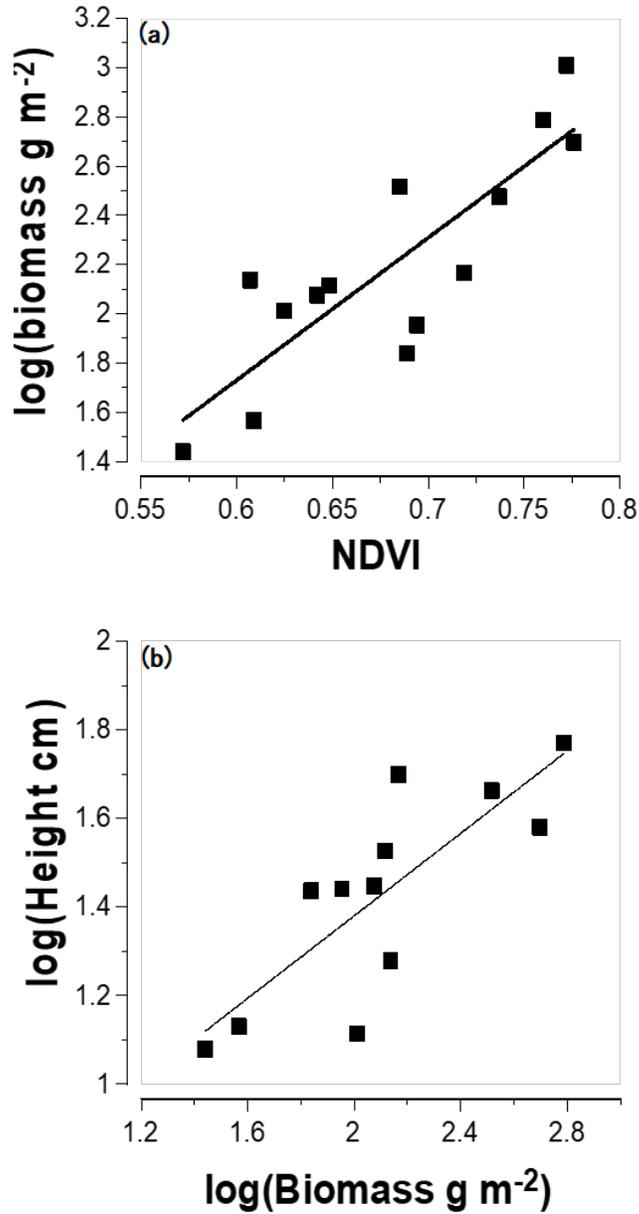


Figure 2.1. Relationships among NDVI, vegetation biomass (g m^{-2}), and vegetation height (cm). a) Linear relationship between NDVI and \log_{10} (vegetation biomass): $\log_{10}(\text{biomass}) = 5.79 \times \text{NDVI} - 1.74$, $P < 0.001$, $R^2 = 0.715$. b) Linear relationship between vegetation biomass (g m^{-2}) and vegetation height (cm): $\log_{10}(\text{plant height}) = 0.466 \times \text{Biomass} + 0.449$, $P = 0.002$, $R^2 = 0.613$.

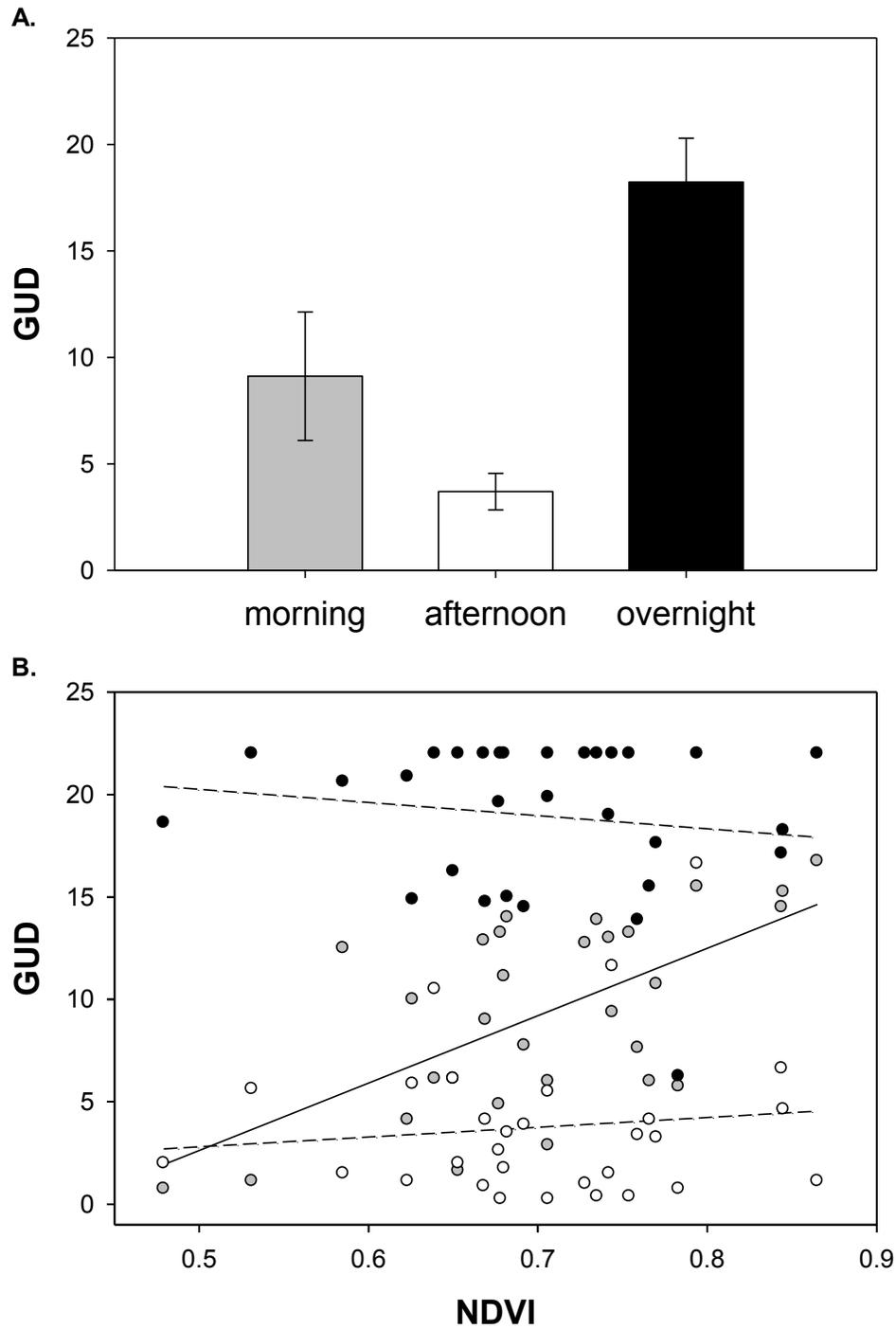


Figure 2.2. a) Mean giving up density (GUD) for each foraging period. Error bars denote ± 1 standard error and significance levels represent differences as revealed by Tukey's HSD pairwise comparisons ($P < 0.05$). b) Relationship between normalized difference vegetation index (NDVI) and giving up densities during different foraging periods. Colors match shading in panel a, whereby morning, afternoon and overnight are represented by grey, white and black circles respectively.

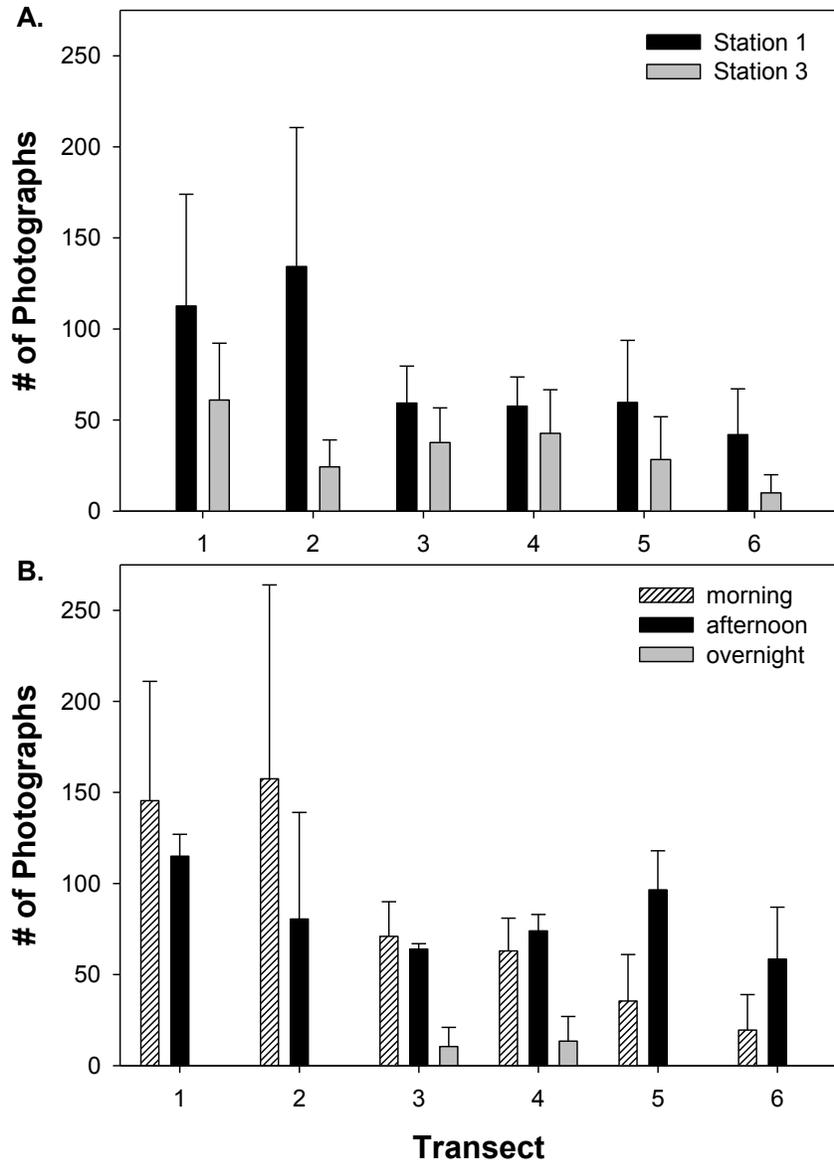


Figure 2.3. a) Number of photographs with Arctic ground squirrels at stations 1 and 3 by transect. Some station 3 photographs of transect 6 include photographs taken at station 5 after the camera was moved to confirm vole foraging (see methods). b) Number of photographs of Arctic ground squirrels per transect subdivided by time of day (morning, afternoon and overnight). Values represent means and error bars denote ± 1 standard error.

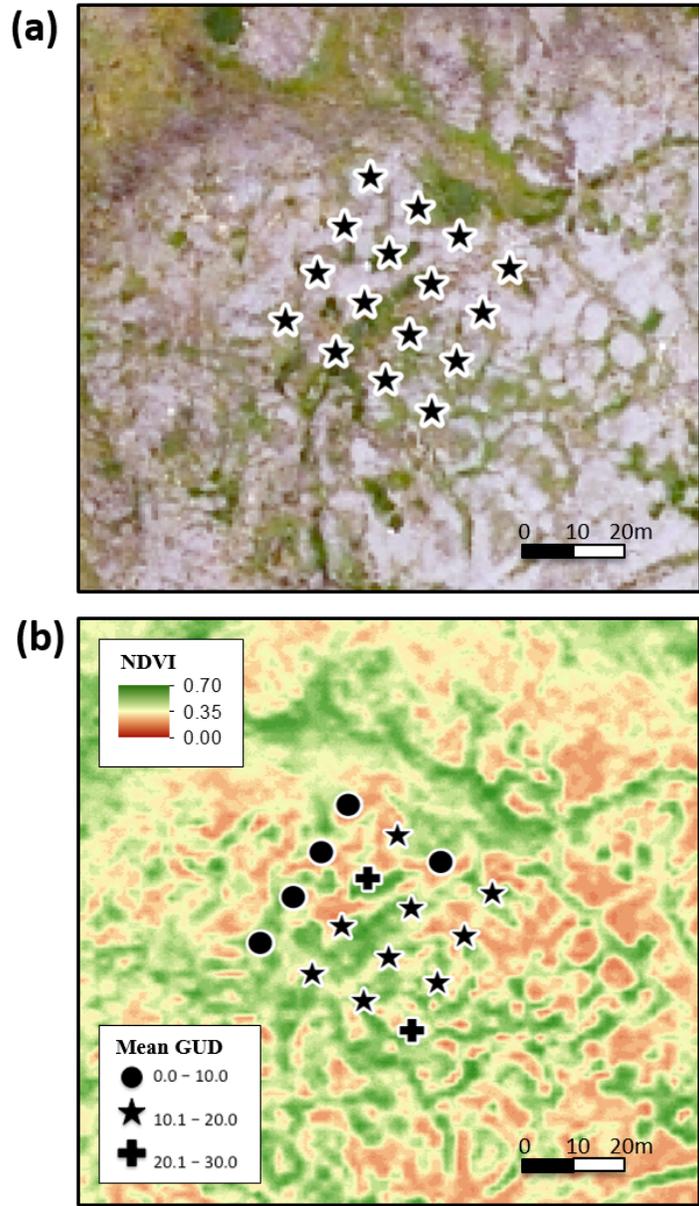


Figure 2.4. Two representations of the 2014 landscape of fear (LOF). a) True color Orthomosaic (60 cm resolution) with stations depicted with stars. Stations are 10 m apart. *Image courtesy of Toolik Field Station GIS.* b) NDVI map (0.3 m resolution) with mean GUD values at each station classified as high risk (cross), moderate risk (star), or low risk (circle). *Image courtesy of the DigitalGlobe Foundation.*

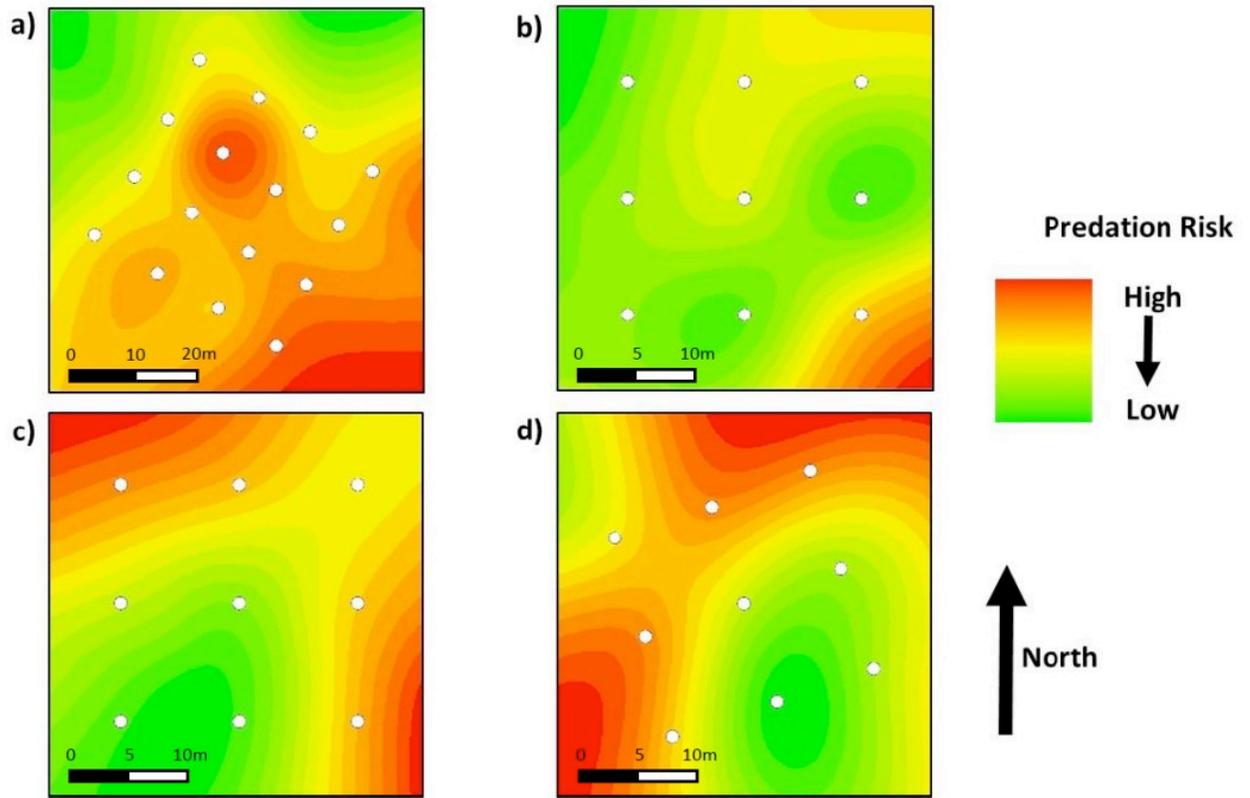


Figure 2.5. “Heat maps” of 2014 and 2015 landscapes of fear (LOF). Colors represent gradients of perceived predation risk based on giving-up densities, with darkest green representing least risk and darkest red representing greatest risk. a) 2014 4 × 4 LOF grid; b), c) & d) the three 3 × 3 grid LOFs in 2015.

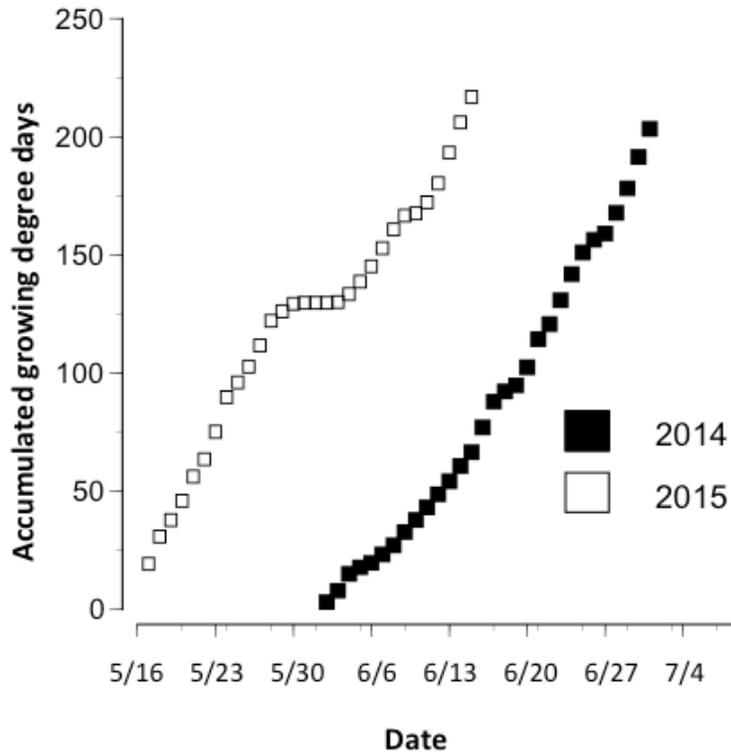


Figure 2.6. Cumulative growing degree days for 2014 and 2015. Growing degree days were calculated beginning with the average date of the recorded snow free dates for all the monitored dry heath plots to mark the start of the growing season until peak greenness for 2014 and 2015.

3. LARGE-SCALE EFFECTS OF THE ARCTIC GROUND SQUIRREL ON LOCAL SHRUB PRODUCTIVITY

3.1 Introduction

Climate change is shifting the structure, composition, and extent of Arctic tundra vegetation, transitioning from dwarf shrub vegetation to canopy-forming shrubs (Myers-Smith et al. 2011a; Tape et al. 2006, 2012). To monitor this amplification and encroachment, aerial photos and satellite imagery have been widely used through both the comparative analysis of repeat photography (Sturm et al. 2001; Tape et al. 2006, 2012) and seasonal fluctuations in Normalized Difference Vegetative Index (NDVI; Tape et al. 2012, Pettoirelli et al. 2005), a numerical index of plant density and greenness related to photosynthetic activity.

Abiotic mechanisms driving shrub amplification have been widely studied (Chapin et al. 1995, Myers-Smith & Hik 2013, Myers-Smith et al. 2011a, Tape et al. 2006, 2012), and include variables such as temperature and moisture. However, comparatively, it is less understood the role of biotic agents on vegetation dynamics in the Arctic tundra. Field studies have analyzed the direct effects of vertebrate herbivory on local changes in aboveground biomass (Chapin et al. 1995), plant community composition (Bråthen et al. 2007, Pajunen et al. 2012), and nutrient allocation (Bryant et al. 1983), but only a few studies have used satellite imagery to quantify the large-scale effects of herbivory in the Arctic (Olofsson et al. 2012) or to help model herbivore populations (Newton et al. 2014).

Herbivores may also influence shrub productivity through fertilization via nutrient deposition of urine and feces (Barthelemy et al. 2015, 2017; Mckendrick et al. 1980) or by affecting plant chemistry and local soil conditions (Barrio et al. 2016, Price 1971, Van Der Wal et al. 2004), having dramatic local impacts (Gharajehdaghipour et al. 2016). Yet no studies to date have analyzed the local effects of mammalian nutrient deposition on plant productivity as large-scale patterns via satellite imagery.

The abundant and omnivorous Arctic ground squirrel (*Urocitellus parryii*; AGS) serves as an excellent candidate for landscape-scale satellite analysis. As ecosystem engineers, AGS collectively drive large-scale effects on their environment (McKendrick et al. 1980). The soil bioturbation and the excretion of feces and urine that characterize burrow systems should enhance shrub productivity, including NDVI, shrub height and biomass when compared with areas with no burrows. These changes should be detectable with satellite imagery (Olofsson et al. 2012). With pan-Arctic distribution, their collective influences on productivity can be effectively scaled.

Accounts of patterns of plant productivity near AGS burrows differ. AGS favor habitats with clear sight lines and low shrub density to minimize predation risk (Chapter 2, Karels et al. 2000, Wheeler & Hik 2014). This behavior will favor the selection of areas with low mean greenness values (Barker & Derocher 2010, Karels & Boonstra 1999). Though more recent research has found a positive correlation between burrow selection, increased forb cover, and shrubs less than 50 cm tall (Wheeler et al. 2015). This disconnect can be attributed to a knowledge gap in whether AGS are actively engineering their local ecosystem or merely selecting for favorable attributes.

Specifically, in this study, I investigated 1) patterns of local shrub productivity associated with AGS burrow systems using satellite imagery and 2) the role of AGS as ecosystem engineers on local shrub productivity. Using satellite-derived NDVI of vegetation and light detection and ranging (LiDAR) derived shrub height and biomass measurements, I predict that NDVI, shrub height, and shrub biomass will be higher near ground squirrel resident burrows than control plots. To then attribute this productivity to AGS, an analysis of local nutrient dynamics of both plant and soil samples will clarify whether AGS provide nutrient inputs to neighboring shrubs near burrows. I predict that concentrations of soil and plant organic N and $\delta^{15}\text{N}$ will be higher near burrows than in nearby, non-burrow plots.

3.2. Methods

3.2.1 Study area

The study took place at Toolik Field Station, located in the foothills of the Brooks Range on Alaska's North Slope (68°38'N, 149°36'W elevation 760 m). The site consists predominantly of dry heath and moist tussock tundra. Vegetation consists of non-tussock forming sedges and grasses, tussock-forming graminoids intermixed with low stature and canopy-forming willow and birch species. The study was restricted to a roughly 1 km² area near the Arctic Observing Network – International Tundra Experiment (AON-ITEX) dry heath fence, an area of high AGS densities.

3.2.2 Study species

AGS are the northernmost species of ground squirrel with pan-Arctic distribution Alaska, Canada, and Siberia. This semi-fossorial rodent inhabits Arctic tundra, alpine meadow, and boreal forest habitats, preferring sloped terrain with adequate drainage, permafrost depth up to 1 m, and sparse vegetation for burrowing. They are generalist foragers with a broad diet consisting of plants, fungi, invertebrates, small vertebrates, birds, carrion and sometimes their own species. Diet selectivity has been demonstrated via examination of caching behavior and stomach contents (Gillis et al. 2005, Zazula et al. 2006), showing a preference for forbs, deciduous shrubs and forage with high water content and avoidance of evergreen shrubs and lichens. AGS concentrate foraging directly adjacent to burrow entrances up to 30 m of openings (Batzli & Sobaski 1980).

3.2.3 Remote sensing data collection

Data layers – As inputs for shrub productivity, aboveground shrub biomass and shrub height estimates were obtained from layers described in Greaves et al. (2016), with a resolution of 0.80 m and 0.20 m respectively. To derive the NDVI layer, a WorldView-3 image (WV-3; acquired on August 7, 2015) of the Toolik Field Station research grid was obtained through an imagery grant awarded via the Digital Globe Foundation (www.digitalglobe.com). The

WV-3 imagery provided a 31 cm panchromatic resolution and 1.24 m multispectral resolution. The spectral and spatial resolution properties of the imagery are detailed in Table 3.1.

To enhance the resolution of the multispectral image, the two images (panchromatic and multispectral) were merged and processed in ERDAS Imagine. The image was then Brovey transformed with bilinear interpolation resampling (unsigned 16 bit and selecting all layers – bands 1-8). The resulting multispectral image was roughly 1 km² with a resolution of 0.31 m. NDVI was then calculated in ArcGIS (10.3.1; ESRI, Redlands, CA) by floating Bands 5 (Visible Red Light; VIS) and 7 (Near Infrared; NIR) using the following equation to create an NDVI subset layer:

$$NDVI = (NIR - VIS) / (NIR + VIS)$$

Within the boundaries delimited by the available satellite imagery (approximately 1 km²), the area was then systematically surveyed by foot for AGS burrows, including water tracks and riparian areas, which are unsuitable for squirrels. Waypoints were collected within areas of high AGS activity via GPS (n=37; Trimble Geo7x, with 2m antenna). Waypoints were taken at 1 m height at the intersection of the midway point between the farthest active burrows and the nearest active resident burrow with the greatest soil throw. Active burrows were defined by the evidence of fresh digging and fecal matter.

Habitat modeling – To restrict the evaluation of shrub productivity to known characteristics of AGS preferred habitat (Barker & Derocher 2010, Batzli & Sobaski 1980, Carl 1971, Wheeler et al. 2015), 30 m resolution land cover classes of vegetation, surficial geology, and surficial geomorphology were built into a habitat model (Walker et al. 2006; www.arcticatlas.org; Fig. 3.1). This aided in eliminating areas of high shrub productivity associated with water tracks and riparian areas, areas typically unsuitable for ground squirrels and likely not influenced by AGS activities.

Using the burrow GPS points collected, polygons of each of the land cover classes associated with each layer were evaluated for their intersection with the collection of GPS points.

The vegetation cover classes that best encapsulated the GPS points consisted of dry tundra (*Salix* spp., *Arctous alpine*, *Dryas integrifolia*) and low and dwarf-shrub tundra. Surficial geology classes consisted of glacial till and glaciofluvial deposits. Finally, surficial geomorphology classes included stony and gelifluction polygons. The total modeled area was then extracted by mask. All model components were analyzed and masked in ArcGIS (Fig 3.2).

Data extraction and analysis – To determine patterns of vegetation productivity in relation to areas of heightened AGS activity, multi-ring buffers were built around each waypoint at 1 m increments up to 30 m within the masked habitat model. The non-overlapping buffers represented independent measurements of the pixels found within each buffer. NDVI, shrub height, and shrub biomass data were extracted using the Focal Statistics as Table tool in ArcGIS.

For comparison, random points were also generated within the modeled site (n=37) to serve as a control. The control points were generated using the Random Points Tool in ArcGIS with a minimum allowed distance of 30 m from burrow GPS points.

For both the burrow and control sites, distance intervals were grouped into 5 m increments (6 total). The mean pixel values were evaluated per each distance interval using a Kruskal-Wallis rank sum test with a Dunn's post hoc test and Bonferroni correction. Burrow and control data were then compared using a Spearman's rank correlation to determine the association between the two ranked variables. We then performed separate regressions of burrow and control data and distance. All data were analyzed in R (version 3.2.3).

3.2.4 Abiotic and stable isotope data

To compare potential abiotic differences between AGS and non-AGS sites, volumetric moisture, temperature and thaw depth were measured at each of the sampling sites. Volumetric moisture was measured at a depth of 12 cm with a soil moisture probe (HydroSense II, Campbell Scientific, Logan, UT). Temperature was also measured at a depth of 12 cm using a soil thermometer (Hanna Instruments, Woonsocket, RI). Five measurements were taken at random

within the 1 m² quadrats and averaged. The measurements were then square-root transformed to achieve assumptions of normality. The data from within colonies and in control plots were then compared using a Welch's T-test.

Plant, soil, and fecal samples were collected in early August 2016 within nine independent, active squirrel colonies approximately 150 m apart. For each colony site, paired samples were collected in nearby, undisturbed plots approximately 10 m away from the colony collection site. Active burrow sites were defined by the evidence of fresh digging and fecal matter within burrow entrances.

At each active burrow site, leaf and stems samples were collected from both *Salix* spp. and *Betula* spp. when present. Six subsamples (stems and leaves) were taken from each shrub within 1 m² quadrats centered around an active burrow. Stems with evidence of current herbivory or deformity from previous season herbivory were avoided. Stems and leaves were then separated, choosing only the primary, apical growth of the current growing season for analysis. Six stem subsamples were also taken from shrubs in the control plots and similarly processed.

Three 10 cm deep soil cores were collected at each site: 1) within the entrance of the active burrow 2) directly adjacent to each burrow within the 1 m² quadrat and 3) in the nearby, control plots with no burrows approximately 10 m from burrows. Cores were separated into the top and bottom 5 cm and stored at -20°C until processed. Fresh fecal samples were collected from each of the colony sites and also kept frozen until analysis.

All samples were dried to a constant weight at 55°C and homogenized in a ball mill (SPEX SamplePrep Mixer/Mill 8000D). Once dry, soil samples were passed through a 2 mm sieve to remove rocks and bulk organic material. Stem, leaf, and fecal samples were then weighed at 4 mg and soils were weighed at 15-20 mg (depending on organic material content) into tin cups. C and N content (%), $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ values were then determined using a Thermo Delta V isotope ratio mass spectrometer (IRMS) interfaced to a NC2500 elemental analyzer. All analyses were conducted at the Cornell University Stable Isotope Laboratory.

To examine the differences by species and location for stem and leaf samples, we tested for differences in elemental and isotopic values using two-way ANOVAs with location (burrow and control) and species (*Salix* spp. and *Betula* spp.) as group variables, and the interaction effect between location and species.

To examine the differences in elemental and isotopic values by depth, the overall N and $\delta^{15}\text{N}$ of the top and bottom 5 cm soil cores were first analyzed using a Welch's T-test. C and N content, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were then analyzed using a one-way ANOVA to determine differences within the top 5 cm for each location (burrow, adjacent, and control). N content values were \log_{10} transformed to achieve assumptions of normality. We also examined the role of the abiotic variables (thaw depth, temperature and moisture) on N content and $\delta^{15}\text{N}$ of the total core (10 cm) using separate ANCOVAs with N content and $\delta^{15}\text{N}$ as dependent variables, location as a grouping variable, and thaw depth, temperature, and moisture as covariates.

3.3 Results

3.3.1 Satellite data

Burrow NDVI differed significantly by distance from burrow center ($H=29.961$, $P<0.001$; Fig. 3.3). The NDVI of control plots did not differ by distance ($H=4.206$, $P=0.52$; Fig. 3a). The post hoc analysis of the burrow sites revealed that NDVI is highest within the first 15 m (Table 2). Burrow shrub height also differed significantly with distance ($H=30.4503$, $P<0.001$). Heights were generally lower between 5 and 15 m from all other distances within the 30 m radius of burrows (Table 3.2). Control shrub heights did not differ with distance ($H=4.732$, $P=0.45$). Burrow shrub biomass differed significantly with distance ($H=12.851$, $P=0.02$) but only between the first 5 m and 10 m ($P=0.015$). The first 5 m did, however, differ from all other distances at the 90% confidence interval (Table 3.2).

Burrow NDVI was negatively correlated with control sites ($R_s=-0.528$, $P=0.003$; Fig. 4a). Burrow shrub biomass was negatively correlated with control sites ($R_s=-0.576$, $P=0.001$; Fig.

4b). In contrast, burrow shrub height and control shrub height were positively correlated ($R_s=0.393$, $P=0.032$; Fig. 4c). With the linear regression, we found a higher intercept for NDVI at burrow sites. But the intercept for height and biomass was higher in control sites versus burrow sites (Figure 3.5).

3.3.2 Abiotic data

Volumetric water content was significantly lower near burrows than in non-burrow control plots (Welch's T-test, $t_{106,01}=-4.508$, $P<0.001$; Figure 3.6). Mean water content near burrows was $13.92\% \pm 0.88$ versus $20.77\% \pm 1.25$ near controls at 12 cm. Thaw depth and temperature were significantly higher near burrows than in control plots (Welch's T-test, $t_{95,936}=10.894$, $P<0.001$ and $t_{94,044}=3.645$, $P<0.001$, respectively; Figure 3.6). Thaw depth near burrows was, on average, 20.3 cm deeper than controls. Burrows were 1.72°C warmer than controls at 12 cm.

3.3.3 Elemental and isotope data

Stems and leaves – Nitrogen content of stems was significantly greater near burrows than in control plots (ANOVA $F_{1,26}=9.594$ $P=0.005$) with a higher concentration of N in *Salix* spp. near burrows. The mean N content of *Salix* spp. was $1.57\% \pm 0.05$ (s.e.m) near burrows versus $1.35\% \pm 0.06$ near controls. The $\delta^{15}\text{N}$ value was significant between location and species (ANOVA $F_{1,26}=5.751$, $P=0.024$). Mean $\delta^{15}\text{N}$ values in *Salix* spp. were higher near burrows than controls ($F_{1,10}=9.806$, $P=0.012$). The mean $\delta^{15}\text{N}$ of *Salix* was -1.25 ± 0.74 and -4.10 ± 0.53 per mil in burrows and controls, respectively. There was no significant difference with *Betula* spp. ($F_{1,16}=0.36$, $P=0.557$).

There was a significant difference in C content in leaves by species ($F_{1,27}= 8.702$, $P=0.006$), with an overall higher C concentration in *Betula* spp. ($51.1\% \pm 0.17$) than in *Salix* spp. ($49.9\% \pm 0.43$). $\delta^{13}\text{C}$ differed by species ($F_{1,27}=28.823$, $P<0.001$). Mean $\delta^{13}\text{C}$ was lower in *Betula*

spp. Values were lower at both burrow (-29.3 ± 0.17) and controls (-29.0 ± 0.21) versus *Salix* spp. burrow (-27.7 ± 0.46) and controls (-27.7 ± 0.29).

The N content of leaves differed significantly by location ($F_{1,27}=5.608$, $P=0.025$) and species ($F_{1,27}=11.997$, $P=0.002$), and was higher in *Salix* spp. near burrows (Fig. 3.7). The interaction between location and species on $\delta^{15}\text{N}$ was significant ($F_{1,26}=4.314$, $P=0.045$). Values were higher in *Salix* spp. near burrows ($F_{1,10}=9.148$, $P=0.012$; Fig. 3.7).

Soil – Among the three locations, soil N content was higher in the top 5 cm versus the bottom 5 cm amongst all sites (Welch's T-test $t_{46,653}=2.596$, $P=0.013$). Within the bottom 5 cm core, N content and $\delta^{15}\text{N}$ values did not differ by location. Within the top 5 cm, N content was significantly lower near burrows (ANOVA $F_{2,24}=13.07$, $P<0.001$), compared to the adjacent (Tukey's HSD $P=0.031$) and control sites (Tukey's HSD $P<0.001$). However, $\delta^{15}\text{N}$ values were significantly higher near burrows (ANOVA $F_{2,24}=8.491$, $P=0.002$; 3.07 ± 0.180 per mil, mean \pm s.e.m) than the adjacent (Tukey's HSD $P=0.012$; 2.05 ± 0.398) and the control sites (Tukey's HSD $P=0.002$; 1.78 ± 0.532 ; Fig. 3.8).

Results of the ANCOVA revealed no relationship between location and moisture on $\delta^{15}\text{N}$ values ($F_{2,21}=0.155$, $P=0.858$), thaw depth ($F_{2,21}=0.450$, $P=0.644$), or soil temperature ($F_{2,21}=0.1065$, $P=0.363$). For the N content, results of the ANCOVA showed no interaction between moisture and location on N content ($F_{2,21}=0.796$, $P=0.464$) or thaw depth ($F_{2,21}=0.169$, $P=0.846$). There was a significant interaction between temperature and location on N content (ANCOVA $F_{2,21}=3.982$, $P=0.034$). N content increases with increasing temperature within burrows (ANOVA $F_{1,7}=6.229$, $P=0.041$).

3.4 Discussion

Analysis of the satellite imagery revealed higher NDVI and shrub biomass near burrows than non-burrow sites (Figs. 3a and 3c, respectively). Mean NDVI values were significantly higher within the first 15 m of burrows (0.42) than from 15-30 m (0.41). Mean biomass values

were significantly greater within 5 m of burrows (302.5 g/m^2) than after 5 m (232.2 g/m^2). Heights were significantly shorter near burrows (Fig. 3b). Mean height in the first 15 m was lower (0.027 m) versus after 15 m (0.028 m). Our results taken together suggests and influence of AGS on ecosystem structure to at least a 30 m radius from colony centerpoints.

NDVI metrics (Figs. 4a and 5a, respectively) support the notion that AGS affect local productivity. NDVI shows both a negative correlation with controls ($R_s = -0.528$, $P = 0.003$) and a higher intercept than control values (Fig. 4a). Results of the elemental and isotopic analysis mirror this trend, suggesting a fertilization effect in shrubs near burrows. Soil $\delta^{15}\text{N}$ values were significantly more enriched near burrows than in control plots, which is also consistent with animal fertilization via fecal matter and urine deposits. Stem and leaf $\delta^{15}\text{N}$ values were specifically enriched in *Salix* spp. Taken together, it is possible that AGS are actively engineering their local ecosystem and promoting the growth of *Salix* spp within the dry heath.

To date, climate manipulation studies within the dry heath have not confirmed a species-specific advantage in *Betula* or *Salix* to fertilization or warming when grown together (Gough et al. 2002, Graglia et al. 1997, Grellmann 2002). Studies typically analyze species together within a functional group (i.e. deciduous shrubs). Graglia et al. (1997) found an effect of fertilization, warming, and shading on the productivity of *Salix polaris* within fellfield habitats, though not within the dry heath. Alternatively, ecosystem manipulation studies in the moist acidic tundra highlight the physiologically competitive advantage of *Betula* spp. in response to both fertilization and warming (Bret-Harte et al. 2001, Chapin et al. 1995, Shaver et al. 2001), playing a dual role with secondary metabolites in the suspected proliferation of species high in defense compounds (Bryant et al. 2014). Our results therefore suggest that shrub expansion may be treatment (fertilization and warming) and habitat-specific. Expansion will therefore be spatially heterogeneous, with the potential for AGS to contribute to this heterogeneity.

Recent research confirms that encroachment is not ubiquitous throughout the Arctic. Some shrub patches are rapidly expanding (infilling and increasing in extent) while others remain stable (Myers-Smith et al. 2011b, Tape et al. 2012). This landscape heterogeneity is attributed to several abiotic factors within microhabitats including growing season temperature, precipitation, host soil characteristics, surficial geology and topography (Tape et al. 2012). Expanding shrub patches are typically lower in standing soil moisture (both organic and mineral), higher in soil temperatures and have greater thaw depths than nearby, stable patches (Tape et al. 2012). Likewise, areas near AGS burrows sustain significantly lower soil moisture, higher soil temperature and greater thaw depths than nearby, non-burrow controls (Fig. 3.6), therefore potentially priming soils for growth. The positive effect of warming on nutrient cycling near AGS burrows was indeed confirmed via the significant increase in N content near burrows related to higher temperatures (Fig. 3.8).

AGS-induced fertilization of *Salix* spp. may provide an important ecosystem service to Arctic herbivores that preferentially forage on *Salix*. *Salix* is relatively fast growing, typically lower in plant secondary metabolites, and highly tolerant to herbivory, making it a preferred forage of many Arctic species (Chapter 1). Additionally, by significantly increasing the N content and lowering the C/N ratio of *Salix* spp., this will help improve litter quality and increase nitrogen mobility, creating a positive feedback on localized NPP (Olofsson & Oksanen 2002). By promoting the success of *Salix* spp., this may have important ramifications for the anticipated spread of *Betula* subspecies that are higher in lignans and plant secondary metabolites, through a depression via interspecific competition for resources.

It is important to note that the possible influence of AGS on NDVI may be more robust than illustrated. NDVI values within the immediate vicinity of burrows include exposed soil and earthen piles (low NDVI), thereby lowering the NDVI signal of the plot compared to controls. Our study also used NDVI values derived via satellite acquired slightly after peak growing season due to cloud cover (imagery dated August 7). Additionally, 2015 was both warmer and drier

across Alaska than average, resulting in early senescence at Toolik Field Station. Peak fall occurred in early August in 2015 versus late August in 2016, as reported by the Toolik Lake Field Station Environmental Data Center (https://toolik.alaska.edu/edc/biotic_monitoring/plant_phenology.php). Our results are therefore conservative yet still highlight the role of AGS on shrub abundance and growth.

3.5 Future Research

NDVI available via satellite imagery and LiDAR-derived metrics are valuable tools for monitoring shrub encroachment and vegetation productivity, especially in relation to small mammal habitats. The purpose of this study was to highlight the potential positive influence of AGS activities (nitrogen deposition and bioturbation) on nearby plant vitality, attempting to determine whether AGS will serve as drivers of global change-induced Arctic shrub expansion.

Future research could utilize hyper-spectral imagery to help identify species-specific spectral signatures, better clarifying vegetation species-specific patterns in relation to AGS burrows at broader scales. To refine the results of the isotopic analysis and contribution of AGS to nutrient dynamics, isotopically labeled foods could be used in a $\delta^{15}\text{N}$ -enriched tracer study to determine the output of urine and fecal matter and uptake into plants (Barthelemy et al. 2017). Additionally, research could include a temporal component to determine changes in NDVI, biomass and height associated with AGS emergence and mating (April), pup-weaning (mid-June), and peak growing season (late July), as well as changes in soil and foliar N content and $\delta^{15}\text{N}$.

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3.7 References

- Barker OE, Derocher AE (2010) Habitat selection by arctic ground squirrels (*Spermophilus parryii*). *J Mammal* 91:1251–1260. doi: 10.1644/10-MAMM-A-030.1
- Barrio IC, Bueno CG, Gartzia M, et al (2016) Biotic interactions mediate patterns of herbivore diversity in the Arctic. *Glob Ecol Biogeogr*. doi: 10.1111/geb.12470
- Barthelemy H, Stark S, Michelsen A, Olofsson J (2017) Urine is an important nitrogen source for plants irrespective of vegetation composition in an Arctic tundra: Insights from a ¹⁵N-enriched urea tracer experiment. *J Ecol* 1–12. doi: 10.1111/1365-2745.12820
- Barthelemy H, Stark S, Olofsson J (2015) Strong responses of subarctic plant communities to long-term reindeer feces manipulation. *Ecosystems* 18:740–751. doi: 10.1007/s10021-015-9856-y
- Batzli GO, Sobaski ST (1980) Distribution, abundance, and foraging patterns of ground squirrels near Atkasook, Alaska. *Arct Alp Res* 12:501–510.
- Bråthen KA, Ims RA, Yoccoz NG, et al (2007) Induced shift in ecosystem productivity? Extensive scale effects of abundant large herbivores. *Ecosystems* 10:773–789. doi: 10.1007/s10021-007-9058-3
- Bret-Harte MS, Shaver GR, Zoerner JP, et al (2001) Developmental plasticity allows *betula nana* to dominate tundra subjected to an altered environment. *Ecology* 82:18–32. doi: 10.1890/0012-9658(2001)082[0018:DPABNT]2.0.CO;2
- Bryant JP, Chapin, F Stuart I, Klein DR (1983) Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* 40:357–368. doi: 10.2307/3544308
- Bryant JP, Joly K, Chapin FS, et al (2014) Can antibrowsing defense regulate the spread of woody vegetation in arctic tundra? *Ecography (Cop)* 37:204–211. doi: 10.1111/j.1600-0587.2013.00436.x
- Carl EA (1971) Population control in arctic ground squirrels. *Ecology* 52:395. doi: 10.2307/1937623
- Chapin FS, Shaver GR, Giblin AE, et al (1995) Responses of Arctic tundra to experimental and observed changes in climate. *Ecology* 76:694–711. doi: 10.2307/1939337
- Gharajehdaghypour T, Roth JD, Fafard PM, Markham JH (2016) Arctic foxes as ecosystem engineers: increased soil nutrients lead to increased plant productivity on fox dens. *Sci Rep* 6:24020. doi: 10.1038/srep24020
- Gillis EA, Morrison SF, Zazula GD, Hik DS (2005) Evidence for selective caching by Arctic ground squirrels living in alpine meadows in the Yukon. *Arctic* 58:354–360.
- Gough L, Wookey PA, Shaver GR (2002) Dry heath Arctic tundra responses to long-term nutrient and light manipulation. *Arctic, Antarct Alp Res* 34:211–218.
- Graglia E, Jonasson S, Michelsen A, Schmidt IK (1997) Effects of shading, nutrient application

and warming on leaf growth and shoot densities of dwarf shrubs in two arctic-alpine plant communities. *Ecoscience* 4:191–198. doi: 10.2307/42900727

- Greaves HE, Vierling LA, Eitel JUH, Boelman NT, Magney TS, Prager CM, Griffin KL (2016) High-resolution mapping of aboveground shrub biomass in Arctic tundra using airborne Lidar and imagery. *Remote Sens Environ* 184: 361–373. doi:10.1016/j.rse.2016.07.026.
- Grellmann D (2002) Plant responses to fertilization and exclusion of grazers on an arctic tundra heath. *Oikos* 98:190–204. doi: 10.1034/j.1600-0706.2002.980202.x
- Karels TJ, Boonstra R (1999) The impact of predation on burrow use by arctic ground squirrels in the boreal forest. *Proc Biol Sci* 266:2117–2123. doi: 10.1098/rspb.1999.0896
- Karels TJ, Byrom AE, Boonstra R, Krebs CJ (2000) The interactive effects of food and predators on reproduction and overwinter survival of Arctic ground squirrels. *J Anim Ecol* 69:235–247. doi: 10.1046/j.1365-2656.2000.00387.x
- Mckendrick JD, Batzli GO, Everett KR, et al (1980) Some effects of mammalian herbivores and fertilization on tundra soils and vegetation. *Arct Alp Res Arct and Alpine Res* 12:565–578. doi: 10.2307/1550501
- Myers-Smith IH, Forbes BC, Wilking M, et al (2011a) Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environ Res Lett* 6:45509. doi: 10.1088/1748-9326/6/4/045509
- Myers-Smith IH, Hik DS (2013) Shrub canopies influence soil temperatures but not nutrient dynamics: An experimental test of tundra snow-shrub interactions. *Ecol Evol* 3:3683–3700. doi: 10.1002/ece3.710
- Myers-Smith IH, Hik DS, Kennedy C, et al (2011b) Expansion of canopy-forming willows over the twentieth century on Herschel Island, Yukon Territory, Canada. *Ambio* 40:610–623. doi: 10.1007/s13280-011-0168-y
- Newton EJ, Pond BA, Brown GS, et al (2014) Remote sensing reveals long-term effects of caribou on tundra vegetation. *Polar Biol* 37:715–725. doi: 10.1007/s00300-014-1472-3
- Olofsson J, Oksanen L (2002) Role of litter decomposition for the increased primary production in areas heavily grazed by reindeer: a litterbag experiment. *Oikos* 96:507–515. doi: 10.1034/j.1600-0706.2002.960312.x
- Olofsson J, Tømmervik H, Callaghan T V. (2012) Vole and lemming activity observed from space. *Nat Clim Chang* 2:880–883. doi: 10.1038/nclimate1537
- Pajunen A, Virtanen R, Roininen H (2012) Browsing-mediated shrub canopy changes drive composition and species richness in forest-tundra ecosystems. *Oikos* 121:1544–1552. doi: 10.1111/j.1600-0706.2011.20115.x
- Pettorelli N, Vik JO, Myrsetrud A, et al (2005) Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends Ecol Evol* 20:503–510. doi: 10.1016/j.tree.2005.05.011

- Price LW (1971) Geomorphic effect of the Arctic ground squirrel in an alpine environment. *Source Geogr Ann Ser A, Phys Geogr* 53:100–106.
- Shaver GR, Bret-Harte MS, Jones MH, et al (2001) Species composition interacts with fertilizer to control long-term change in tundra productivity. *Ecology* 82:3163–3181. doi: 10.1890/0012-9658(2001)082[3163:SCIWFT]2.0.CO;2
- Sturm M, Racine C, Tape K (2001) Climate change. Increasing shrub abundance in the Arctic. *Nature* 411:546–547. doi: 10.1038/35079180
- Tape K, Sturm M, Racine C (2006) The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Glob Chang Biol* 12:686–702. doi: 10.1111/j.1365-2486.2006.01128.x
- Tape KD, Hallinger M, Welker JM, Ruess RW (2012) Landscape heterogeneity of shrub expansion in Arctic Alaska. *Ecosystems* 15:711–724. doi: 10.1007/s10021-012-9540-4
- Van Der Wal R, Bardgett RD, Harrison KA, Stien A (2004) Vertebrate herbivores and ecosystem control: Cascading effects of faeces on tundra ecosystems. *Ecography* 27:242–252. doi: 10.1111/j.0906-7590.2004.03688.x
- Wheeler HC, Chipperfield JD, Roland C, Svenning JC (2015) How will the greening of the Arctic affect an important prey species and disturbance agent? Vegetation effects on arctic ground squirrels. *Oecologia* 178:915–929. doi: 10.1007/s00442-015-3240-7
- Wheeler HC, Hik DS (2014) Giving-up densities and foraging behaviour indicate possible effects of shrub encroachment on arctic ground squirrels. *Anim Behav* 95:1–8. doi: 10.1016/j.anbehav.2014.06.005
- Zazula GD, Mathewes RW, Harestad AS (2006) Cache selection by arctic ground squirrels inhabiting Boreal-steppe meadows of southwest Yukon territory, Canada. *Arctic, Antarct Alp Res* 38:631–638. doi: 10.1657/1523-0430(2006)38[631:CSBAGS]2.0.CO;2

Table 3.1. Spectral and spatial resolution of WV-3 imagery acquired on August 7, 2015.

Layer	Spatial Resolution (m)	Band	Band Range	Band Name
WorldView-3	0.31	Pan	450-800	Panchromatic
	1.24	1	400-450	Coastal
		2	450-510	Blue
		3	510-580	Green
		4	585-625	Yellow
		5	630-690	Red
		6	705-745	Red Edge
		7	770-895	NIR1
		8	860-1040	NIR2

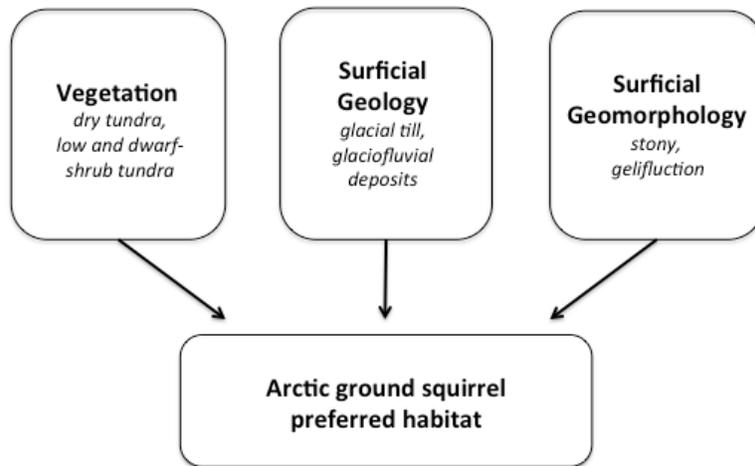


Figure 3.1. Arctic ground squirrel habitat model inputs.

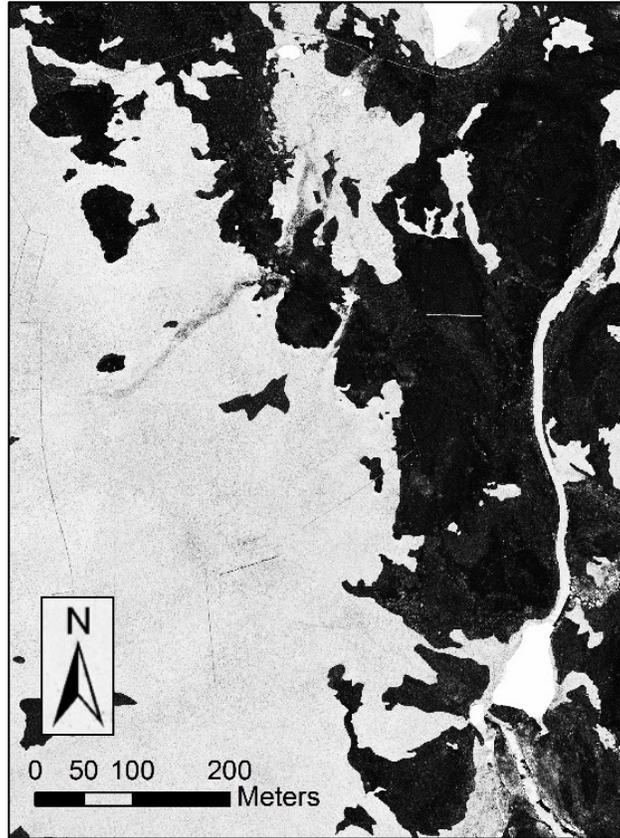


Figure 3.2. Total study area. Modeled Arctic ground squirrel habitat shown in dark. *Image courtesy of the DigitalGlobe Foundation.*

Table 3.2. Results of the Dunn's post hoc with Bonferroni correction for pair-wise comparisons for all burrow distances. *P*-values shown 95% confidence. Asterisks 90% confidence intervals.

Layer	Distance	Mean \pm s.e.m		Z-score	P-value
NDVI	5-20	0.421 \pm 0.003	0.041 \pm 0.001	-3.109	0.014
	5-25	0.421 \pm 0.003	0.423 \pm 0.002	-3.328	0.007
	5-30	0.421 \pm 0.003	0.413 \pm 0.002	-2.928	0.026
	10-20	0.423 \pm 0.002	0.041 \pm 0.001	3.295	0.007
	10-25	0.423 \pm 0.002	0.423 \pm 0.002	3.507	0.003
	10-30	0.423 \pm 0.002	0.413 \pm 0.002	3.099	0.015
	15-20	0.423 \pm 0.002	0.041 \pm 0.001	2.971	0.022
	15-25	0.423 \pm 0.002	0.423 \pm 0.002	3.188	0.011
	15-30	0.423 \pm 0.002	0.413 \pm 0.002	2.827	0.035
Height (m)	5-30	0.03 \pm 0.015	0.029 \pm 0.0007	2.837	0.034
	10-20	0.026 \pm 0.001	0.028 \pm 0.0007	-3.019	0.019
	10-25	0.026 \pm 0.001	0.027 \pm 0.001	-3.722	0.002
	10-30	0.026 \pm 0.001	0.029 \pm 0.0007	-4.587	<0.001
	15-25	0.027 \pm 0.001	0.027 \pm 0.001	-2.747	0.045
	15-30	0.027 \pm 0.001	0.029 \pm 0.0007	-3.656	0.002
Biomass (g/m ²)	5-10	303 \pm 14	241 \pm 10	-3.068	0.016
	5-15	303 \pm 14	236 \pm 9	-2.630	0.064*
	5-20	303 \pm 14	232 \pm 8	-2.476	0.099*
	5-25	303 \pm 14	236 \pm 9	-2.559	0.079*

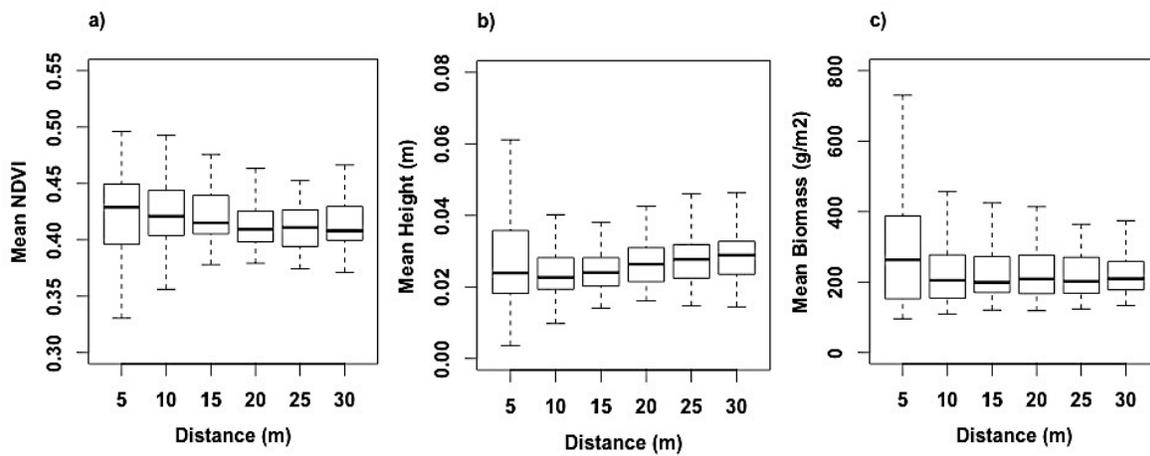


Figure 3.3. Effect of distance on a) mean NDVI b) mean height and c) mean biomass by distance within areas of high AGS activity.

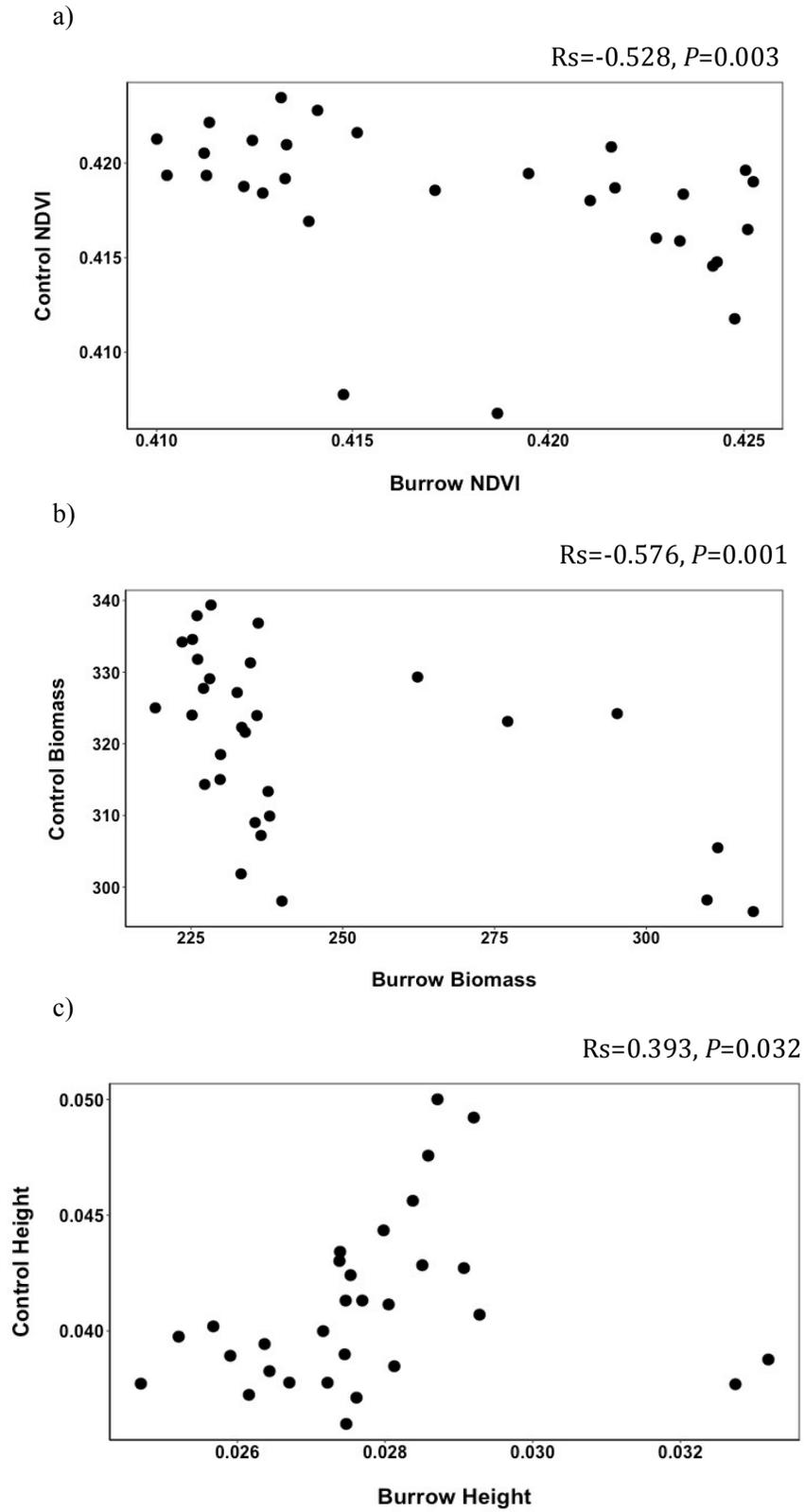


Figure 3.4. Spearman's rank order correlation of a) NDVI b) biomass and c) height for control (n=37) and burrow (n=37) sites.

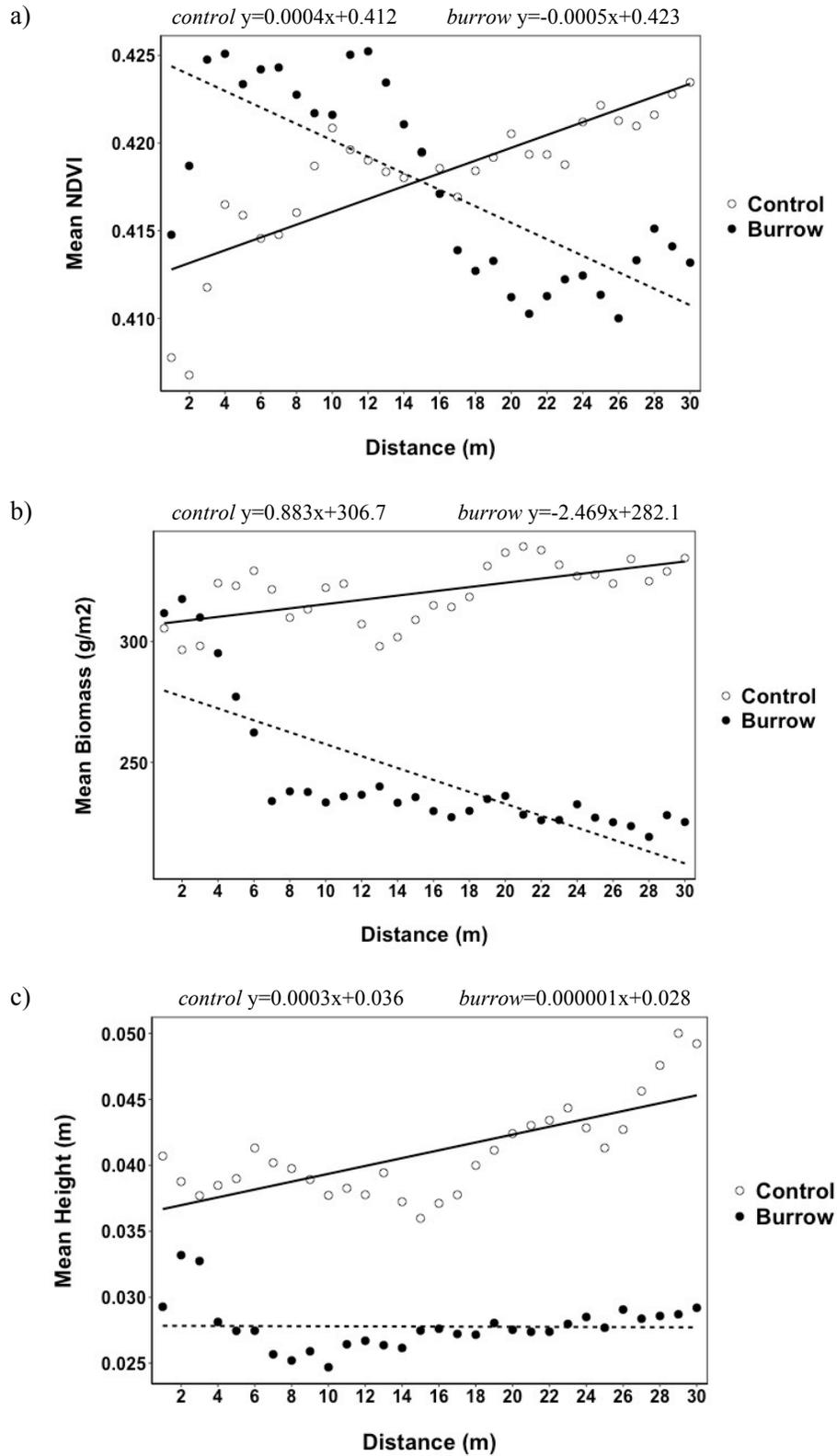


Figure 3.5. Regression of mean pixel values per distance for a) NDVI b) biomass and c) height for control (n=37) and burrow (n=37) sites.

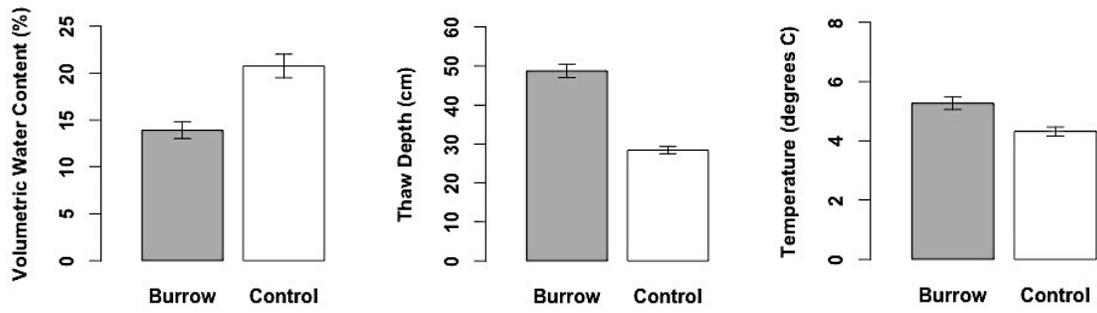


Figure 3.6. Mean \pm s.e.m burrow versus control values of volumetric water content, thaw depth and temperature.



Figure 3.7. N content (%) and $\delta^{15}\text{N}$ values in leaves sampled within colonies and in nearby, non-burrow locations.

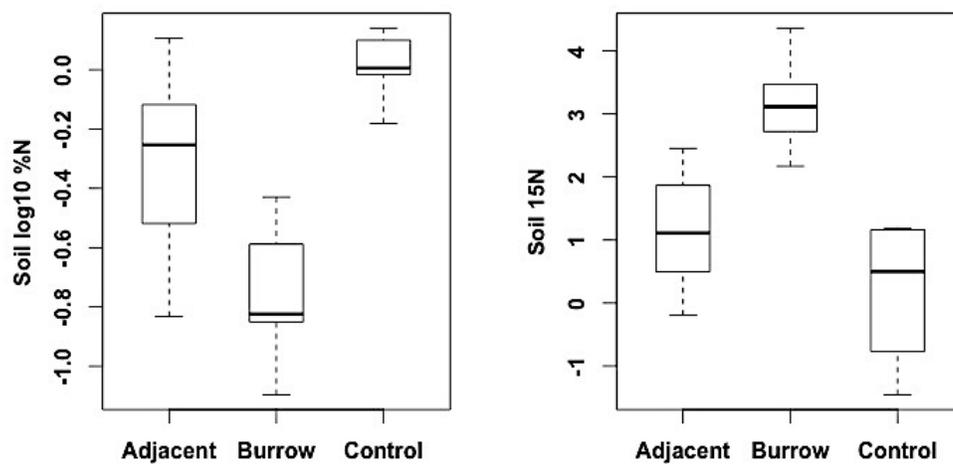


Figure 3.8. Log₁₀ soil N content (%) and δ¹⁵N values within the top 5 cm of each of the cored locations (adjacent, burrow and control).

VITA

NAME Jennifer E. Dalton

EDUCATION B.A. Communications Studies
University of Michigan, Ann Arbor, MI
1996-2000

TEACHING EXPERIENCE

BIOS 230 Ecology and Evolution (Spring 2017)
BIOS 220 Mendelian and Molecular Genetics (Fall 2016)
BIOS 101 Populations and Communities (Fall 2015, Spring 2016)

PUBLICATIONS

Flower CE, Dalton JE, Brown JS, Gonzalez-Meler MA, and Whelan CJ. 2017. Patch use in the Arctic ground squirrel: Implications for projected shrub encroachment (*Submitted*).

Flower CE, Dalton JE, Knight KS, Brikha M, Gonzalez-Meler MA. 2015. To treat or not to treat: Diminishing effectiveness of emamectin benzoate tree injections in ash trees heavily infested by emerald ash borer. *Urban Forestry and Urban Greening*. 14(4): 790-795.

POSTERS/PRESENTATIONS

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GRANTS/AWARDS

UIC Graduate Teaching Award – 2017, 2016
NSF Graduate Research Fellowship Program – Honorable Mention – 2016
Digital Globe Foundation Imagery Grant – WorldView-3 image of the North Slope of Alaska – 2016
American Society of Mammalogists Grants-In-Aid – 2016

VOLUNTEER ACTIVITIES AND MEMBERSHIPS

Northwestern University Science in Society – Science Club Mentor – August 2016-May 2017
Lincoln Park Zoo – Animal Behavior Monitor – April 2015-February 2016
Girls Empowered by Math and Science (GEMS) – Presenter/Session Leader – April 2016
Chicago Botanic Garden – Volunteer Fruit and Vegetable & Berm Gardens – 2012-2013

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