NTNU
Norwegian University of
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Master's thesis

2020

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Science and Technology
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Herbivory Moderates the Positive Effect of Climate Warming on Shrub Growth in Northern Interior Alaska

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Natural Resources Management
Submission date: May 2020
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Abstract

Climate warming is a primary driver of observed increases in shrub growth and productivity across the circumpolar arctic. This proliferation of shrub biomass has altered the structure and composition of northern plant communities with cascading effects on arctic ecosystems. However, the extent to which vertebrate herbivores moderate shrubs growth responds to warming remains unclear. In this study, I used a dendroecological approach to disentangle the relative effects and interactions of climate and herbivory on the radial growth of the deciduous shrubs at Alaska's boreal tundra ecotone. I established annual radial growth chronologies for 323 stem samples from two deciduous shrubs with markedly different growth habits and palatability, dwarf birch (*Betula nana*) and willow (*Salix spp.*). I used these chronologies to determine the growth response of each species to mean summer temperature and precipitation as well as browsing pressure from moose, snowshoe hare and ptarmigan. The results of my analysis revealed positive growth trends for both shrub species over the 28-year study period, which were sensitive to temporal variation in both climate and herbivore abundance. I found that climate, specifically summer temperature, is a strong driver of observed increases in the radial growth of both dwarf birch and willow shrubs. Furthermore, I provide evidence that spatial and temporal fluctuations in the abundance of moose, snowshoe hare and ptarmigan interact with and partially offset the positive effect of summer temperature on shrub growth. However, when the influence of herbivory is considered relative to summer temperature, I find that summer temperature is generally a stronger driver of shrub growth. Thus, I conclude that at current densities herbivores moderate but do not fully counteract the positive effects of climate warming on deciduous shrub growth in northern interior Alaska. This study illustrates that herbivores, even at low densities, can impact shrub's growth response to climate warming, and highlights the need to consider herbivory in future efforts to model or predict vegetation state transitions at the boreal-tundra ecotone.

Keywords: Willow, Dwarf Birch, Moose, Snowshoe Hare, Ptarmigan, Climate Change, Boreal, Tundra, Dendroecology

Preface

This master thesis was written at the Norwegian University of Science and Technology (NTNU) University Museum in Trondheim with financial support from the Disentangle project. This project was written and developed by Dr. James Speed and was funded through the Research Council of Norway's FRIPRO Young Research Talents program (#262064). Portions of the data presented here will be utilized in the doctoral thesis of the author's co-supervisor Katariina Vuorinen as well as in subsequent manuscripts to be submitted for publication by the author and his advisors.

Fieldwork for this research was conducted on lands administered by the United States Bureau of Land Management Central Yukon Field Office. Prior to fieldwork, a proposal for sites access and destructive sampling was sent to and reviewed by Bureau of Land Management staff. The proposed activities were determined to qualify as *casual use* of public lands; defined under 43 CFR §2920.0-5(k) as "short term non-commercial activity which does not cause appreciable damage or disturbance to the public lands, their resources or improvements, and which is not prohibited by closure of the lands to such activities." Official documentation of this determination was carried at all times during fieldwork.

Acknowledgements

I would like to sincerely thank my advisors Dr. James Speed and Katariina Vuorinen for their continued support and instruction throughout this project. Dr. Speed's prudent guidance has helped usher this project through times of uncertainty to successful completion. Katariina has been an invaluable source of knowledge on the lab work, data analysis and finer details of this study. Both advisors have provided timely insight and patiently mentored me as I developed this project. Working with them has broadened my knowledge and competence as a scientist, and for that I am truly grateful.

I would also like to thank William Hedman and Sheri Wilson with the Bureau of Land Management Central Yukon Field Office for helping me obtain the necessary permitting to conduct my fieldwork on public lands. Tanja Peterson helped ensure my safety during fieldwork by acting as my point of contact for daily check-ins. Jack Reakoff invited me into his home in Wiseman and shared his deep knowledge of the area's ecology, and I thank him for his time and expertise. My fellow master's student on the Disentangle project, Hans Ivar Hortman provided many hours of helpful discussion and injected levity into otherwise arduous tasks.

Finally, a very special thanks to my fiancé Gillian for her constant support during my graduate studies, I couldn't have done it without you!

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List of Abbreviations

ADFG	Alaska Department of Fish and Game
BAI	Basal Area Increment
BLM	Bureau of Land Management
GMU	Game Management Unit
MSP	Mean Summer Precipitation
MST	Mean Summer Temperature
NTNU	Norwegian University of Science and Technology
SNAP	Scenarios Network for Alaska & Arctic Planning

1 Introduction

Tundra and boreal plant communities are changing rapidly as a result of global climate change (Myneni et al., 1998; Walker et al., 2006; Bunn et al., 2007; Post et al., 2009; Bhatt et al., 2010; Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Tape et al., 2012). Across the circumpolar arctic, one of the most apparent and ecologically significant shifts in vegetation is the poleward expansion of shrubs at boreal-tundra ecotones (Tape et al., 2006; Myers-Smith et al., 2011; Ropars and Boudreau, 2012). The expansion of tall deciduous shrub, for example, alder (*Alnus viridis*), dwarf birch (*Betula nana*), and willow (*Salix spp.*), into alpine and arctic tundra, coupled with drought-induced declines in productivity in the boreal forest are consistent with the early stages of a northward biome shift (Beck et al., 2011; Mann et al., 2012; Epstein et al., 2013). With this vegetation transition, the predicted changes in the structure and composition of northern plant communities will result in biotic and abiotic feedbacks which significantly alter nutrient cycles, hydrologic processes, surface energy dynamics and plant-herbivore interactions in this region (Chapin et al., 2005; D Blok et al., 2011; Myers-Smith et al., 2011; Yu et al., 2011; Lara et al., 2012; DeMarco, Mack, et al., 2014; Vowles and Björk, 2019).

At the root of this observed vegetation shift is an increase in shrub growth, resulting in taller shrubs and greater annual biomass production, often at the expense of bryophytes and lichens (Beck and Goetz, 2011; Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe, et al., 2012; Epstein et al., 2012). Increases in shrub growth have been documented across the circumpolar arctic through recurrent vegetation surveys (Joly et al., 2007; Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012), repeat photography (Tape et al., 2006; Brodie et al., 2019), remote sensing (Epstein et al., 2013; Naito and Cairns, 2015) and dendrochronological analyses (D. Blok et al., 2011; Tape et al., 2012; Myers-Smith, Elmendorf, et al., 2015; Ackerman et al., 2018). Yet, the patterns of shrub growth observed in these studies are not homogeneous; suggesting that there are spatial and temporal variations in shrub growth across the circumpolar arctic. The primary driver of this variability is thought to be temperature, with other abiotic factors such as precipitation, snow dynamics, and soil conditions mediating the effect of warming on shrub growth (Strum et al., 2005; Tape et al., 2012; Myers-Smith, Elmendorf, et al., 2015; Li et al., 2016; Ackerman et al., 2017; Martin et al., 2017; Myers-Smith and Hik, 2018; Weijers et al., 2018).

However, shrub growth is not dictated solely by abiotic drivers (Martin et al., 2017); herbivores exert considerable top-down trophic control on shrub communities, and as such, they have a central role in mediating the growth response of arctic shrubs to climate warming (Olofsson et al., 2009; Speed et al., 2011; Plante et al., 2014; Christie et al., 2015; Bråthen et al., 2017; Løkken et al., 2019; Vuorinen et al., 2020). Herbivores influence shrub growth directly through selective browsing and trampling as well as indirectly through the deposition of nutrients and the alteration of plant-plant competitive interactions (Jefferies et al., 1994; Hester et al., 2010; Bernes et al., 2015). Through these effects, herbivores may be able to counteract or moderate the vegetation state shifts occurring at forest-tundra ecotones (Speed et al., 2011; Vowles, 2017; Olofsson and Post, 2018). However, the magnitude and direction of herbivores' effect on shrub growth depend on spatial and temporal fluctuations in herbivore abundance and browsing pressure as well as regional shrub characteristics such as palatability and browsing tolerance (Mulder, 1999; Myers-Smith et al., 2011; Christie et al., 2015). Therefore, the degree to which herbivores can moderate shrub's growth response to climate warming is expected to vary across the circumpolar arctic (Bryant et al., 2014; Christie et al., 2015).

Among arctic ecosystems, northern interior Alaska hosts a uniquely diverse assemblage of vertebrate herbivores which occupy a wide variety of functional niches (Speed et al., 2019), potentially broadening their cumulative effects on shrub growth. As tall shrubs have expanded northward from Alaska's boreal-tundra ecotone (Tape et al., 2006; Naito and Cairns, 2015), three widely dispersed northern browsers, moose (*Alces alces*), snowshoe hare (*Lepus americanus*) and ptarmigan (*Lagopus lagopus* & *L. muta*), have followed, expanding their range and their potential influence on shrub growth (Tape, Christie, et al., 2016; Tape, Gustine, et al., 2016; Zhou et al., 2017). Through a combination of exclosure experiments and observational studies, browsing by these three herbivore species has been shown to have a strong effect on shrub's growth, architecture and reproduction; which in turn alter the species composition, canopy structure, soil chemistry and nutrient cycling in shrub-dominated communities (Post and Klein, 1996; Kielland, J. P. Bryant, et al., 2006; Butler and Kielland, 2008; Gough et al., 2012; Christie et al., 2014).

In recent years, dendroecology has increasingly become the tool of choice to study the response of arctic shrub growth to fluctuations in environmental variables such as climate and herbivory (Myers-Smith, Hallinger, et al., 2015). Shrubs, like other woody plants in seasonal environments, add radial layers of woody tissue to their stems during the growing season each year. The resulting annual growth rings, provide a record of shrub growth through time which can be used to ground truth remotely sensed trends in shrub productivity (D. Blok et al., 2011; Tape et al., 2012; Weijers et al., 2018), document shrub expansion at ecotones (Myers-Smith and Hik, 2018) and most importantly for this study, quantify the sensitivity of shrub growth to environmental factors (Myers-Smith, Elmendorf, et al., 2015; Young et al., 2016; Gamm et al., 2018). Several dendroecological studies have assessed the drivers of shrub growth in northern interior Alaska (Tape et al., 2012; Ackerman et al., 2017, 2018), however, these studies only take into account abiotic factors, leaving the potential moderating effect of herbivory unaccounted for. The few studies from other regions, which have employed this technique to disentangle the effects climate and herbivory on shrub growth (Speed et al., 2011, 2013; Le Moullec, 2019; Vuorinen et al., 2020), focus primarily on domesticated or heavily managed herbivore systems.

Therefore, in this study, I seek to assess the relative effects and interactions of climate and herbivory on the radial growth of deciduous shrubs at the boreal-tundra ecotone in northern interior Alaska using a dendroecological approach. This region of Alaska, while broadly impacted by the effects of global climate change (Hinzman et al., 2005), has remained largely untrammeled by other anthropogenic incursions (Trammell and Aisu, 2015). This provides a unique opportunity to further our understanding of the drivers influencing shrub growth in Alaska, while providing a counterpoint to similar dendroecological studies conducted in regions of higher human intervention. Understanding the effect that climate and herbivory have on shrub growth will have important implications for predicting the impact of future state shifts at the boreal-tundra ecotone and will help to inform potential herbivore management strategies for this region. By assessing changes in the radial growth of shrubs under different climatic and browsing pressures, I seek to address the following hypotheses: (1) Increased temperature and precipitation will have a positive effect on shrub radial growth, (2) Increased abundance of moose, snowshoe hare and ptarmigan will have a negative effect on shrub radial growth, (3) The effects of temperature and herbivory will interact such that as temperature increases the negative effect of herbivory on shrub radial growth will decrease and be eventually negated.

2 Methods

2.1 Study Area

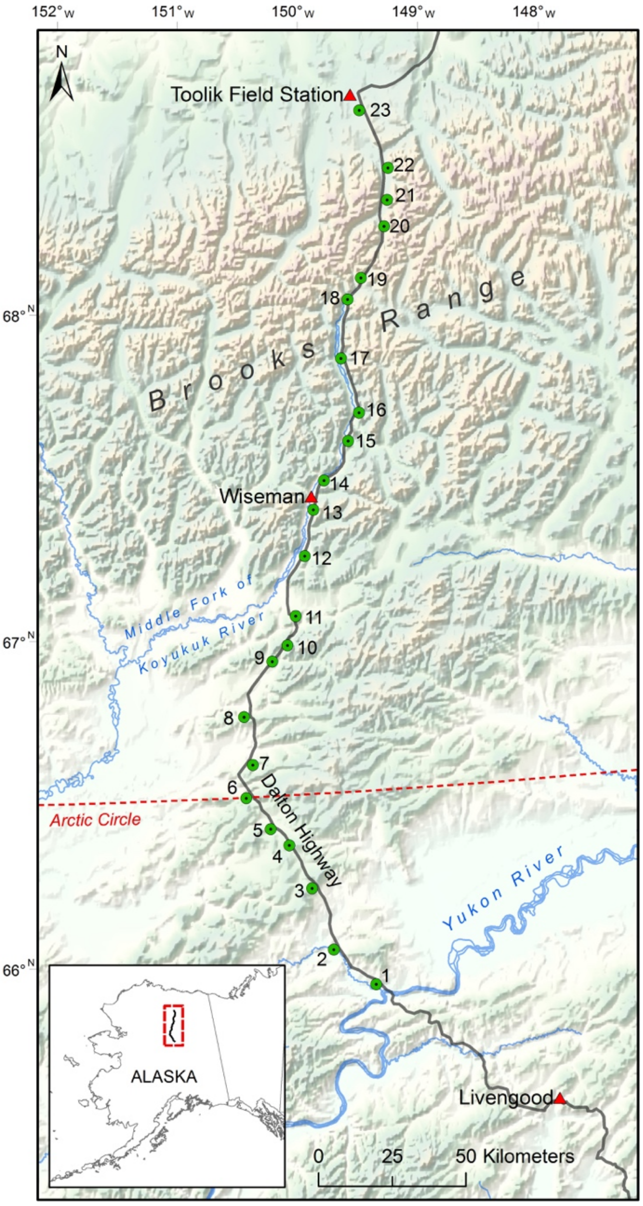

Figure 1. Map of study area showing sampling sites along the Dalton Highway (green points)

This study was conducted along a 370 kilometer stretch of the Dalton Highway (Figure 1), in northern interior Alaska, between the Yukon River (N 65.879, W 149.717) and the Toolik Field Station (N 68.633, W 149.551). The Dalton Highway is a north-south thoroughfare that transects the latitudinal gradient between Alaska's boreal, alpine and tundra biomes. Portions of the study area south of the Brooks Range are underlain by discontinuous permafrost with vegetation cover dominated by mixed white spruce (*Picea glauca*) and black spruce (*Picea mariana*) boreal forest, with alpine tundra at elevations above 800 to 900 meters (Huryn and Hobbie, 2013). To the north, through the Brooks Range and onto Alaska's North Slope, permafrost becomes continuous and the vegetation transitions from the alpine to arctic tundra where the dominant woody species include dwarf birch (*Betula nana*), willows (*Salix spp.*) and Siberian alder (*Alnus viridis*). The study area is within Alaska's interior climatic zone, which is characterized by extreme seasonal temperature fluctuations, from average summer maximum temperatures of 21.9°C, to average winter minimum temperatures of -29.3°C. The mean annual temperature across the study area between 1987 and 2015 was -6.9°C. Mean annual precipitation during this period was 19.1 cm, with the majority of precipitation occurring during the growing season between June and August (Cherry et al., 2014; SNAP, 2019). Variation in climatic and environmental characteristics across the study area are shown in Appendix 1.

2.2 Site Selection

To obtain an even distribution of shrub samples, the study area was broken into 23 16-km sections from north to south. In each of these 23 sections, one site was selected for sampling. Given the size and diversity of vegetation types present across the study area, sampling sites were identified through a process of stratified random selection via a GIS suitability analysis. Suitable sampling areas were identified within each section using the following six criteria:

1. *Vegetation Type:* The objective of this study was to sample from similar shrub-dominated communities that occurred throughout the study area. Using the Alaska Center for Conservation Science's vegetation classification map for northern, western and interior Alaska (Boggs et al., 2016), areas classified as "Tall Shrub" or "Low Shrub" were included in the sampling area.
2. *Distance from the Dalton Highway:* Road dust from the Dalton Highway causes physical damage to vegetation within 10-20 m of the road and dust accumulation can cause early snowmelt, altered plant phenology and increased soil pH up to 100 m from the road (Walker and Everett, 1987; Auerbach et al., 1997; Myers-Smith et al., 2006). To avoid these potential anthropogenic effects, areas less than 250 m from an established road were excluded from the sampling area. Furthermore, due to the logistical constraints of site access, areas more than 2 km from the Dalton Highway were also excluded from the sampling area.
3. *Distance from the Trans-Alaska Pipeline*: The Trans-Alaska Pipeline runs parallel to the Dalton Highway. To avoid any residual influence from the pipelines construction and ongoing maintenance, areas within 50 m of the pipeline were excluded from the sampling area.
4. *Distance from Riparian Areas*: Shrub communities in riparian areas differ significantly in structure and composition from upland shrub communities. The aim of this study was to assess the drivers of shrub growth in upland shrub communities; therefore areas within 100 m of surface waters documented by the National Hydrography Dataset (U.S. Geological Survey, 2019) were excluded from the sampling area.
5. *Position Relative to Major Rivers*: The Middle Fork of the Kuyukuk, the Jim River and the Dietrich River run near or parallel to the Dalton Highway for 169 km of the 370 km long study area. Crossing these major rivers to collect samples was deemed an unnecessary risk, therefore areas requiring a river crossing to access were excluded from the sampling area.
6. *Private Property*: Permits for sampling were obtained from the United States Bureau of Land Management (BLM), which administers 92% of the lands within the study area. All areas owned or administered by parties other than the BLM were excluded from the sampling area.

In total 12.6% of the study area (183 of 1,445 km^2) met the established suitability criteria. Within the suitable areas of each section, five points were randomly generated, of which one was selected at random as the primary sampling site. The remaining four points were reserved as alternatives in the event that the primary sampling site was deemed unsuitable during fieldwork, primary sites were utilized in 21 of 23 sections.

2.3 Sampling Methods

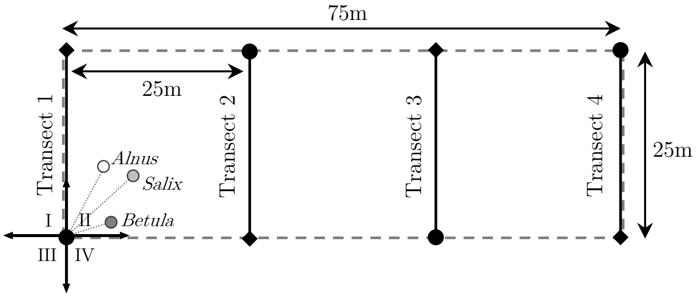

Figure 2. Diagram of sampling transects. At the ends of each transect (indicated by a circle), a point centered quarter was established and the closest individuals of the three study genera within a 10-meter radius were sampled.

Fieldwork was conducted during the month of July in 2019. The 23 sampling sites were numbered sequentially from south to north (Figure 1). To avoid confounding the effects of latitude with phenology, I began by sampling odd numbered sites while traveling north along the Dalton Highway and sampling the remaining even numbered sites while returning south.

At each site, beginning at the randomly established sampling point, four parallel 25 m transects were established at intervals of 25 m along the primary contour of the landscape (Figure 2). Environmental covariates including slope, aspect and vegetation type were measured at each site. Observed vegetation type was classified using the key to Alaska vegetation published by Boggs et al. in 2016. To assess site-level herbivory, the four transects were walked in alternating directions recording the presence of moose, snowshoe hare and ptarmigan pellets within a 2 m band (Barrio et al., 2016).

At alternating ends of the four transects, the point centered quarter method (Mitchell, 2010) was used to characterize browsing intensity and sample shrubs for dendroecological analysis. The nearest alder (*Alnus viridis*), dwarf birch (*Betula nana*) and willow (*Salix spp.*) shrubs in each quadrant within 10 m of the center point were recorded (Figure 2). When multiple willow species were present in a quadrant, I preferentially sampled from the most abundant species across the site to ensure I obtained an adequate sample size. To avoid sampling genetically similar individuals, shrubs of the same species were not sampled unless separated by at least 5 m. Shrubs over 3 m in height or with a stem basal diameter greater than 100 mm were not sampled as they were assumed to have partially escaped the impacts of browsing. Shrubs with a stem basal diameter less than 5 mm were also excluded from sampling as they were unlikely to have a sufficient number of annual rings to support dendroecological analysis.

At each shrub, vertical height, stem length and diameter at the root collar were measured on the main stem (tallest by vertical height). The main stem was used because it has been found to be more responsive to climate and often contains a longer record of growth (Karlsson et al., 2004). Canopy cover was measured at each shrub using the Canopy Survey app (Mignanelli, 2018). Canopy reference photos were taken 50 cm off the ground at the base of each shrub and processed with the app to determine the proportion of canopy cover above the shrub.

Figure 3. Herbivore browsing marks on willow shrubs. (A) Moose browse mark characterized by a ragged and broken twig. (B) Snowshoe hare browse mark with sharp diagonal cuts. (C) Ptarmigan browse marks on small twigs and buds.

Browsing intensity of moose, snowshoe hare and ptarmigan was quantified at each shrub as the proportion of twigs browsed by each species on the main stem. This was determined by counting the number of browsed and unbrowsed twigs (Christie et al., 2014; Zhou et al., 2017). Each of these three herbivores leave distinct browsing marks when feeding on woody plants (Figure 3). Moose browsing can be recognized by the ragged broken tips of browsed twigs, whereas snowshoe hare leave a sharp diagonal cut on the twig. Ptarmigan primarily consume buds or feed on tiny twigs (Christie et al., 2014).

After shrub measurements and browsing intensity were recorded, the main stem was cut with a fine-toothed saw directly above the root collar then cut again 10-15 cm above the first cut. The resulting stem segments were tagged with a unique ID and air dried in paper bags at room temperature prior to being processed for dendroecological analysis. In total 792 shrubs (168 *Alnus viridis*, 348 *Betula nana* and 276 *Salix spp.* (239 *S. pulchra, 25 S. glauca & 12 S. bebbiana*)) were sampled across the 23 study sites. A detailed assessment of shrub characteristics and browsing intensity observed across the study area is presented in Appendix 2

2.4 Dendroecological Methods

Shrub radial growth was measured using dendroecological methods for a subset of the total samples collected in the field. I was unable to quantify radial growth for all sampled shrubs due to time constraints associated with sample processing and measuring. In order to obtain a representative subsample, two dwarf birch and two willow samples were selected at random from each transect. Alders were not included in this analysis, as their distribution across the study area was not consistent and therefore the sample size was not as robust when compared to the other two shrub species. Of the 792 shrubs sampled, 337 were utilized in the dendroecological analysis (181 *Betula nana* and 151 *Salix spp*).

Samples were prepared for growth ring analysis by taking 20-30 μm thick cross sections from the base of stem segments using a GSL1 microtome (Gärtner and Schweingruber, 2013). Cross sections were then stained for 3 minutes using a solution of aqueous Astra Blue (1g/1000 ml) and aqueous Safranin O Dye (1g/1000 ml) at a ratio of 1:1 (Gärtner and Schweingruber, 2013). This treatment stained lignified tissues pink and the cellulose or non-lignified tissues blue allowing for better visualization and measurement of the growth rings (Vazquez-Cooz and Meyer, 2002; Myers-Smith, Hallinger, et al., 2015). Stained sections were rinsed with tap water to remove residual stain, then dehydrated with ethanol (Gärtner and Schweingruber, 2013), and permanently mounted on

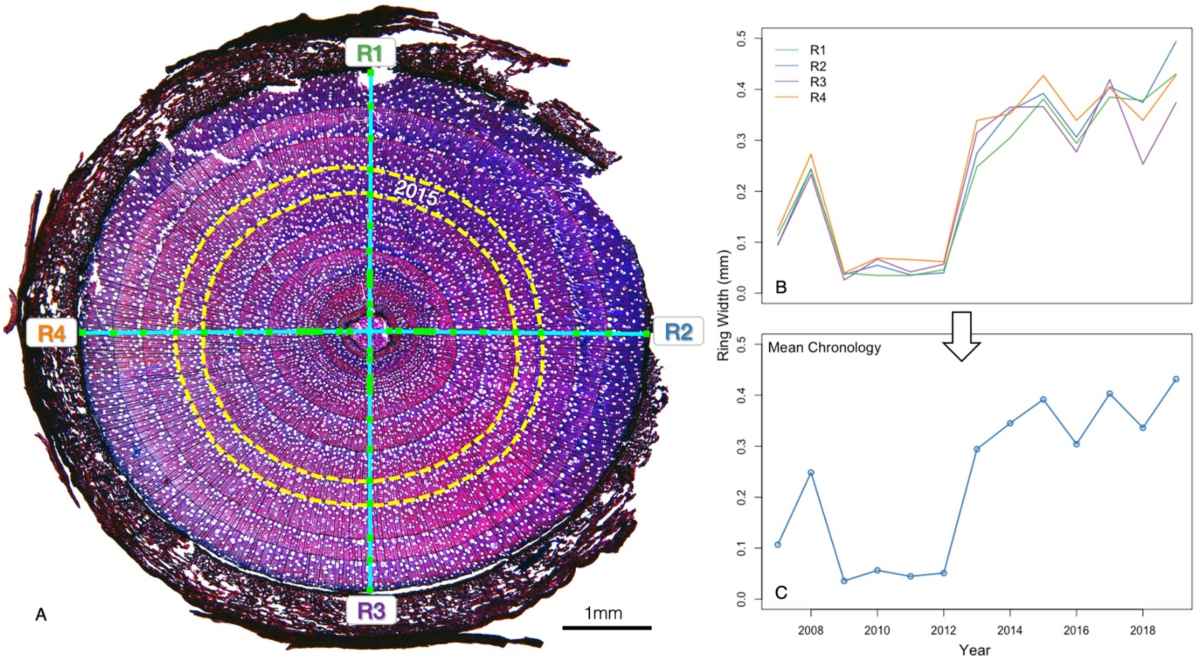

Figure 4. Graphical representation of the development of shrub chronologies. (A) Stem section with growth rings measured in 4 radii separated by 90°, shown as blue lines labeled R1, R2, R3 & R4. Shrubs were cross dated by identifying pointer years, indicated as yellow dashed lines, which were used to align the growth series. (B) Growth series of the four radii graphed over time. (C) Mean chronologies were developed by averaging the four radial growth series.

microscope slides with Canada Balsam. Mounted slides were dried in an oven at 60°C for at least 12 hours (Gärtner and Schweingruber, 2013; Tardif, 2015).

Stem sections were photographed using a Leica M165 C microscope system with MV170 HD camera (Leica Microsystems). Photographs were imported into the image processing software Fiji (Schindelin et al., 2012) where growth ring widths were measured using the Tree Rings package within the Object J plugin (Vischer and Nastase, 2019). To account for irregularities in shrub growth, growth rings were measured in 4 radii separated by 90° (Myers-Smith, Hallinger, et al., 2015). For large or partial sections, where four radii were not visible, only 2 radii separated by 180° were measured. These radial growth series were visually crossdated within each section (Figure 4a) to ensure correct alignment between the radii (Myers-Smith, Hallinger, et al., 2015). The four radial growth series were averaged into a mean chronology for each shrub (Figure 4c). Ring width measurements from mean chronologies were converted to basal area increment (BAI) using bai.in function from the dplR-package (Bunn, 2008) as ring areas represent overall shrub growth better than linear ring widths (Biondi and Qeadan, 2008).

Shrub growth exhibited a strong age trend, as BAI generally declined with age. To account for this, I removed the first five years of growth from each BAI series. I then standardized the biological age trend by fitting linear models to log transformed BAI values for each species (Speed et al., 2011). The residuals from these linear regressions were used as the response variable representing shrub growth in my analyses. The resulting age standardized BAI chronologies from 363 shrubs, revealed a consistent positive growth trend in both dwarf birch and willow over the last 30 years (Figure 5a).

2.5 Temproal Herbivore Data

Moose densities across the study area are generally low, ranging from 0.1 to 0.6 moose/km^2 (Osborn, 1992; Dale et al., 1995; Lawler et al., 2006). Moose populations are monitored by the state of Alaska Department of Fish and Game (ADF&G) within broad geographic districts referred to as Game Management Units (GMU). The study area spans portions of three GMUs, with sites 1 through 3 in GMU 20F, sites 4 through 19 in GMU 24A and sites 20 through 23 in GMU 26B. Within each GMU, data on moose population dynamics and harvest rates are published biannually by the ADF&G in Moose Management Reports (Hollis, 2018; Lenart, 2018; Stout, 2018). The data on moose population densities in these reports are collected periodically via aerial surveys following the protocol developed by Gasaway et al. (1986). Here I utilize these density estimates to represent the fluctuation of moose population between 1987 and 2015 in each GMU (Figure 5b). Given the periodic nature of these surveys, years without a density estimate were interpolated assuming a linear trend between existing density estimates.

Snowshoe hare populations fluctuate across their range in nine to ten cycles driven primarily by predator abundance and forage availability (Hodges, 2000; Krebs et al., 2001). In the study area, data on snowshoe hare populations have been collected around the town of Wiseman by staff from Gates of the Arctic National Park & Preserve since 1997 (DiFolco and Maier, 2015). Park Service staff have monitored local population cycles by integrating winter track surveys, pellet counts and live trapping data with traditional ecological knowledge from lifelong Wiseman resident and trapper, Jack Reakoff. The resulting dataset indicates that snowshoe hare populations at the northern end of their range have longer cycles between major peak densities, occurring roughly every 18 to 20 years with minor peaks occurring at the midpoint of 9 to 10 years. The last major peak in the study area occurred between 1998 and 2001, with a minor peak occurring between 2008 and 2009. In the summer of 2019, the study area was experiencing another major peak in snowshoe hare density (pers. commun. Reakoff 2019). Studies on the spatial synchrony of snowshoe hare cycles across western North America indicate that fluctuations in snowshoe hare populations are synchronous at spatial scales of 200-400 km, with synchrony declining with distance (Krebs et al., 2013). Given this, I expect snowshoe hare cycles to be largely synchronous across the study area. To quantify these cycles for this analysis I developed a simple numerical index to represent the major phases of the snowshoe hare cycle: increase, peak, decline and low (Hodges et al., 2001). Values of 1 were assigned to low years; values of 2 were assigned to years of increase or decline surrounding a major peak as well as minor peak years and lastly values of 3 were assigned to major peak years (Figure 5c).

Research on ptarmigan in northern Alaska has focused primarily on their movement and diet, while the dynamics of their populations remain largely unknown. Ptarmigan migrate annually across the study area from summer nesting grounds north of the Brooks Range through Anaktuvuk Pass to winter habitat in the boreal forests south of the Brooks Range (Irving et al., 1967). While observing this migration over the course of 15 years, Irving et al. found no evidence of cyclic variation in ptarmigan populations, as are observed in other portions of the ptarmigans range (Irving et al., 1967). Given the lack of understanding and available data on the temporal population dynamic of ptarmigan in this region, a temporal variable for ptarmigan density was not included in this analysis.

2.6 Climate Data

Temporal climate data for the study area was obtained from the Scenarios Network for Alaska & Arctic Planning group (SNAP, 2019). I utilized gridded climate datasets containing historical estimates of monthly climate variables, which had been downscaled from the global Climate Research Unit time series v. 4.0 (Harris et al., 2014; Walsh et al., 2018). This data covers the state of Alaska at a spatial resolution of 1 km^2 and spans the time period from 1901 to 2015. Of the eight climatic variables in the SNAP dataset, I included mean air temperature and precipitation during the growing season in this analysis as these have been identified in relevant literature as primary climatic drivers of shrub growth (D. Blok et al., 2011; Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe, et al., 2012; Jørgensen et al., 2015; Myers-Smith, Elmendorf, et al., 2015; Li et al., 2016; Weijers et al., 2018). Monthly mean air temperature and precipitation were extracted for the 23 sampling sites. The extracted data was then used to calculate annual mean temperature and precipitation during the summer growing season (June- August), which were used as the climatic parameters in this analysis (Figure 5d & 5e).

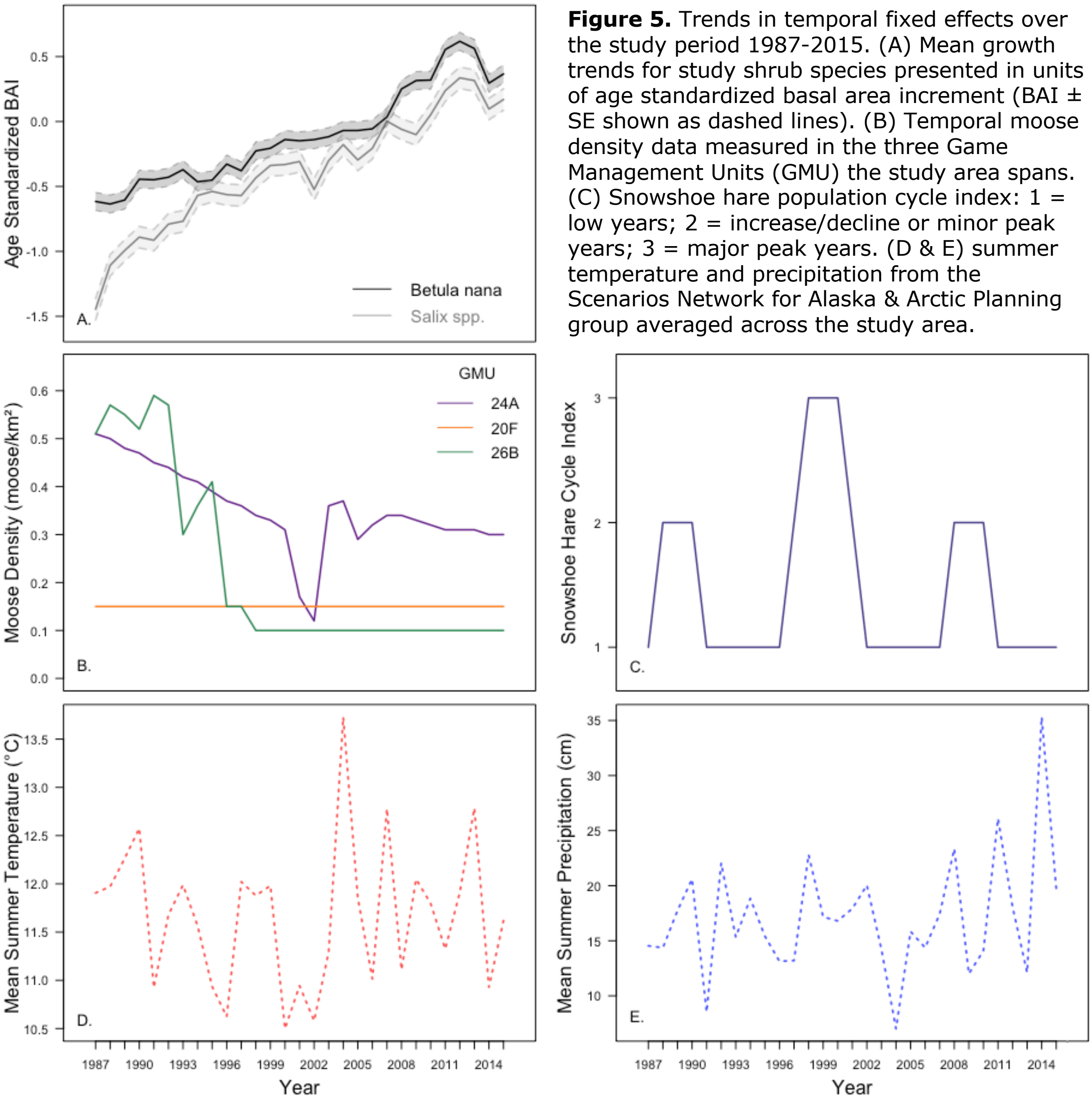

Figure 5. Trends in temporal fixed effects over the study period 1987-2015. (A) Mean growth trends for study shrub species presented in units of age standardized basal area increment (BAI ± SE shown as dashed lines). (B) Temporal moose density data measured in the three Game Management Units (GMU) the study area spans. (C) Snowshoe hare population cycle index: 1 = low years; 2 = increase/decline or minor peak years; 3 = major peak years. (D & E) summer temperature and precipitation from the Scenarios Network for Alaska & Arctic Planning group averaged across the study area.

2.7 Statistical Analyses

Data analysis was carried out in R version 3.5.2 (R Core Team, 2018). I assessed the influence of herbivory and climate on shrub growth through a linear mixed model analysis using the R-package nlme (Pinheiro et al., 2017). To optimize the overlap in temporal herbivore data, climatic data and shrub chronologies, the full range of the dataset was delimited to a study period between 1987 and 2015. I started by developing full models for both dwarf birch and willow, with age standardized BAI as the response variable. These models were fit with the fixed effects I hypothesized would influence shrub growth, namely: mean summer temperature (MST), mean summer precipitation (MSP) and different measures of spatial and temporal herbivore abundance. Spatial herbivory variables included moose, snowshoe hare and ptarmigan browsing intensity observed at the site-level during sampling, while temporal herbivory variables included ADF&G moose density estimates and my snowshoe hare population cycle index. Interactions between these herbivory variables and mean summer temperature were also included in the models. To avoid overfitting the full models with multiple measures of herbivore abundance, I developed two model sets for each species to assess the effects of (1) spatial browsing intensity separately from the effects of (2) temporal herbivore abundance. The four full models used in this analysis and their parameters are presented in Appendix 3 (Tables A3.1 & A3.2). To control for the hierarchical structure of the data, random intercepts were fitted to each model for the nesting of shrub individuals within sites. To aid in the interpretation and comparison of fixed effects and their interactions in the model, the fixed effects were normalized at the shrub level by centering (subtracting the mean) and standardizing (dividing by standard deviation) the data (Schielzeth, 2010). Prior to running the models, I calculated the variance inflation factors (VIF) for the fixed effects, which were all below 1.6 (see also appendix 4 for explanatory variable correlations), suggesting collinearity would not influence the analysis (Graham, 2003).

I began the analysis by preforming full model tests to compare each of the four full models to their respective intercept-only models using likelihood ratio tests. This was done prior to model selection in an effort to control for Type I errors (Forstmeier and Schielzeth, 2011). Fixed effects were then selected through backward elimination from the full models. Wald tests were used to assess the significance of individual fixed effects in each model, and parameters not found to be significant at $\alpha = 0.05$ were eliminated in a stepwise fashion until reaching a minimal adequate model (Figures A3.1 & A3.2). After model selection, the final models were refitted with restricted maximum likelihood estimation to calculate slope estimates.

3 Results

Age standardized BAI chronologies for both dwarf birch and willow (Figure 5a) showed a coherent positive growth trend over the study period from 1987-2015. The results of the mixed model analysis showed that the radial growth of dwarf birch and willow was significantly correlated with variation in mean summer temperature and precipitation (Tables 3; for full model outputs and details on model selection see Appendix 3). These models also indicate that radial growth for both species was related to temporal fluctuations in the abundance of moose and additionally snowshoe hare for willow. Furthermore, these models show that the growth of both shrubs is influenced by interactions between mean summer temperature and herbivory parameters, specifically, spatial ptarmigan browsing intensity for willow and snowshoe hare index for dwarf birch.

Table 1. Coefficients for selected mixed effects models for *Betula nana* and *Salix spp.* Models fitted with spatial browsing intensity variables are presented in Table A. Models fitted with temporal herbivore density variables are presented in Table B. Sample size (*n*) indicates the number of radial growth observations taken as the response variable in the model. Conditional R^2 values show the proportion of variance in age standardized explained by each model (Nakagawa and Schielzeth, 2013). Coefficients for the full models from which the models here were derived are presented in Tables A3.1 & A3.2.

A.		**Estimate**	**SE**	**_t_-value**	**_P_-value**
Salix spp. **Radial growth**	Intercept	0.18	0.14	1.28	0.201
(n=1655)	Mean Summer Temperature	0.25	0.06	4.37	**<0.001**
R^2 = 0.69	Mean Summer Precipitation	0.05	0.02	2.14	**0.033**
	Ptarmigan Browsing Intensity	0.25	0.16	1.56	0.134
	Ptarmigan x MST Interaction	0.14	0.05	3.13	**0.002**

B.		**Estimate**	**SE**	**_t_-value**	**_P_-value**
Betula nana **Radial growth**	Intercept	0.29	0.13	2.28	0.023
(n=2875)	Mean Summer Temperature	0.14	0.04	3.68	**<0.001**
R^2 = 0.64	Mean Summer Precipitation	0.04	0.02	2.38	**0.018**
	Moose Density	-0.19	0.02	-10.75	**<0.001**
	Snowshoe Hare Index	-0.02	0.01	-1.29	0.196
	Snowshoe Hare x MST Interaction	0.03	0.01	2.45	**0.014**
Salix spp. **Radial growth**	Intercept	0.11	0.16	0.72	0.470
(n=1655)	Mean Summer Temperature	0.21	0.05	4.53	**<0.001**
R^2 = 0.73	Moose Density	-0.15	0.03	-6.16	**<0.001**
	Snowshoe Hare Index	-0.05	0.02	-3.57	**<0.001**

3.1 Factors Influencing Shrub Growth

3.1.1 Climate

Climate sensitivity was observed in the annual radial growth of both dwarf birch and willow. In both species, mean summer temperature was positively related to age standardized BAI (Table 1). For dwarf birch, the response of shrub growth to mean summer temperature was significant in interaction with snowshoe hare index. The coefficient of this interaction indicates that the positive effect of summer temperature was greatest in years of peak snowshoe hare abundance. For willow, the effect of mean summer temperature was strong in both models. In the temporal herbivory model, summer temperature had the greatest effect on willow growth among significant model parameters and exhibited no interactions with herbivore abundance (Figure 6a). In the spatial herbivory model, an interaction was observed between summer temperature and ptarmigan browsing intensity, with the greatest positive effect of summer temperature occurring in sites with heavy ptarmigan browsing. These interactions between summer temperature and herbivory parameters will be discussed in greater detail in the herbivory section of the results.

A positive growth response to mean summer precipitation was also observed in both shrub species, however the effect of precipitation on radial growth was much weaker than summer temperature (Tables 3). The response of dwarf birch growth to increases in summer precipitation was marginal (Figure 6b). Mean summer precipitation was narrowly eliminated during selection for the willow temporal model (Figure A3.2). However, when assessed in the full model, the effect of summer precipitation on radial growth was similar to that observed in the spatial herbivory model (Table A3.2b), suggesting that

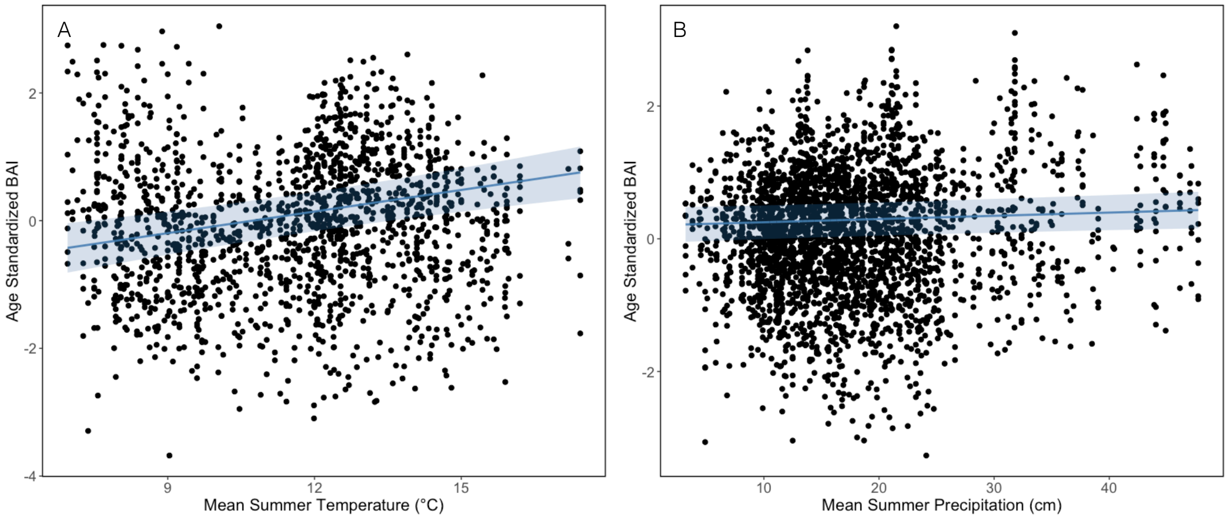

Figure 6. Pairwise plots of (A) age standardized BIA for willow plotted against mean summer temperature and (B) age standardized BIA for dwarf birch plotted against mean summer precipitation. Black dots represent raw data while the blue line depicts the linear relationship (± SE shaded in blue) based on temporal herbivory models for both species.

summer precipitation has a small positive effect on willow radial growth, despite the lack of statistical support in the temporal herbivory model.

3.1.2 Herbivory

Variation in shrub growth was not independently explained by spatial browsing intensity from any of the study herbivores (Table A3.1). Only the interaction between mean summer temperature and ptarmigan browsing intensity in the willow model was found to have a significant effect on growth (Table 1). Model based predictions of this interaction suggests that the effect of ptarmigan browsing intensity shifts with changes in mean summer temperature. In this case as mean summer temperature increases, ptarmigan browsing intensity has an increasingly positive effect on shrub growth (Figure 7). When

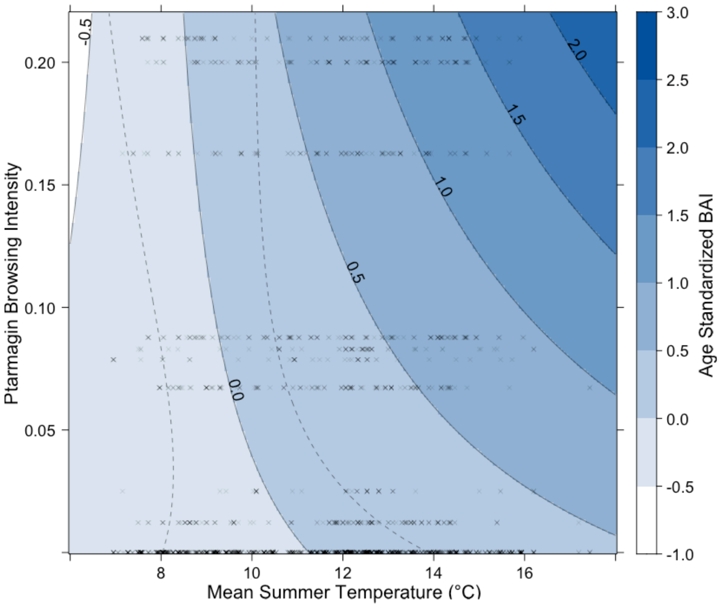

Figure 8. Contour plots showing *Salix spp* age standardized basal area increment (BAI) predicted over the range of ptarmigan browsing intensity and mean summer temperature. Predictions were calculated using the selected spatial herbivory model for *Salix spp* growth (Table 1). Color gradient represents age standardized BAI, with darker values denoting greater predicted annual growth. Standard errors are plotted as dashed lines around the contour line at 0 age standardized BAI. Observation points are plotted to indicate the coverage of data input into the model.

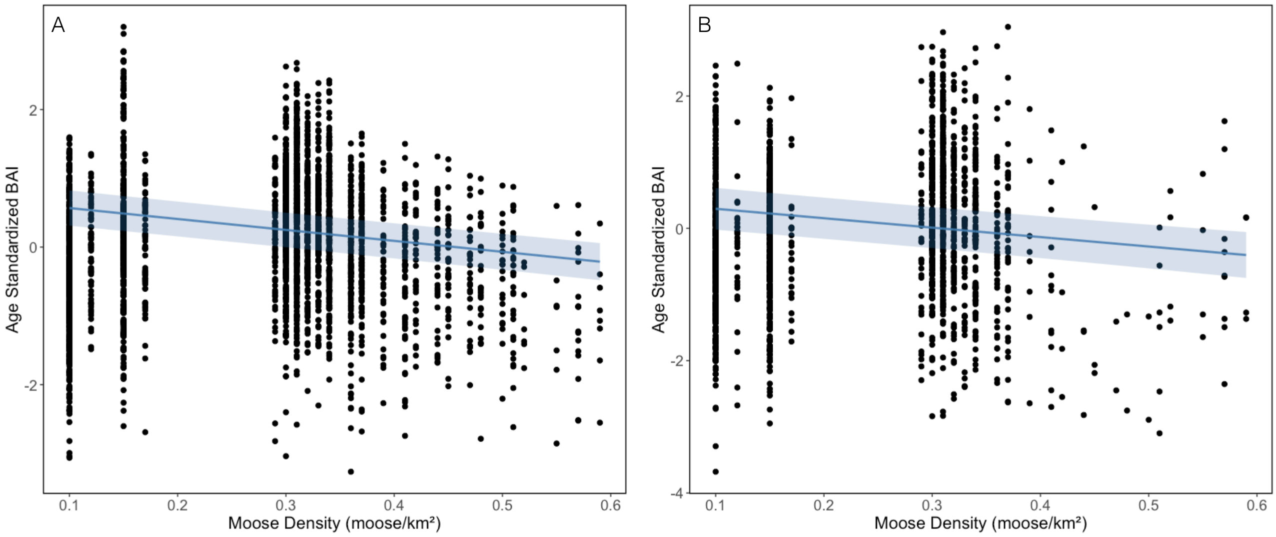

Figure 7. Age standardized BAI plotted against of moose density for (A) *Betula nana* and (B) *Salix spp.* Black dots represent raw data while the blue line depicts the linear relationship (± SE shaded in blue) based on temporal herbivory models.

mean summer temperatures are low, below approximately 8°C, the direction of this effect reverses, and high levels of ptarmigan browsing would have a negative effect on growth. However, the data is limited at the extremes of the mean summer temperature spectrum, where the effect of ptarmigan browsing is predicted to be greatest. Where the data is more abundant, the effect of ptarmigan browsing intensity is relatively weak when compared to mean summer temperature, as shown by the nearly vertical slope of the isoclines (Figure 7).

The models suggest that temporal herbivory parameters had a more pronounced effect on shrub growth when compared to the spatial herbivory parameters. Moose density had a negative effect on radial growth in both dwarf birch & willow (Figure 8). For dwarf birch moose density had the largest estimated effect on radial growth (Table 1). When considering the relative effect size of standardized variables, we see that this was the only instance where a significant herbivory variable had a larger estimated effect on radial growth than mean summer temperature. Fluctuations in snowshoe hare abundance, as represented by an index, had a small negative effect on the radial growth of willow; suggesting that growth was slower in years when snowshoe hare populations were at the peak of their cycle. However, model-based predictions of willow growth show that the effects of moose density and snowshoe hare index are very limited in relation to the effect of mean summer temperature (Figure 9).

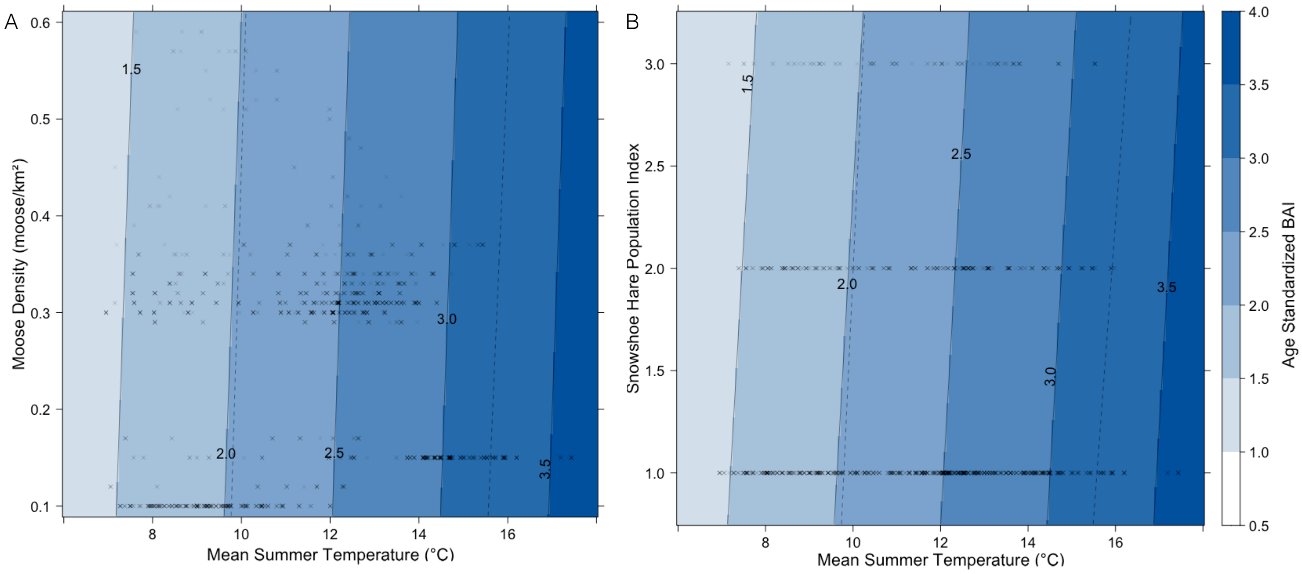

Figure 9. Contour plots showing *Salix spp* age standardized basal area increment (BAI) predicted over the range of (A) moose density or (B) snowshoe hare index and mean summer temperature. Predictions were calculated using the selected temporal herbivory model for *Salix spp* growth (Table 1). Color gradient represents age standardized BAI, with darker values denoting greater predicted annual growth. Standard errors are plotted as dashed lines around the contour line at 2.5 age standardized BAI. Observation points are plotted to indicate the coverage of data input into the model.

The only significant interaction in the temporal herbivore models was the relationship between mean summer temperature and snowshoe hare index as they relate to dwarf birch radial growth (Table 1). This interaction is visualized in Figure 10, where it is evident that the effect of high snowshoe hare abundance reverses along the gradient of summer temperature. The model predicts that when mean summer temperatures are above approximately 12°C, peak snowshoe hare densities have an increasingly positive effect on dwarf birch radial growth. While, when mean summer temperatures are below approximately 12°C, peak snowshoe hare densities have the opposite, increasingly negative effect on growth. Despite the statistical support for this interaction, the predicted size of snowshoe hares' effect is very small as indicated by the near vertical orientation of the isoclines along the mean summer temperature axis.

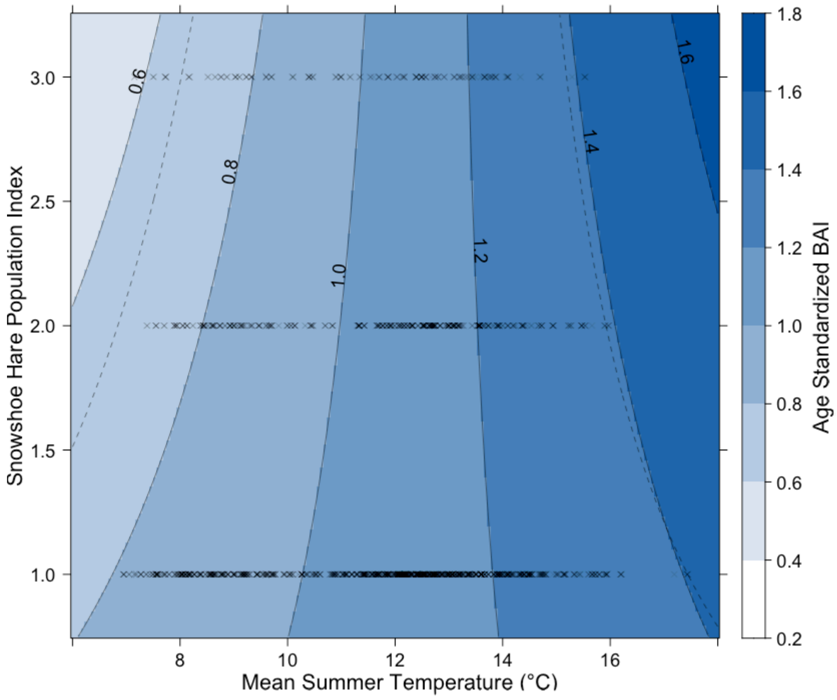

Figure 10. Contour plot showing *Betula nana* age standardized basal area increment (BAI) predicted over the range of snowshoe hare index and mean summer temperature. Predictions were calculated using the selected temporal herbivory model for *Betula nana* growth (Table 1). Color gradient represents age standardized BAI, with darker values denoting greater predicted annual growth. Standard errors are plotted as dashed lines around the contour line at 1 age standardized BAI. Observation points are plotted to indicate the coverage of data input into the model.

4 Discussion

Using a dendroecological approach, this study reveals that shrub growth at Alaska's boreal-tundra ecotone is sensitive to temporal variation in both climate and herbivore abundance. Consistent with past dendroecological research from this region (Tape et al., 2012; Ackerman et al., 2017, 2018), I find that climate, specifically summer temperature, is a strong driver of observed increases in the radial growth of both dwarf birch and willow shrubs. Furthermore, I provide evidence that spatial and temporal fluctuations in the abundance of moose, snowshoe hare and ptarmigan interact with and partially offset the positive effect of summer temperature on shrub growth. However, when the influence of herbivory is considered relative to summer temperature, I find that summer temperature is generally a stronger driver of shrub growth. This supports the conclusions established by past research on the regulatory role of browsers on shrub growth (Gough et al., 2012; Bryant et al., 2014; Christie et al., 2015); suggesting that herbivory moderates but does not completely counteract the positive effects of climate warming on deciduous shrub growth in northern interior Alaska.

4.1 Effects of Climate on Shrub Growth

There is significant evidence linking trends in summer temperature, and to a lesser extent summer precipitation, to observed increases in arctic shrub growth (Martin et al., 2017). In a meta-analysis of these climatic drivers, Myers-Smith et al. (2015) found that growth sensitivity to summer temperature was common in shrubs across the circumpolar arctic, but that the magnitude and direction of this sensitivity varied by species and location. Furthermore, the authors suggest that the magnitude of summer temperatures effect on shrub growth is positively related to precipitation via its relationship to soil moisture (Myers-Smith, Elmendorf, et al., 2015). At a regional scale, across northern Alaska & the Yukon Territory, dendroecological assessments of *Salix pulchra* (Ackerman et al., 2017, 2018; Weijers et al., 2018), *Salix spp*. (Myers-Smith and Hik, 2018) and *Alnus viridis* (Tape et al., 2012) show a consistent positive growth response to summer temperature. The results of this study further support these findings and confirm my first hypothesis, suggesting that annual variation in summer temperature correlates positively with radial growth trends in both dwarf birch and willow. However, I found that the strength of this temperature response varied between the two study species.

For willow, I found a strong positive growth signal from summer temperature in both models, which is consistent with past dendroecological analyses of this genus (D. Blok et al., 2011; Ackerman et al., 2018; Myers-Smith and Hik, 2018; Weijers et al., 2018).

Assessing trends in willow growth across Alaska’s north slope, Ackerman et al. (2018) found that the response of willows to variation in summer temperature was remarkably coherent, regardless of topographic position or site-level edaphic conditions. Thus, it is reasonable to suspect that the summer temperature sensitivity found in my willow samples could be applied beyond the upland communities I sampled, to the mesic riparian shrub communities in the study area.

For dwarf birch I also observed a positive effect of summer temperature, though its relationship to growth was less pronounced and varied with herbivore pressure from snowshoe hare (temperature-herbivory interactions will be discussed in subsequent sections). To my knowledge, this is the first dendroecological assessment of dwarf birch growth in northern Alaska. However, experimental studies conducted at the Toolik Field Station, which is located at the northern end of the study area (Figure 1), also detected a positive temperature-growth relationship in dwarf birch subjected to artificial warming (Bret-Harte et al., 2001; DeMarco, MacK, et al., 2014). Dendroecological studies of dwarf birch growth from northeastern Siberia also found a positive relationship between summer temperature and growth (D. Blok et al., 2011; Li et al., 2016). Consistent with finding presented here, Blok et al. (2011) suggest that the positive effect of summer temperature is less pronounced in dwarf birch than in willow. The authors propose that this discrepancy arises from differences in growth strategy, citing the tendency for dwarf birch to allocate resources towards stem elongation rather than radial growth under favorable conditions (Bret-Harte et al., 2001), which may reduce the climate signal within its annual growth rings. Despite this, other dendroecological assessments of dwarf birch reveal similar positive relationships between summer temperature and radial growth, but suggest that this effect is moderated by other environmental factors such as local topography (Ropars et al., 2015). Analysis of a 100 year chronology built from dwarf birch shrubs in western Greenland found that shrub growth was strongly correlated to both summer and winter temperature, emphasizing the importance of winter warming as a “co-driver” of shrub growth in their study system (Hollesen et al., 2015). In this study, the relatively small effect of summer temperature on dwarf birch growth may indicate that other climatic or environmental factors have contributed to the observed positive trend in radial growth. During the study period, warming trends in northern interior Alaska have been considerably stronger in the winter than in the summer (Walsh and Brettschneider, 2019), thus it is plausible that the dynamics of winter climate may also explain some of the observed variation in shrub growth.

In addition to the positive effects of summer temperature, the data also show a positive response of radial growth to mean summer precipitation in both dwarf birch and willow. While this precipitation-growth relationship was significant in the models, the effect of precipitation was marginal when compared to summer temperature. I expect that summer precipitation mediates shrub growth by influencing the amount of available soil moisture during the growing season. However, the limited importance of summer precipitation in the models suggests that other factors, such as snow cover, permafrost, topography and soil characteristics (Seneviratne et al., 2010), may be stronger determinants of soil moisture availability in this study system. Studies which have also assessed direct precipitation-growth relationships in dwarf birch and willow find little consensus on the magnitude and timing of precipitations' effect on growth. Some studies, suggest that the effects of precipitation are present but limited (Myers-Smith and Hik, 2018) while others find that the effects of precipitation vary in relationship to temperature (Li et al., 2016), interannual timing (D. Blok et al., 2011) or seasonality (Hollesen et al., 2015; Ropars et al., 2015). Given the variability of these results, it appears that the effect of precipitation on shrub growth is more heterogeneous and context specific than the effect of temperature. Therefore, the positive effect of summer precipitation which I observed at regional scales across the study area may be marginalized by site-level heterogeneity in shrubs precipitation-growth response.

Another facet within the relationship between climate and shrub growth is the potential for a non-linear growth response to summer temperature. Several studies have found that shrub growth exhibits a negative second-order relationship to summer temperature, in which the positive effect on radial growth slows and eventually saturates with increasing temperature, presumably due to moisture limitation (Speed et al., 2011; Ackerman et al., 2017, 2018). Ackerman et al. (2018) found that willow radial growth consistently slowed during warmer summers across Alaska's north slope in both upland and riparian landscapes. This suggests that the positive effects of warming on shrub growth are not boundless and can be limited by finite resources such as water and nutrients (Ackerman et al., 2018; Gamm et al., 2018). While I did not assess this kind of relationship here, it seems plausible given the results presented by Ackerman et al. (2017 & 2018) that the upland willow shrubs in this study could exhibit a similar temperature induced moisture limitation.

4.2 Effects of Herbivory on Shrub Growth

Vertebrate herbivores exert significant influence on arctic and boreal shrub communities through selective browsing and trampling, and are therefore expected to moderate the growth response of shrubs to climate change (Pedersen and Post, 2008; Gough et al., 2012; Bryant et al., 2014; Ravolainen et al., 2014; Christie et al., 2015; Myers-Smith, Elmendorf, et al., 2015; Olofsson and Post, 2018). The data presented here support this conjecture and provide evidence that temporal fluctuations in the abundance of moose and snowshoe hare correlate negatively with trends in shrub radial growth. These results support my second hypothesis and suggest that at regional scales increases in the abundance of moose and snowshoe hare limit the radial growth of willow and potentially dwarf birch shrubs.

Among the shrubs found in interior Alaska, willows are considered highly palatable and as such they are the preferred forage of the three study herbivores (Christie et al. 2015; Zhou et al. 2017; also see Appendix 2). The impact of browsing from moose and snowshoe hare on willows can manifest at multiple levels; from changes in individual leaf chemistry, growth structure and longevity (Bryant, 1987; Butler and Kielland, 2008), to landscape scale changes in age distributions, nutrient cycling and successional dynamics (Bryant et al., 1985; Bryant and Chapin, 1986; Kielland et al., 1997; Kielland, J. Bryant, et al., 2006; Butler and Kielland, 2008). Therefore, it was not surprising to find that willow radial growth was negatively correlated to both moose and snowshoe hare abundance. When comparing the relative effects of these two herbivores in the model, I found that temporal variation in moose density had a stronger effect on the radial growth of willows than cyclic fluctuations in snowshoe hare abundance. The reason for this discrepancy may arise from the more varied diet of snowshoe hares (Christie et al. 2015; Zhou et al. 2017; also see Appendix 2), which could distribute browsing pressure to other shrub species during periods of high abundance and reduce the cumulative effect on willow growth. Although their relative effects differ, strong overlap in the diet and habitat preferences of moose and snowshoe hare (Figure A2.2) may indicate their effects on willow growth are additive at the landscape scale (Zhou et al. 2017; also see Appendix 2). Despite the clear influence that these herbivores have on willow growth, the models suggest that the negative effects of herbivory are not enough to counteract the growth increases associated with summer warming. However, increasing shrub abundance and earlier snowmelt in northern interior Alaska may bolster moose and snowshoe hare populations in the future (Tape, Christie, et al., 2016; Tape, Gustine, et al., 2016), which could presumably affect the magnitude of these herbivore-growth relationships going forward.

The moderating effect of herbivory on shrub growth is expected to vary based on a shrubs palatability, browsing tolerance, and exposure to browsing pressure (Myers-Smith et al., 2011; Christie et al., 2015). Therefore, the effect of herbivory on shrub growth is likely to be concentrated primarily on highly palatable willows, affording a growth advantage to well defended species such as dwarf birch and alder (Bryant et al., 2014; Christie et al., 2015). My data on browsing intensity support this hypothesis, as sampled willows were 4 times more likely to be browsed than dwarf birch, and on browsed shrubs, the proportion of twigs removed was on average 2.4 times greater on willow than on dwarf birch (see Appendix 2). Given this, it was surprising to find a strong negative correlation between temporal moose density and dwarf birch radial growth. Indeed, the relationship between moose density and radial growth appears to be remarkably consistent in both dwarf birch and willow (Figure 8), despite their considerable differences in growth form and palatability. My data on browsing intensity support the findings of other studies, which indicate that dwarf birch represents an insignificant portion of moose diet in northern Alaska (Christie et al. 2015; Zhou et al. 2017; also see Appendix 2). Exclosure experiments at the Toolik Field Station found no significant herbivory effect on dwarf birch after 9 years of large herbivore exclusion (Gough et al., 2007). In a comprehensive assessment of herbivore effects on dwarf birch growth, Bryant et al. (2014) found no evidence of a significant herbivory effect in the well defended North America subspecies of dwarf birch (*B. nana* subsp. *exilis)*. These findings cast doubt on the ecological relevance of the relationship between moose density and dwarf birch radial growth shown in the model. This paired with the limited climate-growth response of dwarf birch, suggest that there are factors outside the scope of this study which influenced the observed increase in dwarf birch radial growth during the study period.

Unlike temporal fluctuations in herbivore abundance, I found little evidence that variations in spatial browsing intensity influenced the radial growth of study shrubs. Only the interactive effect of ptarmigan browsing intensity and summer temperature as it relates to willow growth was found to be significant. This general lack of explanatory power may stem from the overall low levels of browsing observed (Appendix 2). The frequency and intensity of browsing in the upland shrub communities I sampled was generally lower when compared to studies conducted along riparian corridors in northern interior Alaska (Butler and Kielland, 2008; Christie et al., 2014; Zhou et al., 2017). This finding was not unexpected, as the study herbivores tend to utilize riparian areas more heavily due to the greater abundance tall shrubs (Joly et al., 2015a, 2016; Tape, Christie, et al., 2016). The more concentrated and consistent browsing pressure in riparian systems, may have elicited a stronger herbivory signal in shrubs radial growth, however this hypothesis will need further testing.

When considering the potential effects of herbivory observed in this study, it should be noted that the herbivory data used in this analysis represent two extremes on the continuum of spatial and temporal data resolution, and as such this data has some important limitations. The temporal measures of moose density and snowshoe hare abundance are spatially coarse, representing broad regional population trends, and as such poorly represents the fine scale spatial heterogeneity of browsing pressure across the study area (Joly et al., 2015b). Alternatively, the spatial measures of browsing intensity have high spatial resolution, but completely lack a temporal component and therefore do not capture the potential for interannual variation in browsing intensity. Consequently, extrapolating of the results presented here at finer scales should be done with caution and I recommend future work incorporate more precise spatial and temporal measures of browsing pressure to determine if the regional trends seen here are consistent at finer scales.

4.3 Interactive Effects of Climate & Herbivory

While the independent effects of climate and herbivory on shrub growth are well established, to fully disentangle their relative influence on shrub growth it is necessary to consider how these drivers of shrub growth interact (Speed et al., 2011; Løkken et al., 2019; Vuorinen et al., 2020). My data suggest that the radial growth of both dwarf birch and willow is influenced by the interactive effects of mean summer temperature and herbivory. These findings partially support my third hypothesis, as the models suggest that in warmer summers the negative effect of herbivory on shrub growth can be negated. However, beyond this original hypothesis, I found that at mean summer temperatures above 8 to 12°C, the negative effect of herbivory reverses and becomes increasingly positive. Such positive interactions between summer temperature and herbivory were observed in both shrub species, each interacting with different herbivores. In both observed interactions, the effects of herbivory were limited in relation to summer temperature, suggesting that the favorability of climatic conditions dictate the effect of browsing on shrub growth.

For willows, the positive effect of ptarmigan browsing during warmer summers is potentially the result of a compensatory growth response to herbivory. When conditions are favorable, willows have a unique propensity to tolerate browsing through compensatory growth (Bowyer and Neville, 2003; Christie et al., 2014). During the winter months, willow buds are a primary food source for ptarmigans and through repeated browsing ptarmigan can alter the architecture and reproductive capacity of willows (Tape et al., 2010; Christie et al., 2014, 2015; Christie and Ruess, 2015). Christie et al. (2014) found that moderate ptarmigan browsing on willows induced a compensatory growth response, shown in higher rates of bud production, increased shoot length/diameter and greater overall biomass. While seasonal browsing intensity from ptarmigan can be very intensive in riparian areas (Christie et al., 2014; Zhou et al., 2017), ptarmigan browsing in the upland areas I sampled was more moderate (Appendix 2). Therefore, it seems plausible that under favorable temperature conditions and moderate ptarmigan browsing, the interactive response observed in the model predictions (Figure 7) could be attributed to a compensatory growth response.

For dwarf birch, the tendency of growth to increase during warm summers with high snowshoe hare abundance is more challenging to interoperate. Unlike willow, dwarf birch has limited palatability and invests heavily in defensive compounds to deter herbivory (Christie et al., 2015). As discussed in the previous section, there is limited evidence that herbivores influence dwarf birch growth (Gough et al., 2012; Bryant et al., 2014). There is evidence from studies in Quebec, which found that shrub birch (*Betula glandulosa*) exhibited a compensatory growth response, by increasing leaf biomass, when subjected to simulated browsing of up to 25% of available shoots (Champagne et al., 2012). In my study area, it is not uncommon for snowshoe hare to browse on dwarf birch (Christie et al. 2015; Zhou et al. 2017; also see Appendix 2), but it does not appear to comprise a significant portion of their diet. Even during the current major peak, my browsing intensity data suggest that snowshoe hare browsed only 11% of sampled dwarf birch with a mean browsing intensity of 7%. Given the limited amount of observed browsing by snowshoe hare on dwarf birch, it seems unlikely that a compensatory growth response would be evident in the radial growth of dwarf birch at regional scales. A more plausible explanation, considering the negative relationship between snowshoe hare index and willow radial growth, could be a release from competition during peak snowshoe hare densities, allowing dwarf birch to utilize the favorable temperature conditions and increase its radial growth. Indeed, in the exclosure experiments performed by Gough et al, (2007), they attribute the observed increase in dwarf birch growth outside of the exclosure to a release from competition stemming from selective grazing by voles on graminoids. Despite a more generalist diet, my browsing intensity data suggest that snowshoe hare preferentially feed on willows. At high densities, snowshoe hare can limit willow growth, increasing the availability of light and nutrients for other species (Bryant et al., 1985; Bryant, 1987). Thus, I suspect that the slight positive effect of high snowshoe hare abundance during favorable temperature conditions is the result of reduced interspecific competition between dwarf birch and willow.

4.4 Broader Implications

In northern interior Alaska, tundra ecosystems appear to be at a "tipping point", as a warmer climate increases shrub growth, promoting shifts in vegetation towards shrub dominance (Sturm et al., 2001; Naito and Cairns, 2011). Climate projections suggest that in the coming decades, summer temperature and precipitation will continue to increase across northern Alaska, which is expected to perpetuate the ongoing vegetation shift at Alaska's boreal-tundra ecotone (Euskirchen et al., 2009). The positive relationship observed between summer climate and shrub growth supports these predictions and suggests that with its current trajectory, the climate in interior Alaska will become increasingly favorable for deciduous shrub growth. Furthermore, these results indicate that while at current densities the top-down control exerted by moose, snowshoe hare and ptarmigan will moderate the growth of deciduous shrubs but will not fully negate the positive effects of climate warming. Given my results, it seems likely that shrub growth in interior Alaska will continue to increase in the near term, unless limited by factors unaccounted for in this analysis (e.g. soil moisture and nutrient availability, see Martin et al., 2017 for a more comprehensive list of potential controlling factors). While increases in the radial growth of shrubs do not have direct implications on the tundra ecosystems, past studies have identified an allometric relationship between radial growth and above ground biomass in both dwarf birch and willow in Alaska (Berner et al., 2015). Therefore, I expect that shrub biomass has also increased during the study period and will continue to increase, which will have more tangible implications on the structure and function of the shrub tundra in northern interior Alaska. Increased shrub biomass has been implicated in a number of potentially significant and interrelated feedbacks at local and global scales, including alterations in carbon budgets, fire regimes, snow cover and permafrost thaw (Myers-Smith et al., 2011). Additional research is needed to determine how the projected increases in shrub growth and biomass will impact ecosystem functioning at Alaska’s boreal-tundra ecotone.

Going forward, future studies should investigate the effect that increased shrub biomass will have on herbivore populations in northern Alaska. With shrub expansion over the past half century, moose and snowshoe hare have expanded their range northward into previously unviable habitat (Tape, Christie, et al., 2016; Tape, Gustine, et al., 2016). Yet, in the current analysis there does not appear to be a direct relationship between increased shrub growth and herbivore density. In this region, studies indicate that predation and disease, rather than resource limitation, drive low population densities in moose (Gasaway et al., 1992) as well as the population cycles in snowshoe hare (Krebs et al., 2017). While the spatial range of these herbivores may change in response to increasing shrub biomass, it seems unlikely given the strong top-down control from predators, that herbivore densities will substantially increase in the study area. Furthermore, climate does not act solely on shrubs, an increasingly dynamic winter climate and more extreme summer temperatures will also have a strong direct effect on herbivore populations as well (Albon et al., 2017). Further research on the population dynamics of the three study herbivores, particularly ptarmigan, is needed to fully understand how these herbivores will react to the vegetation state shifts and climatic changes occurring in northern interior Alaska.

The overall capacity for herbivores to limit vegetation state shifts in the tundra is highly context dependent (Bryant et al., 2014; Christie et al., 2015; Olofsson and Post, 2018). In the context of this study, I found that at low densities during favorable climatic conditions, a diverse set of three wild herbivores had a slight moderating effect on shrub growth. However, in contrast to the results presented here, studies conducted in northern Europe and Fennoscandia, demonstrate that herbivory can fully negate climate induced increases in shrub growth (Ravolainen et al., 2014; Bråthen et al., 2017; Vuorinen et al., 2020). The key difference in these studies seems to be the high densities of domesticated or heavily managed herbivores, bolstered by predator suppression, which greatly increases the potential limiting effect of herbivory on shrub growth. While the differing effect of herbivore abundance is clear in these examples, other climatic and environmental contexts must also be considered. The arctic climate is predicted to become increasingly dynamic; as temperatures continue to rise (Anisimov et al., 2007) the growth response of shrubs is not expected to be consistent across the circumpolar arctic (Myers-Smith, Elmendorf, et al., 2015). Recent remotely sensed trends in vegetation productivity suggest that while northern interior Alaska has continued its 30-year "greening trend", areas of the Eurasian arctic are beginning to "brown", as a result of reduced summer warmth index (Bhatt et al., 2013) and increased extreme weather events (Phoenix and Bjerke, 2016). In environments where the underlying climatic conditions are unfavorable, it's likely that even low densities of wild herbivores can significantly limit shrub growth. For example, Gamm et al. (2018) found that both birch and willow shrubs responded negatively to increasing summer temperatures in western Greenland, which they attribute to a combination of moisture limitation and increased browsing from muskoxen. These examples highlight the need to consider both herbivore abundance and underlying climatic and environmental context when studying the effect herbivores have on arctic shrub growth.

4.5 Conclusions

Using a dendroecological approach, I show that herbivory interacts with climate to determine the radial growth of deciduous shrubs at the boreal-tundra ecotone in northern Interior Alaska. In this relationship, I show that climate, specifically mean summer temperature, is the preeminent driver of variation in the radial growth of both dwarf birch and willow. Counteracting the positive effects of climate, I show that fluctuations in moose and snowshoe hare abundance relate negatively to shrub growth at regional scales.

My findings indicate that at current densities, vertebrate herbivores at Alaska's boreal-tundra ecotone exert measurable top-down influence on shrub growth, which can partially offset climate induced growth increases in deciduous shrubs. With this study I provide evidence that the population dynamics of a diverse set of wild browsers can influence large scale patterns in arctic shrub growth. Though herbivory is often cited as a likely driver of shrub growth, this study is to my knowledge, the first dendroecological study in the North American Arctic to assess the effects of herbivory relative to the climatic drivers of shrub growth.

Predictive models of future vegetation dynamics in northern Alaska (Euskirchen et al., 2009) and the Panarctic (Pearson et al., 2013) currently only consider abiotic drivers in their predictions. These models predict that shrub biomass will greatly increase in the ensuing decades resulting in significant abiotic and biotic feedbacks. Given the observed relationships between herbivore abundance and shrub growth, I stress the need for future predictions of vegetation state transitions to incorporate the limiting effects of herbivory in their models. My results highlight regional correlations between herbivory, climate and shrub growth; to improve their predictive power, future studies would be well served to assess these relationships at a finer scale, incorporating higher resolution herbivory data.

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Appendices

Appendix 1: Latitudinal Variation in Site Level Covariates

Appendix 2: Shrub Characteristics & Browsing Intensity

Appendix 3: Model Selection via Backward Selection

Appendix 4: Correlation Matrix of Model Parameters

Appendix 1: Latitudinal Variation in Site Level Covariates

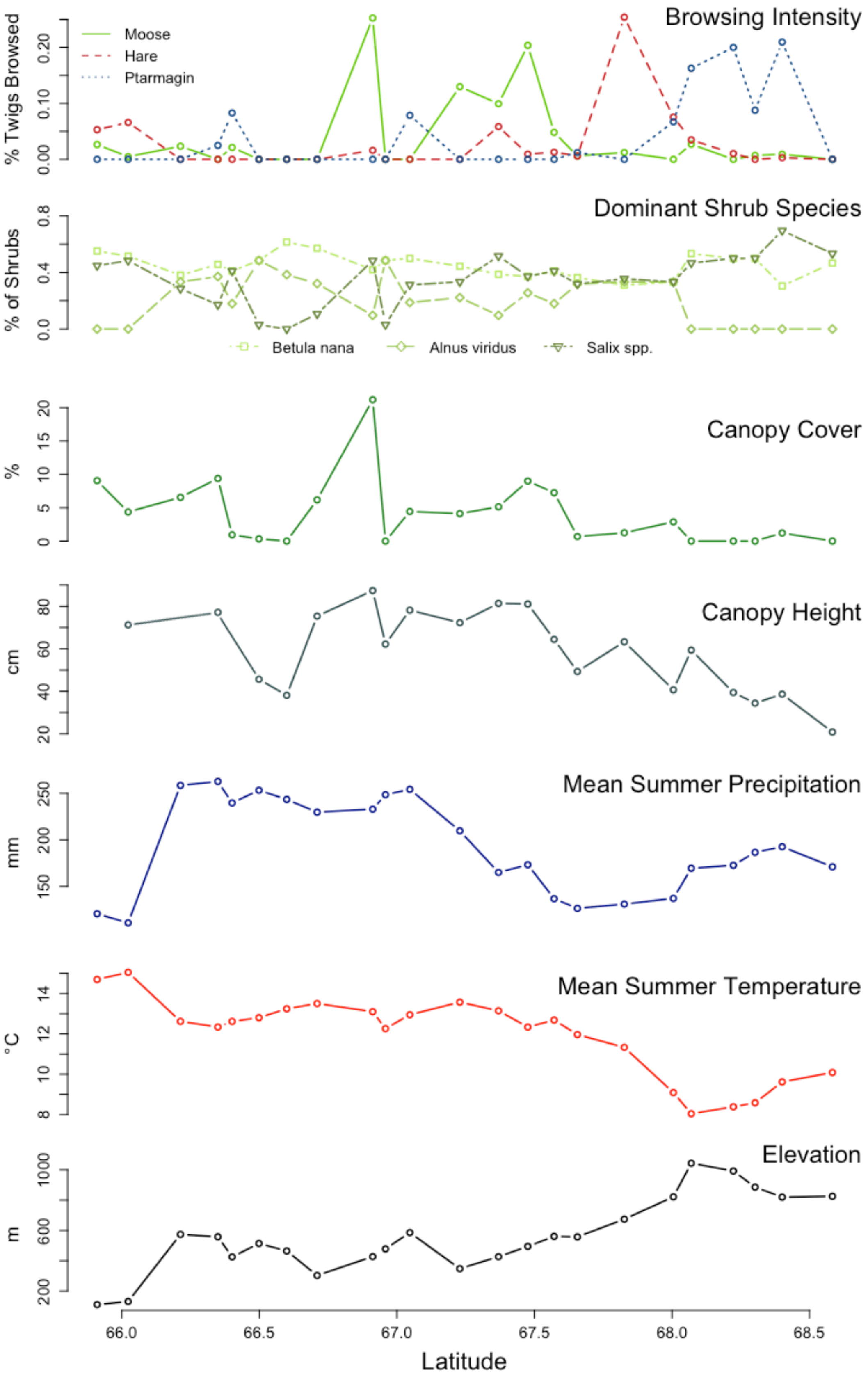


Figure A1. Site-level covariates plotted against latitude

Appendix 2: Shrub Characteristics & Browsing Intensity

The composition of shrubs in the full sample (n=792) was 43% *Betula nana*, 34% *Salix spp.* and 21% *Alnus viridis* (Table A2.1). The occurrence of both dwarf birch and willow was consistent across all sampling sites, while alder occurred at only 16 of the 23 sites. Average vertical height of sampled shrubs was 73.8 cm (*SE*=1.6) and the average canopy cover at individual shrubs was 7.2% (*SE*= 0.8). Five vegetation types were observed during sampling, ordered here by frequency: Low Shrub, Tall Shrub, Black Spruce Woodland, Low Shrub-Tussock Tundra and Tussock Tundra. In total, 88% of sampled sites were classified as either low or tall shrub.

Table A2.1. Summary of shrub characteristics and site-level browsing intensity.

	Sample Size	Height (cm)		Median Browsing Intensity (IQR) (% Twigs Browsed)		
Shrub Species	*n*	Mean (SE)	Range	Moose	Hare	Ptarmigan
Alnus viridis	168	133.2 (2.9)	63-240	0 (0.8)	0 (0.8)	0 (0.3)
Betula nana	348	44.4 (0.8)	12-91	0 (0.1)	0 (1.8)	0 (0)
Salix spp.	276	79.7 (5.9)	18-177	0.9 (6.9)	0.9 (4.0)	0 (9.7)
Salix bebbiana	12	-	-	7.3 (-)	-	-
Salix glauca	25	74.8 (4.9)	36-121	1.6 (1.7)	3.7 (12.0)	4.5 (17.3)
Salix pulchra	239	74.1 (2.3)	18-177	0.8 (6.2)	0.9 (4.0)	0 (9.9)

Of the 792 shrubs sampled, 141 were browsed by moose (18%), 159 were browsed by snowshoe hare (20%) and 113 were browsed by ptarmigan (14%). As expected, all three herbivores browsed more on willows (75% of shrubs browsed) than on the less palatable dwarf birch (19% of shrubs browsed) or alder (28% of shrubs browsed). Across the sampling area, browsing marks and feces pellets were observed at 21 of 23 sites and these metrics of site-level browsing were highly correlated for all three herbivore species (Moose: r = 0.70, Hare: r = 0.86, Ptarmigan: r = 0.90). Browsing overlap was observed between moose and snowshoe hare on 51 shrubs across 11 sites, moose and ptarmigan on 17 shrubs across 5 sites and ptarmigan and hare on 24 shrubs across 5 sites (Figure A2.2).

While all three herbivores were observed throughout the study area, their site-level browsing intensity was spatially heterogeneous (Figure A2.2). To better understand the factors influencing the observed spatial variation in browsing intensity, a pairwise spearman rank correlation analyses was used to assess the relationship between browsing intensity, shrub characteristics and site-level covariates. Understanding the factors which dictate spatial browsing intensity between shrub species will help us identify where herbivores may have the greatest influence on shrub growth. This variance appears to be dictated by different factors for each herbivore species (Table 2).

Table A2.2. Correlation between observed mean browsing intensity and site characteristic. The Spearman's rank correlation coefficient (ρ) and P-value (0 - 0.001: ***, 0.001- 0.01: **, 0.01- 0.05: *) are provided. ^{1} Canopy height represents mean shrub height at the site-level. ^{2} Percent alder, dwarf birch and willow represent the proportion of that species out of the total shrubs sampled at a site.

Browsing Intensity	*Canopy Height* ^{1}	*Canopy Cover*	*Latitude*	*% Alder* ^{2}	*% Dwarf Birch*	*% Willow*
Moose	0.45 *	0.46 *	-0.01	-0.33	-0.35	0.39 *
Snowshoe Hare	0.21	-0.23	0.17	0.33	-0.27	0.44 *
Ptarmigan	-0.36	-0.37 *	0.46 *	-0.36 *	-0.01	0.31

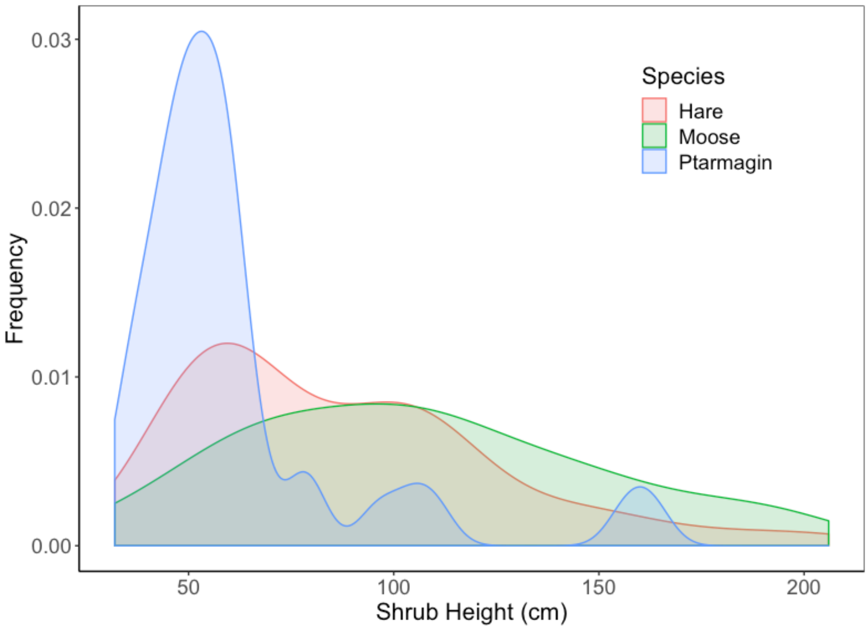


Figure A2.1. Browsing frequency (proportion of total shrubs browsed) by moose, snowshoe hare and ptarmigan across the range of observed shrub height.

As expected, all three herbivores browsed more in sites dominated by willows (75% of shrubs browsed) and browsed less in sites dominated by less palatable dwarf birch (19% of shrubs browsed) or alder (28% of shrubs browsed). A positive correlation was observed between moose browsing and both shrub height and canopy cover, while the opposite trend was observed in ptarmigan browsing. This relates to the observed spatial distribution of ptarmigan browsing, which occurred more frequently in northern sites, that tended to have a shorter canopy height and less canopy cover. There were no strong relationships between snowshoe hare browsing and the environmental covariates I measured, aside from an apparent preference for sites with high proportions of willow.

When looking at the relationship between shrub height and browsing frequency, there are evident patterns in browsing preference which emerge for each herbivore (Figure A2.1). Browsing by all three herbivores was observed across the spectrum of shrub heights. However, ptarmigan browsing was concentrated primarily on lower shrubs; the average height of which was 61 cm. Moose browsing was more evenly distributed across the spectrum of shrub heights, but the majority of browsing occurred on taller shrubs with an average height of 99.8 cm. Snowshoe hare browsing was more intermediate, overlapping considerably with both moose and ptarmigan, with a mean browsing height of 86.4 cm. The distribution of snowshoe hare browsing across shrub species is more uniform than moose or ptarmigan which seem to largely prefer willow (Table A2.1). This coupled with the broad range of shrub heights browsed suggest that snowshoe hare are more generalist feeders than moose or ptarmigan.

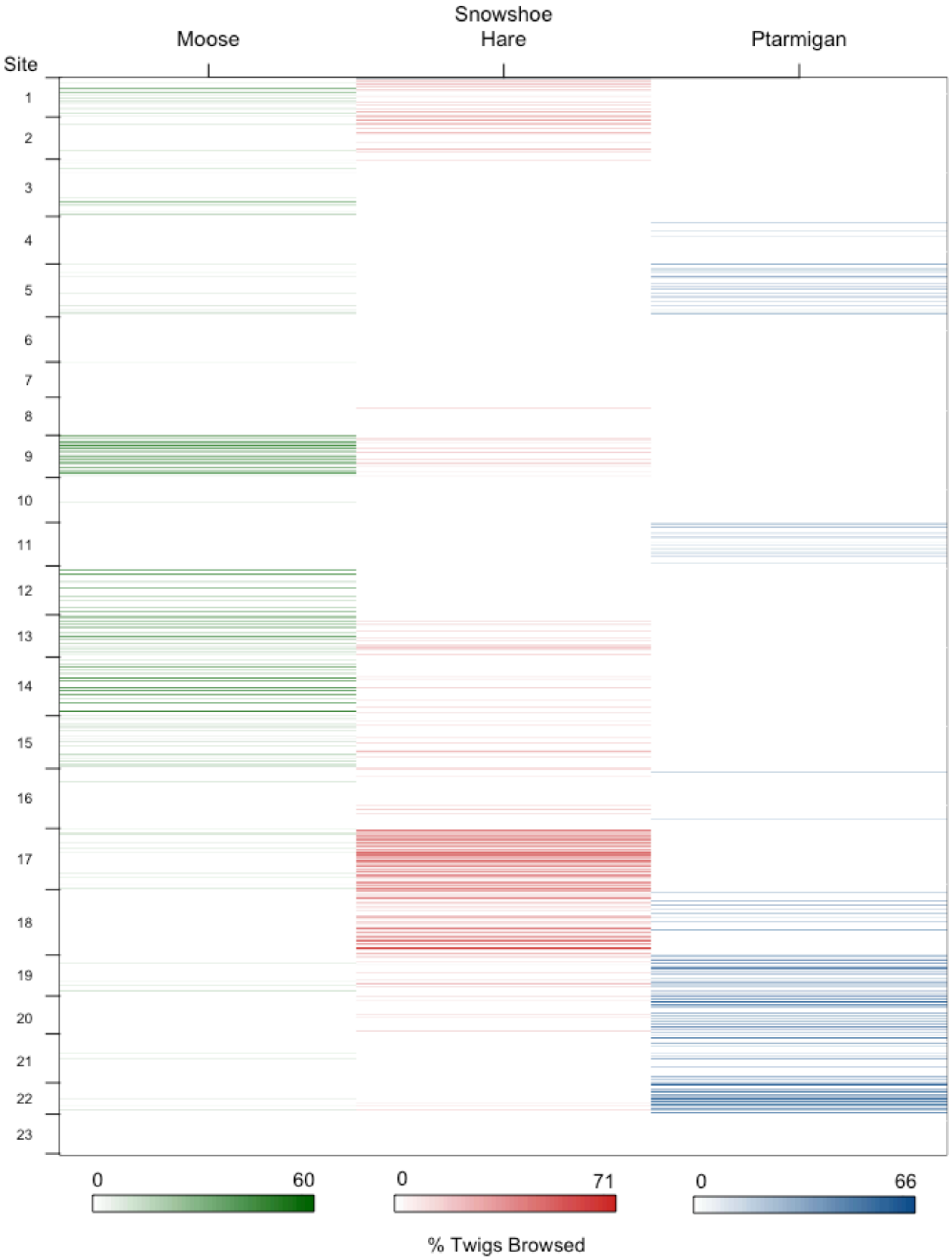


Figure A2.2 Shrub level browsing intensity plotted for moose, snowshoe hare and ptarmigan. Horizontal lines represent the individual shrubs sampled (n = 792) within the 23 sampling sites. The color of the lines indicates the species of herbivore which browsed the shrub and the color's opacity represents the observed browsing intensity on that shrub.

Appendix 3: Model Selection via Backward Selection

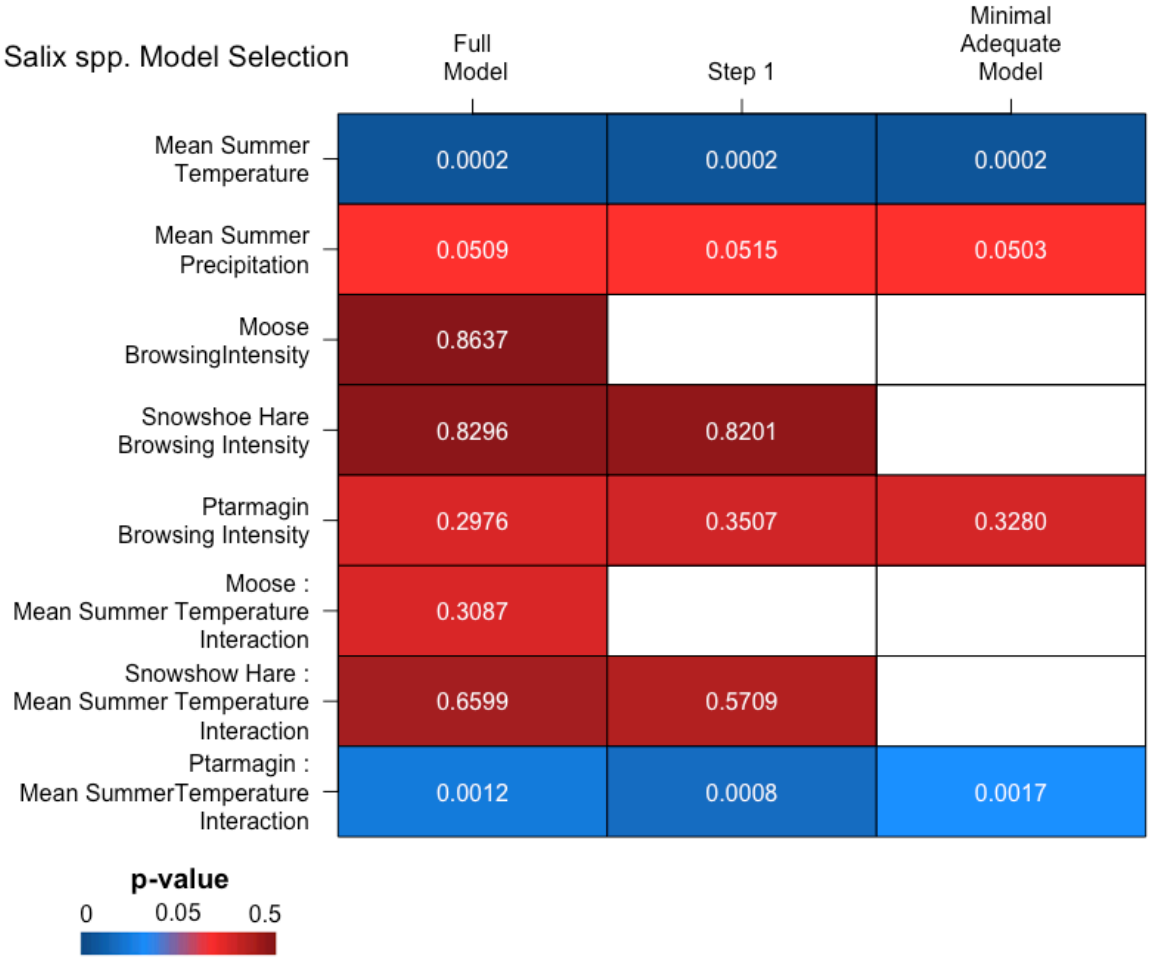
Table A3.1 Fixed effects parameters from full models for (A) *Betula nana* and (B) *Salix spp* fitted with climate and spatial herbivory variables. Sample size (*n*) indicates the number of radial growth observations taken as the response variable in the model. Full model tests, comparing the full models to their respective intercept-only model using likelihood ratio tests, are presented at the base of the tables. The full model for dwarf birch growth fit with spatial herbivory variables (A) was dropped from the analysis as it did not provide significant improvement in model fit when compared to the intercept-only model.

A.		**Estimate**	**SE**	***t*-value**	***P*-value**
Betula nana **Radial growth**	Intercept	0.32	0.12	2.55	0.011
(n=2875)	Mean Summer Temperature	0.06	0.04	1.44	0.150
	Mean Summer Precipitation	0.04	0.02	2.17	0.030
	Moose Browsing Intensity	-0.10	0.13	-0.80	0.432
	Snowshoe Hare Browsing Intensity	-0.04	0.13	-0.30	0.771
	Ptarmigan Browsing Intensity	-0.18	0.14	-1.29	0.212
	Moose x MST Interaction	-0.01	0.04	-0.39	0.696
	Snowshoe Hare x MST Interaction	-0.02	0.04	-0.66	0.507
	Ptarmigan x MST Interaction	0.02	0.04	0.59	0.553

Full Model Test: Likelihood Ratio = 10.04, P-Value = 0.262

B.		**Estimate**	**SE**	***t*-value**	***P*-value**
Salix spp. **Radial growth**	Intercept	0.20	0.16	1.28	0.201
(n=1655)	Mean Summer Temperature	0.24	0.06	4.19	<0.001
	Mean Summer Precipitation	0.04	0.02	1.97	0.049
	Moose Browsing Intensity	0.09	0.17	0.54	0.597
	Snowshoe Hare Browsing Intensity	0.02	0.16	0.09	0.926
	Ptarmigan Browsing Intensity	0.28	0.18	1.51	0.148
	Moose x MST Interaction	0.01	0.05	0.21	0.835
	Snowshoe Hare x MST Interaction	0.07	0.05	1.38	0.168
	Ptarmigan x MST Interaction	0.16	0.05	3.24	0.001

Full Model Test: Likelihood Ratio = 30.01, P-Value = <0.001



	Full Model	Step 1	Minimal Adequate Model
Mean Summer Temperature	0.0002	0.0002	0.0002
Mean Summer Precipitation	0.0509	0.0515	0.0503
Moose BrowsingIntensity	0.8637		
Snowshoe Hare Browsing Intensity	0.8296	0.8201	
Ptarmagin Browsing Intensity	0.2976	0.3507	0.3280
Moose : Mean Summer Temperature Interaction	0.3087		
Snowshow Hare : Mean Summer Temperature Interaction	0.6599	0.5709	
Ptarmagin : Mean SummerTemperature Interaction	0.0012	0.0008	0.0017

Figure A3.1 Graphical representation of the model selection process via backward elimination for model of *Salix spp.* growth fit with climate and spatial herbivory variables. Cells values and color represents the p-value obtained for that parameter from a Wald test. Columns represent model iteration in process of stepwise backward selection. White cells indicate fixed effects which have been eliminated.

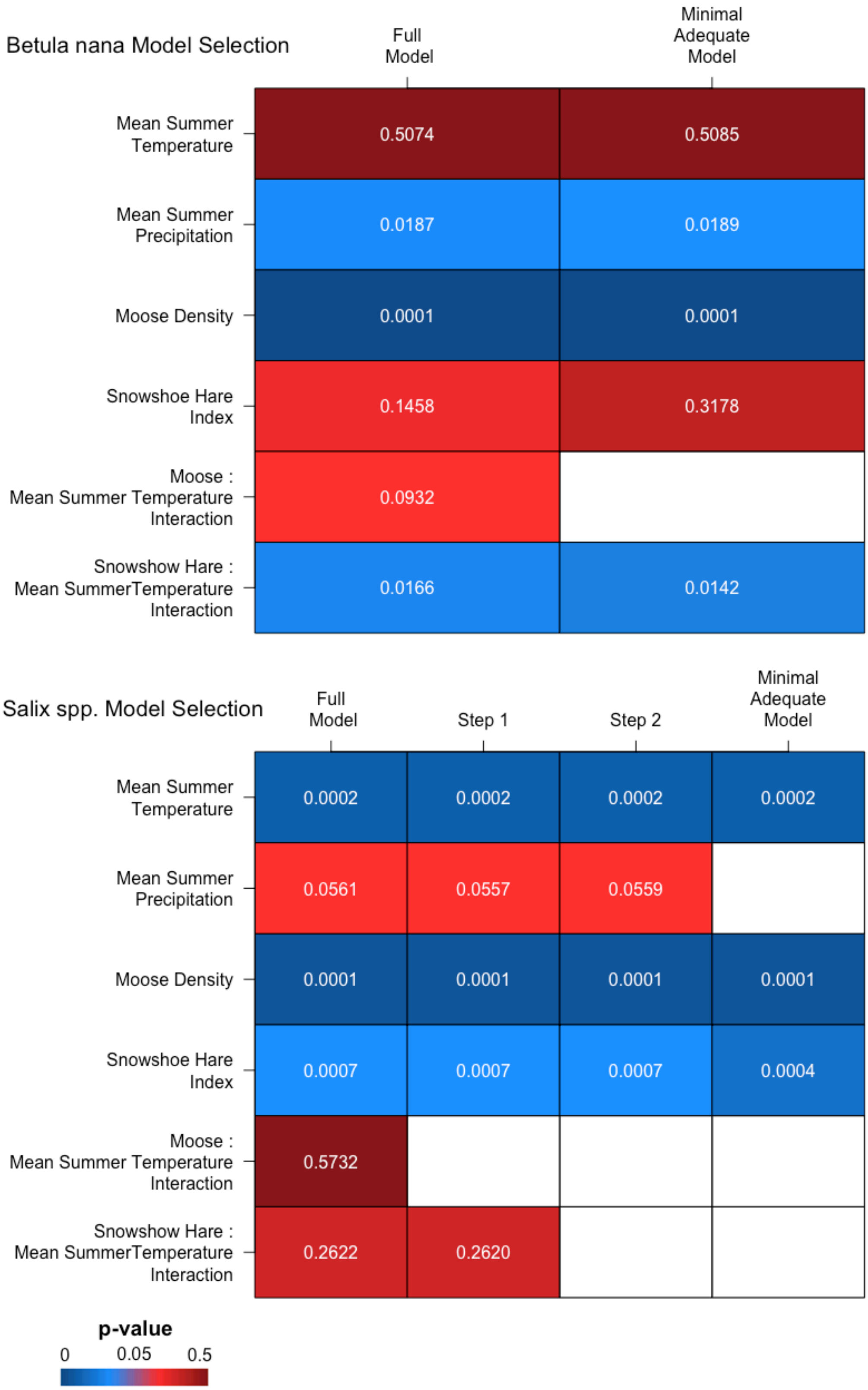
Table A3.2 Fixed effects parameters from full models for (A) *Betula nana* and (B) *Salix spp* fitted with climate and temporal herbivory variables. Sample size (*n*) indicates the number of radial growth observations taken as the response variable in the model. Full model tests, comparing the full models to their respective intercept-only models using likelihood ratio tests, are presented.

A.		**Estimate**	**SE**	***t*-value**	***P*-value**
Betula nana **Radial growth**	Intercept	0.29	0.13	2.30	0.021
(n=2875)	Mean Summer Temperature	0.15	0.04	3.83	<0.001
	Mean Summer Precipitation	0.04	0.02	2.41	0.016
	Moose Density	-0.20	0.02	-10.01	<0.001
	Snowshoe Hare Index	-0.01	0.01	-1.25	0.211
	Moose x MST Interaction	-0.03	0.02	-1.59	0.111
	Snowshoe Hare x MST Interaction	0.03	0.01	2.40	0.017

Full Model Test: Likelihood Ratio = 125.01, P-Value = <.0001

B.		**Estimate**	**SE**	***t*-value**	***P*-value**
Salix spp. **Radial growth**	Intercept	0.10	0.15	0.64	0.521
(n=1655)	Mean Summer Temperature	0.26	0.06	4.72	<0.001
	Mean Summer Precipitation	0.04	0.02	1.94	0.052
	Moose Density	-0.17	0.03	-5.40	<0.001
	Snowshoe Hare Index	-0.05	0.02	-3.38	0.001
	Moose x MST Interaction	-0.02	0.03	-0.57	0.567
	Snowshoe Hare x MST Interaction	-0.02	0.02	-1.13	0.260

Full Model Test: Likelihood Ratio = 68.02, P-Value = <.0001



Betula nana Model Selection

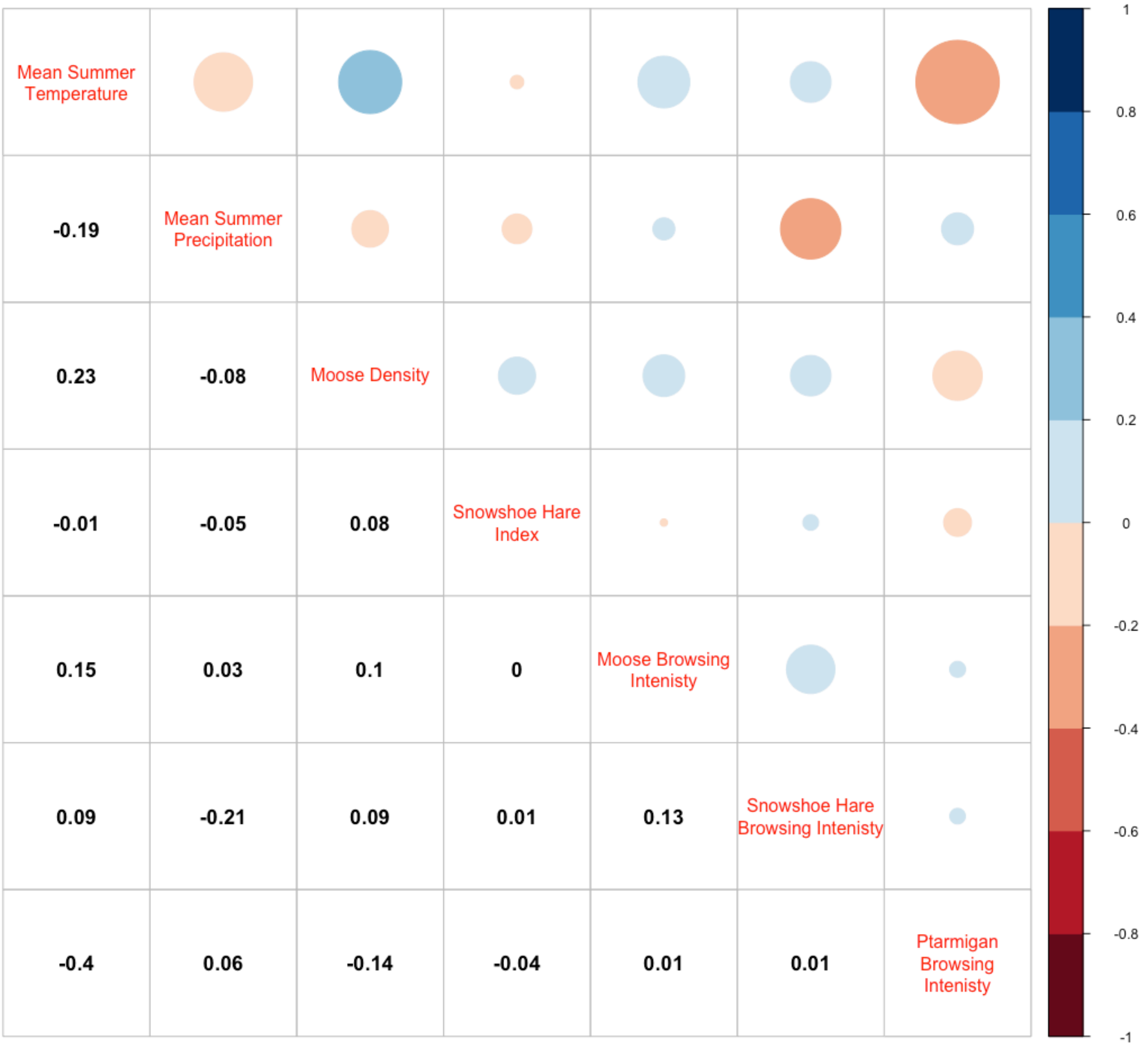
	Full Model	Minimal Adequate Model
Mean Summer Temperature	0.5074	0.5085
Mean Summer Precipitation	0.0187	0.0189
Moose Density	0.0001	0.0001
Snowshoe Hare Index	0.1458	0.3178
Moose : Mean Summer Temperature Interaction	0.0932	
Snowshow Hare : Mean SummerTemperature Interaction	0.0166	0.0142

Salix spp. Model Selection

	Full Model	Step 1	Step 2	Minimal Adequate Model
Mean Summer Temperature	0.0002	0.0002	0.0002	0.0002
Mean Summer Precipitation	0.0561	0.0557	0.0559	
Moose Density	0.0001	0.0001	0.0001	0.0001
Snowshoe Hare Index	0.0007	0.0007	0.0007	0.0004
Moose : Mean Summer Temperature Interaction	0.5732			
Snowshow Hare : Mean SummerTemperature Interaction	0.2622	0.2620		

Figure A3.2 Graphical representation of the model selection process via backward elimination for models of *Betula nana* and *Salix spp.* growth fit with climate and temporal herbivory variables. Cells values and color represents the p-value obtained for that parameter from a Wald test. Columns represent model iteration in process of stepwise backward selection. White cells indicate fixed effects which have been eliminated.

Appendix 4: Correlation Matrix of Model Parameters



Mean Summer Temperature						
-0.19	Mean Summer Precipitation					
0.23	-0.08	Moose Density				
-0.01	-0.05	0.08	Snowshoe Hare Index			
0.15	0.03	0.1	0	Moose Browsing Intenisty		
0.09	-0.21	0.09	0.01	0.13	Snowshoe Hare Browsing Intenisty	
-0.4	0.06	-0.14	-0.04	0.01	0.01	Ptarmigan Browsing Intenisty

Figure A4. Correlation matrix for all climate and herbivory variables included in the mixed model analysis. This figure was produced with the ‘corrplot’ package (Wei et al., 2017) in R and the values represent the spearman rank correlation between each variable.