THE SNOWSHOE HARE FILTER TO SPRUCE ESTABLISHMENT IN BOREAL ALASKA

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Abstract

Interior Alaska is a heterogeneous landscape within the circumpolar boreal forest and is largely composed of black and white spruce (*Picea mariana* and *P. glauca*). Improving our understanding of the factors affecting patterns in spruce regeneration is particularly important because these factors ultimately contribute to shaping the boreal forest vegetation mosaic. Herbivory by snowshoe hares (*Lepus americanus*) is one factor that likely drives patterns in spruce establishment. The interaction between spruce and snowshoe hares provides an opportunity to study how plant-herbivore interactions can affect succession, vegetation community composition, and consequently, how herbivory influences landscape heterogeneity. I explored how herbivory by snowshoe hares alters the survival and growth of spruce seedlings across Interior Alaska's boreal forest. I hypothesized that the survival and growth rate of regenerating spruce is significantly reduced by snowshoe hare herbivory and that snowshoe hare herbivory influences the pattern of spruce establishment across time and space. To address this hypothesis, I conducted research in three distinct vegetation communities across the region: productive lowland floodplains (Chapters 1 and 2), treeline (Chapters 3 and 4), and recently burned stands of black spruce (Chapter 5). Together these five chapters reveal that snowshoe hares affect spruce establishment across much of boreal Alaska. Where and when hares are abundant, spruce can be heavily browsed, resulting in suppressed seedling growth and increased seedling mortality. The results of these studies also reveal a consistent and predictable pattern in which this plant-herbivore interaction takes place. The snowshoe hare filter acts as a 'spatially aggregating force' to spruce establishment, where the potential for optimal regeneration is highest during periods of low hare abundance and where hares are absent from the landscape.

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Introduction

Background and overview

Plant-animal interactions and the landscape mosaic - Vegetation mosaics, reflecting landscape heterogeneity, influence the type of ecosystem services to humans and the kind and number of animal species that can be supported across a landscape (Turner et al. 2013; Stein et al. 2014). Available resources such as specific timber products, ecosystem structure that may provide suitable cover from predators, and habitat types, including the distribution of core habitat or ecotones, are controlled by the plant communities present and their arrangement within a mosaic (Turner 1989). These spatial patterns of vegetation are largely driven by disturbance events and succession interacting with geomorphology and climate.

Plant-herbivore interactions also influence landscape patterns, and this has been demonstrated across many ecosystems (Davidson 1993; Asner and Levick 2012; Christie et al. 2015). For example, the dominance of less palatable grass species throughout remnant tallgrass prairie patches of North America is the legacy of forage selectivity by voles (*Microtus pennsylvanicus*) (Howe et al. 2006). The large ungulates of African savannas reduce the extent of closed-canopy woodlands by consuming tree seedlings, and by elephants (*Loxodonta* spp.) felling mature trees (McNaughton et al. 1988; Asner and Levick 2012). Bark beetles (*Dendroctonus* spp., *Ips* spp., *Scolytus* spp.) cause extensive tree mortality throughout much of western North America's forest ecosystems, which leads to a vast patchwork of standing dead forest stands (Raffa et al. 2008). The activity of each of these herbivores subsequently influences the vegetation mosaic via changes in plant composition or in the patchiness of community types.

The impacts of plant-animal interactions at the landscape level are driven by how individual species of herbivores and plants affect one another. Herbivory is a stress that may facilitate (by consumption of competitors) or harm (direct consumption) a plant’s capacity to establish, or its fitness following establishment (Davidson 1993). The impact of herbivory to a particular plant is affected by the selectivity of the herbivore, and this selection is affected by the defenses of the plant species such as secondary compounds (Bryant et al. 1991). More toxic plants may become dominant in a community because they experience less herbivory and thus gain an advantage over less defended species. The dynamics of this interaction can change plant community composition by shifting it towards greater species evenness or species dominance (Hulme 1996; Butler and Kielland 2008; Feng et al. 2009). The capacity of herbivores to exert an influence on vegetation is also dependent on its simple abundance (and thus feeding intensity) (McNaughton 1984). Similarly, the density of the plant species being consumed also influences the capacity for herbivores to shape the landscape because plants that recruit at high densities may satiate herbivores, limiting the extent to which they alter vegetation composition or structure (Bryant et al. 1991; Crawley and Long 1995). Examples of how herbivores contribute to landscape heterogeneity are widespread in all global biomes, including the boreal forests of North America (Pastor et al. 1988).

Alaska's boreal forest – Interior Alaska is a heterogeneous landscape within the circumpolar boreal forest, bounded by the Alaska mountain range to the south and the Brooks mountain range to the north. As part of the boreal forest ecosystem, it is characterized by a cold and dry climate with a short growing season (Juday et al. 2003), factors that contribute to a low diversity of tree species (Usinowicz et al. 2017). Forests in Interior Alaska are dominated by white and black spruce (*Picea glauca* (Moench) Voss and *P. mariana* (Mill.) B.S.P.), trembling aspen and balsam poplar (*Populus tremuloides* Michx. and *P. balsamifera* L.), and Alaska birch (*Betula neoalaskana* Sarg.). The distribution of these tree species across the landscape is largely described by landscape position, which reflects variation in site drainage and insolation (Mann et al. 1995; Kurkowski et al. 2008; Roland et al. 2013). The occurrence of each tree species in a given location is further driven by processes of disturbance and succession (Kurkowski et al. 2008). Along major rivers, such as the Yukon and Tanana, constant sediment accretion and erosion from channel meandering and flood events control patterns of succession (Walker et al. 1986). New mineral bars are first colonized by willows (*Salix* spp.) and thin leaf alder (*Alnus incana* (L.) Moench ssp. *tenuifolia* (Nutt.) Breitung), while poplar is generally the first tree to dominate the forest canopy, followed several decades later by white spruce (Walker et al. 1986; Hollingsworth et al. 2010). Elsewhere, large expanses of Interior Alaska are dominated by black spruce forests whose age structures, species compositions, and successional trajectories are strongly influenced by fire history. For instance, moderately intense fires can result in black spruce self-replacement following fire whereas severe fires can initiate an alternative successional trajectory that includes a phase of aspen or birch dominance in the many decades following fire (Johnstone and Chapin 2006).

Mean annual temperatures have steadily increased in the region for the last four decades and this has resulted in substantial changes to these patterns of disturbance and succession across the landscape (Kasichke et al. 2010; Juday et al. 2015). For example, productive stands of floodplain white spruce are shifting westward, as eastern Alaska is becoming too warm for optimal growth, whereas further west conditions are now sufficiently warm for more optimal spruce growth and regeneration (Juday et al. 2015; Miller et al. 2017). Fire in stands of black spruce are burning more severely, causing an increase in deciduous tree dominance over spruce dominance (Kasichke et al. 2010; Shenoy et al 2011; Mann et al. 2012). Many of the patterns of change occurring in boreal Alaska reflect changes in the distribution of spruce.

Spruce dominates – The boreal forest of North America is primarily a forest of spruce (Juday et al. 2003; Hollingsworth et al. 2006; Ohse et al. 2009). Consequently, both white and black spruce are well-studied in respect to their life histories (Juday et al. 2003; Viglas et al. 2013), silvicultural properties (Densmore et al. 1999), and in their responses to climate change (Juday et al. 2015; Walker et al. 2015). Despite receiving considerable attention, there are still gaps in our understanding of spruce ecology. One of the largest of these knowledge gaps concerns the impacts of herbivory, in particular the effects of browsing by snowshoe hares (*Lepus americanus*), whose decadal scale irruptions are a striking feature of the boreal forests of Canada and Alaska.

Herbivory is recognized as an important factor affecting patterns of spruce establishment. Heavy browsing of willows by moose reduces suitable microclimates for the establishment of white spruce on river floodplains in Interior Alaska (Angell and Kielland 2009). Conversely, historical exclosure experiments at Isle Royale National Park showed moose browsing facilitates white spruce savanna communities because other competing trees are suppressed by browsing (Pastor et al. 1988). More recent experiments in boreal Canada concluded similar effects of ungulate browsing on forest composition (Hidding et al. 2013). Whereas moose indirectly affect spruce establishment patterns by browsing associated vegetation, snowshoe hares directly browse spruce, resulting in a long record of observations detailing their capacity to severely restrict tree regeneration (Aldous and Aldous 1944; Wolff 1980; Sinclair 2003; Peterson et al. 2005).

Hare ecology in Alaska - The snowshoe hare is known to have a significant impact on vegetation dynamics. In the absence of predators, a significant control over population growth (Feierabend and Kielland 2015), snowshoe hares have been shown to effectively halt the establishment of all tree species in an island setting (Peterson et al. 2005). In the boreal forest, hares can comprise almost half of the total vertebrate biomass (Krebs et al. 2001), and during peaks in their population, their total biomass can exceed that of all other vertebrate herbivores combined (Rexstad and Kielland 2006). It is during peaks in their population that snowshoe hares significantly impact vegetation composition (Turkington et al. 2002; Sinclair 2003).

Interactions between spruce and snowshoe hares provide an opportunity to study how plant-herbivore interactions can affect succession, vegetation community composition, and consequently, how herbivory influences landscape heterogeneity. In order to address the potential impacts of this plant-herbivore interaction on patterns of spruce establishment, I explored how herbivory by snowshoe hares alters the survival and growth of spruce seedlings across Interior Alaska's boreal forest. I hypothesized that the survival and growth rate of regenerating spruce is significantly reduced by snowshoe hare herbivory and that snowshoe hare herbivory influences that pattern of spruce establishment across time and space. In order to address this hypothesis, I conducted research in three distinct vegetation communities across the region.

Chapters 1 and 2: the floodplain – In the first two chapters of my dissertation, I explored how snowshoe hare herbivory influences white spruce establishment along the Tanana River near Fairbanks, Alaska. This reach of the river is representative of many river floodplains in Interior Alaska.

In Chapter 1, I took advantage of long-term exclosure experiments to assess spruce survival and performance in the presence or absence of herbivores. Building on the conclusions of Chapter 1, I ventured beyond the exclosure experiments and sampled herbivory by snowshoe hares at several locations along a 50-km stretch of the Tanana. In Chapter 2, I reconstructed the pattern of white spruce establishment along this stretch of floodplain to see if patterns in hare abundance partly explain patterns in spruce establishment over that last 40 years. Together, Chapters 1 and 2 reveal the capacity for snowshoe hares to significantly influence spruce establishment and growth along the Tanana river floodplain and highlight the importance of the hare cycle and the presence of tall shrub layers in influencing this interaction.

Chapters 3 and 4: hares at treeline – After describing snowshoe hare-white spruce interactions on a river floodplain, I explored how this relationship takes place at the edge of the boreal forest, where treelines are now shifting in response to climate change. Preceding treeline advance there is increasing shrubification, which provides suitable habitat for snowshoe hares in areas well beyond treeline (Tape et al. 2015; Dial et al. 2016). As a result, it is likely that snowshoe hare herbivory will influence patterns of treeline advance.

In Chapter 3, I examined how herbivory by snowshoe hares varies across space and time along an elevational gradient in Denali National Park. In Chapter 4, I incorporated data from latitudinal treeline to explain how herbivory affects spruce height in two regions that reflect the limit of white spruce's distribution. These two studies reveal similarities between what drives variation in browsing of spruce by hares for floodplains and the treeline. I also explained why browsed white spruce are often taller than unbrowsed spruce and suggest this reflects selectivity by hares for older or faster growing seedlings.

Chapter 5: hare browsing of black spruce after fires – Because much of boreal Alaska is dominated by black spruce, I also investigated how herbivory by snowshoe hares affects black spruce establishment. Chapter 5 describes how snowshoe hare herbivory influences patterns of succession following fire. I discuss how browsing by hares reinforces deciduous dominance by suppressing regenerating black spruce under deciduous canopies specifically.

Together these five chapters reveal that snowshoe hares have significant impacts on the spatial and temporal patterns of spruce establishment across much of Interior Alaska. The results of these studies also reveal a consistent and predictable pattern in which this plant-herbivore interaction takes place. The snowshoe hare filter acts as a ‘spatially aggregating force’ to spruce establishment (Herrero et al. 2016), where the potential for optimal regeneration is highest during periods of low hare abundance and where hares are absent from the landscape.

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Chapter 1. Stage-dependent effects of browsing by snowshoe hares on successional dynamics in a boreal forest ecosystem[1]

Abstract

Herbivores transform landscapes and affect succession via selective foraging that alters vegetation composition. In the boreal forest, mammalian herbivores, mainly moose (*Alces alces*), facilitate a shift towards the dominance of heavily defended species over time, such as white (*Picea glauca*) spruce. The effects of moose herbivory are intensified by the browsing of snowshoe hares (*Lepus americanus*). However, unlike moose, snowshoe hares also browse seedlings of white spruce. We quantified herbivory by snowshoe hares on white spruce along the Tanana River, Interior Alaska, and assessed the effects on white spruce demography via two different herbivore exclosure experiments. We hypothesized that both experiments would show reduced plant density and height growth in the presence of hares. We found evidence of extensive browsing of white spruce seedlings by snowshoe hares, which negatively affected white spruce establishment along the Tanana River floodplain. Previous research has indicated that hares facilitate floodplain succession in the forward direction. However, hare herbivory can also retard succession by depressing white spruce establishment and increase the time individual trees spend in the understory. This stage-dependent effect on successional dynamics via a unique temporal variation in snowshoe hare herbivory may contribute to alternative successional trajectories in the boreal forest.

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[1] Olnes, J. and K. Kielland. 2016. Stage-dependent effects of browsing by snowshoe hares on successional dynamics in a boreal forest ecosystem. Ecosphere 7(10): e01475. 10.1002/ecs2.1475

Introduction

Herbivores transform landscapes and affect succession via selective foraging that alters vegetation composition and structure, and nutrient cycling (McNaughton *et al.* 1988; Davidson 1993; Butler *et al.* 2007). Preferences for certain plant species arise from an herbivore's need to meet nutritional requirements while limiting the intake of secondary chemicals (Bryant *et al.* 1991). The degree to which these compounds are present in forage makes some plant species more vulnerable to herbivory than others. The selectivity of herbivores, influenced by plant defensive chemistry, can thus facilitate a shift in community composition towards the dominance of more heavily defended species over time (Bryant *et al.* 1991; Davidson 1993; Feng *et al.* 2009). In the boreal forests of North America, there are numerous examples of how mammalian herbivores facilitate this shift in dominant vegetation. Accelerated succession due to moose (*Alces alces*) browsing has been demonstrated from exclosure studies (Pastor *et al.* 1988; McInnes *et al.* 1992; Kielland *et al.* 1997; Hidding *et al.* 2013), across natural gradients of herbivore densities (Butler & Kielland 2008) and via modeling (Butler *et al.* 2007; Feng *et al.* 2012). Species that are not browsed by moose, including white spruce (*Picea glauca* (Moench) Voss), are thereby thought to dominate the canopy more quickly, despite slower growth rates (Bryant *et al.* 1991; McInnes *et al.* 1992).

The above-mentioned effects of moose herbivory are further intensified from browsing by snowshoe hares (*Lepus americanus*) (Smith *et al.* 1988; Bryant *et al.* 1991). During periods of high abundance, when snowshoe hare biomass can exceed that of all other vertebrate herbivores combined (Rexstad & Kielland 2006), snowshoe hares significantly impact vegetation composition (Fox & Bryant 1984; Turkington *et al.* 2002; Krebs *et al.* 2014). Although hares have similar browsing preferences to moose (Bryant *et al.* 1991), they have also been observed to browse heavily on white spruce seedlings, especially during peaks in their population cycle both in Alaska (Angell & Kielland 2009; Hollingsworth *et al.* 2010) and Canada (Smith *et al.* 1988; Sharam & Turkington 2009). White spruce is a dominant, subarctic tree species found throughout the boreal forests of North America, including Interior Alaska (Ohse *et al.* 2009), and many ecological processes of the boreal forest are affected by the growth and distribution of this conifer (Barber *et al.* 2000). For example, the transition from a deciduous-dominant to spruce-dominant forest is accompanied by substantial changes in plant community composition (Hollingsworth *et al.* 2010) and soil biogeochemical processes (Pastor *et al.* 1988; Kielland *et al.* 2006a, b).

Our objective was to quantify herbivory of white spruce seedlings by snowshoe hares along the Tanana River, Interior Alaska, and assess the potential effects on the demography of white spruce in the context of succession. Two different herbivore exclosure experiments, one with naturally regenerating and the other with planted white spruce, were used to compare individual white spruce seedlings growing in the presence or absence of hare herbivory. We hypothesized that both experiments would show reduced plant density and height growth in the presence of hares. We posit that herbivory of white spruce seedlings by snowshoe hares may facilitate an alternative pathway for herbivores to affect boreal forest succession. Rather than accelerating spruce establishment, hare herbivory may suppress recruitment of spruce and extend the time that deciduous species, such as willow (*Salix*), balsam poplar (*Populus balsamifera* L.), and thin-leaf alder (*Alnus incana* (L.) Moench ssp. *tenuifolia* (Nutt.) Breitung) persist in the canopy.

Materials and Methods

Study area - The Bonanza Creek Long Term Ecological Research (BNZ-LTER) sites are located along the Tanana River in the boreal forest of Interior Alaska, approximately 20 km southwest of Fairbanks. Five major successional stages have been defined for the Tanana River floodplain: Bare sand bars are typically colonized by willows, followed by alder and poplar (Hollingsworth *et al.* 2010; Nossov *et al.* 2011). After approximately 100 – 200 years, white spruce becomes dominant, and depending on landscape position, a mature white spruce stand may persist or succeed into black spruce (*Picea mariana* (Mill.) Britton, Sterns and Poggenb.) (Mann *et al.* 1995).

In 1987, seven vertebrate herbivore exclosures were constructed at early successional sites consisting of willow and alder. The exclosure layout is a randomized block design where at each location, both a treatment (exclosed) and control (unexclosed) plot are present. Plot size varies from 20 m by 20 m to 20 m by 50 m. Fences (5 m high) were built to exclude both moose and snowshoe hare and consist of a wooden frame wrapped using 5 cm chicken wire. These will be denoted as the 'Naturally Regenerating' (NR) exclosures.

Ten additional herbivore exclosures were constructed along the Tanana River floodplain within the BNZ-LTER in September 2002. Each exclosure is 7 m by 7 m and is surrounded by chain-link fence 2 m in height. Within each exclosure, 48 white spruce seedlings were planted, with an equal number planted outside in control plots (unexclosed) also measuring 7 m by 7 m. These exclosures were constructed to examine the indirect effects of moose browsing on white spruce establishment (Angell and Kielland 2009), and the direct impacts of snowshoe hare herbivory on white spruce seedling survival along the floodplain. We denote these as the

‘Artificially Planted’ (AP) exclosures. The AP exclosures were placed along a floodplain terrace age gradient that spans 30 years of floodplain succession (Angell & Kielland 2009), from open willow communities to alder-dominant stands, allowing us to make inferences regarding terrace age, white spruce establishment and hare herbivory. Terrace age was determined from the age of the oldest shrub present (Angell 2007).

Naturally Regenerating exclosures - During the summer of 2014, we measured the height (cm) and basal diameter (mm) of all white spruce found within the seven NR exclosures and adjacent control plots. We also estimated the age of each individual via whorl counting, where age is determined by counting the number of annual apical growth segments along the bole. Height measurements were combined with age estimates and diameter measurements to determine the height-to-age and height-to-diameter ratios for each individual to control for age effects. We evaluated both parameters because the height-to-age ratio is more biologically meaningful, whereas the height-to-diameter ratio has less measurement error. Browsing history was also measured on all white spruce individuals within control and exclosure plots for the NR experiment. Snowshoe hares prefer to browse the apical meristem and the current annual growth of white spruce seedlings. Identification of hare browsing was based on the smooth ~45° angle of the browse scar (Smith *et al.* 1988). Additionally, the density of white spruce was recorded for each exclosure and control plot (individuals m^{-2}), as well as qualitative observations regarding the canopy species present in each plot. We do note, however, that during the past 28 years, the fences at some sites were on occasion damaged by tree falls that allowed hares to enter the exclosures and browse the white spruce seedlings (56% ± 28% browsed, mean ± SE).

Artificially Planted exclosures - For the AP exclosures, we first inventoried each exclosure and control plot to determine the proportion of planted spruce alive in the summer of 2014. For surviving individuals, we measured height (cm) and basal diameter (mm). Because all spruce were of the same age and planted in the same year, we focused on the height-to-diameter ratio as a metric for comparison between exclosure and control plots.

Analysis - All statistical analyses were completed using R statistical software version 3.2.2 (R Core Team 2015). Alpha was set as 0.05 for all statistical tests and means are presented with ± 1 standard error (SE).

We performed paired t-tests to determine the effect of the exclosure treatments on the height-to-age and height-to-diameter ratios of white spruce at the plot level for the NR exclosures (function: t.test). We did not perform a paired t-test to compare density between NR exclosure treatments because a normal quantile plot of the mean differences showed a clear deviation from normality, and this was further confirmed by the Shapiro-Wilks normality test (function: shapiro.test, $W = 0.49$, $p < 0.001$). Therefore, we bootstrapped the median value of density for each treatment, using 1000 resamples each time (library: boot, function: boot). This allowed us to compare the overlap of the bootstrapped 95% confidence intervals around the median to assess treatment effects on spruce density (function: boot.ci). We used the adjusted percentile bootstrap interval (BCa) because this estimate does not assume symmetry around the resampled median.

For the AP experiment, we used multiple regression to assess the effects of the exclosure treatment, terrace age, and their interaction term on the survival and height-to-diameter ratio of planted spruce at the plot level (function: lm). Assumptions for the residuals of these tests were confirmed graphically.

Results

NR exclosures - We measured a total of 877 white spruce trees within seven paired NR exclosures (n = 614) and control plots (n = 263). Canopy cover was either thin-leaf alder, mixed alder and balsam poplar, or balsam poplar-dominant, with nearby white spruce stands that could serve as a seed source varying in distance from each plot (approximately 75 m - >200 m away). We found evidence of significant hare browsing at all locations with 86% ± 13% white spruce browsed in control plots. White spruce within the exclosures mainly recruited between 1991 and 2008, whereas white spruce within the control plots recruited nine years later, between 2000 and 2008 (Figure 1.1).

In addition to differences in recruitment, seedlings exposed to herbivory also had reduced height growth. White spruce within control plots had lower height-to-age ratios (cm year^{-1}) than for white spruce inside exclosures (mean difference: -1.41 ± 1.18 cm year^{-1}, $t_6 = -2.91$, $p = 0.03$, Figure 1.2a). Likewise, the average height-to-diameter ratio for white spruce within the control plots was significantly lower than for white spruce inside exclosures (mean difference: -1.66 ± 0.82 cm mm^{-1}, $t_6 = 4.94$, $p = 0.002$, Figure 1.2b).

We found high variability in white spruce density among exclosure and control plots across sites. Average density inside the exclosures was 0.90 ± 0.80 white spruce m^{-2} compared to 0.21 ± 0.16 white spruce m^{-2} for the adjacent control plots (Figure 1.2c). Although the median density was nearly twice as high for the exclosure treatment (0.09 spruce m^{-2} versus 0.05 spruce

m^{-2} for control plots), the adjusted 95% confidence intervals showed complete overlap given the high variability across sites.

AP exclosures - We sampled a total of 459 individuals and more than half were found within exclosures (292). Five of the control plots (50%) had no surviving white spruce. Average survivorship for the remaining control plots (n = 5, 28% ± 16%) was less than that for the exclosures (n = 10, 50% ± 12%). Seedlings in exclosures (5.34 ± 0.66 cm mm^{-1}) had larger height-to-diameter ratios than for seedlings in control plots (3.65 ± 0.32 cm mm^{-1}). Both our regressions for survival (adj. $r^2 = 0.27$, $F_{3,20} = 3.85$, $p = 0.02$, Figure 1.3a) and for the height-to-diameter ratio (adj. $r^2 = 0.72$, $F_{3,11} = 13.14$, $p < 0.01$, Figure 1.3b) were significant. For exclosure plots, survivorship and the height-to-diameter ratio were positively correlated with floodplain terrace age, but negatively correlated with terrace age in control plots. At older sites where white spruce within exclosures were most successful, a closed canopy of alder was present.

Discussion

We found evidence of extensive browsing of white spruce seedlings by snowshoe hares, which negatively affected white spruce establishment and growth on the Tanana River floodplain. For white spruce that were old enough to sustain multiple browse events, exposure to hare herbivory resulted in decreased height growth, increasing the time required to escape herbivory and reach the forest canopy.

Our results also reflect the varying distance of each NR plot from cone producing stands of mature white spruce. White spruce seeds are heavy and seldom disperse beyond 200 m from the parent tree (Juday, *personal communication*). The high variability in white spruce density across NR exclosure sites is largely attributable to the wide range in distance from cone-producing trees, with plots that were closer tending to have higher seedling density.

Whereas we did not detect a statistically significant browsing effect on density via the NR exclosure experiment, reduced survival of planted spruce in the AP control plots affirms that browsing by hares has important effects on this parameter. Throughout Interior Alaska, including Denali National Park and Preserve, the BNZ-LTER, and in the Brooks Range, we have observed high levels of browsing (Figure 1.4) and seedling mortality for both white and black spruce attributable to snowshoe hares. White spruce seedlings browsed in the first years of establishment are most vulnerable to mortality because a single browse event may suffice to remove all meristematic tissue. As a result, a peak in the snowshoe hare cycle may cause a biologically significant depression in white spruce recruitment. It is plausible that the delayed establishment of white spruce in the NR control plots reflect peak hare abundances in 1990 and 1999, explaining the ten year gap in recruitment observed between most NR exclosures and control plots (Figure 1.1). Recruitment was likely the same within both exclosures and control plots (as the paired plots were equidistant from white spruce seed sources); however, mortalities from browsing by snowshoe hares resulted in a ‘missing record’ of recruitment within the control plots.

The risk of severe browsing that can lead to seedling mortality seems to increase with increasing cover provided by deciduous species over successional time. However, cover is initially important to successful white spruce establishment, as well as for subsequent rates of growth and survival (Angell and Kielland 2009). Older terraces that provide more cover and have lower salt concentrations in the soil are a more suitable microhabitat for white spruce recruitment. Young white spruce seedlings require cover to prevent the risk of overheating or desiccation (Angell and Kielland 2009; Milakovsky *et al.* 2011), though saplings eventually benefit from an opening of the canopy (Milakovsky *et al.* 2011). These findings are consistent with our observations of succession for the Tanana River floodplain, where spruce recruits well under cover, and is released as thick alder canopies give way to more open poplar stands. Snowshoe hares complicate this story, however, because older floodplain sites with increased cover are also better habitat for hares. For example, we found the largest spruce seedlings by far in the AP exclosure on the oldest terrace with the densest willow/alder canopy, but in the adjacent control plot the planted spruce had been completely obliterated by hare browsing. Thus, as microhabitat conditions improve, white spruce must then contend with snowshoe hare herbivory, and this is particularly pronounced under alder canopies.

The convergence of alder canopies, white spruce recruitment, and an abundance of snowshoe hares may present a junction for alternative successional trajectories (Hollingsworth *et al.* 2010, Hidding *et al.* 2013). Nossov *et al.* (2011) found stands of alder that were self-replacing, having continued recruitment for 50 years. These stands may represent one possible trajectory, where alder persists due to a lack of recruiting balsam poplar and white spruce, which may be suppressed due to hare herbivory. They also demonstrated that as alder stands get older, balsam poplar is less likely to be found recruiting, while spruce may recruit at all ages of alder. If hares consume most white spruce seedlings, we assume that balsam poplar seedlings are also consumed but are less able to withstand continued browsing. Therefore, hare browsing may facilitate a novel successional trajectory, whereby alder transitions directly to white spruce (Hollingsworth *et al.* 2010; Nossov *et al.* 2011), essentially representing a “successional skip”. The positive relationship between abundance of hare pellets on the forest floor and the age of alder stands (Nossov *et al.* 2011) is consistent with this hypothesis. Thus, white spruce and hares may interact for long periods of time under alder canopies before the spruce can finally escape.

Our findings recall a comment from Aldo Leopold (1949) regarding oak (*Quercus*) regeneration in Wisconsin, where "each surviving oak is the product of either rabbit scarcity or rabbit negligence." We have demonstrated that, like the oak, white spruce establishment is guided by the presence or absence of hares. Previous research has indicated that hares facilitate floodplain succession in the forward direction by preferentially browsing early successional willow species, thus accelerating the dominance of alder (Kielland & Bryant 1998), which is largely untouched by hares (Bryant *et al.* 1983). However, hare herbivory can also retard succession by reducing white spruce establishment and increasing the time individual trees spend in the understory. This stage-dependent effect on successional dynamics via a unique temporal variation in snowshoe hare herbivory may contribute to alternative successional trajectories that shape the landscape mosaic that is the boreal forest.

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Figures

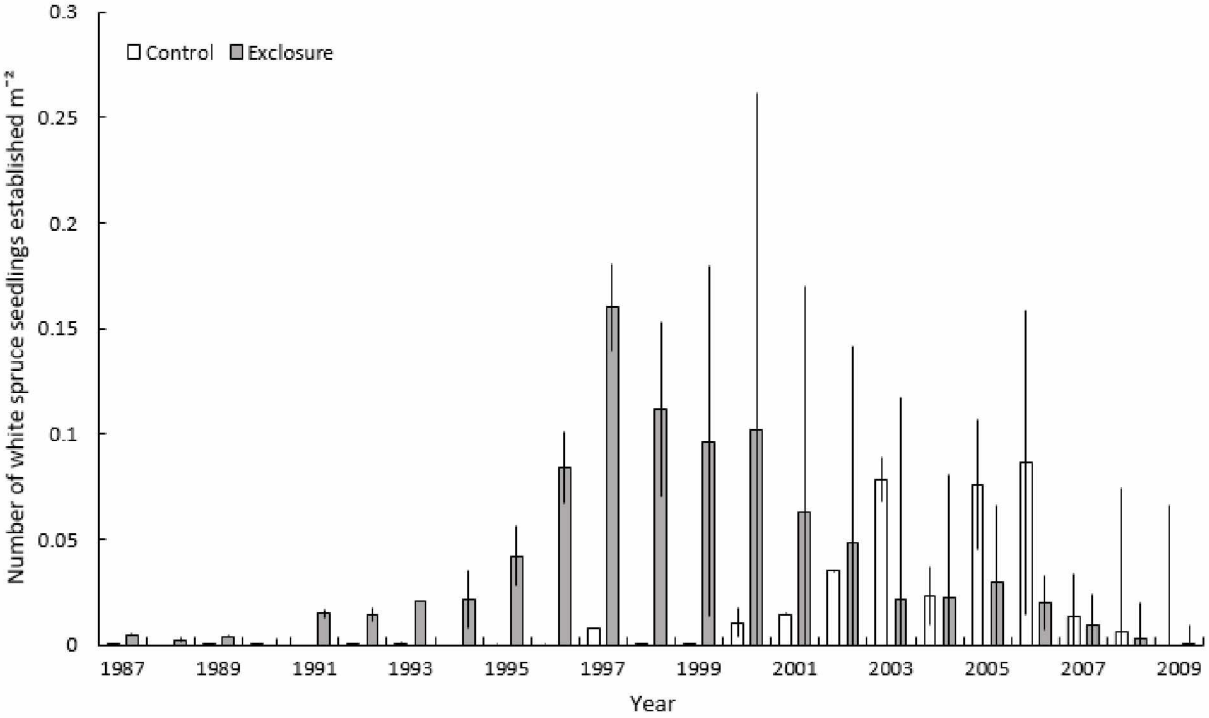

Figure 1.1. Pattern of yearly establishment for white spruce (seedlings established m^{-2}) within NR exclosure plots (grey bars) and control plots (white bars). Mean ± SE, n = 7.

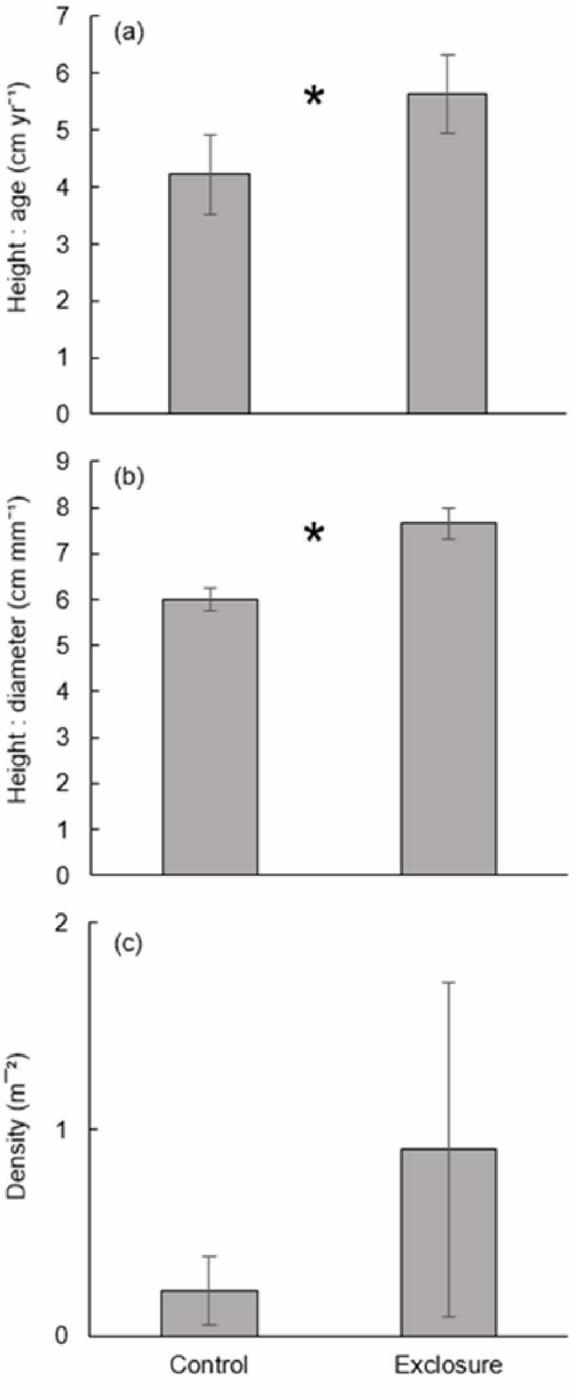

Figure 1.2. White spruce seedlings within NR control plots show reduced height growth and density (Mean ± SE, n = 7). (a) Height-to-age ratio (cm year^{-1}, $t_6 = -2.91$, $p = 0.03$) and (b) Height-to-diameter ratio (cm mm^{-1}, $t_6 = 4.94$, $p < 0.01$) for all NR exclosure and control plots. (c) White spruce density (m^{-2}) for all NR exclosures and control plots.

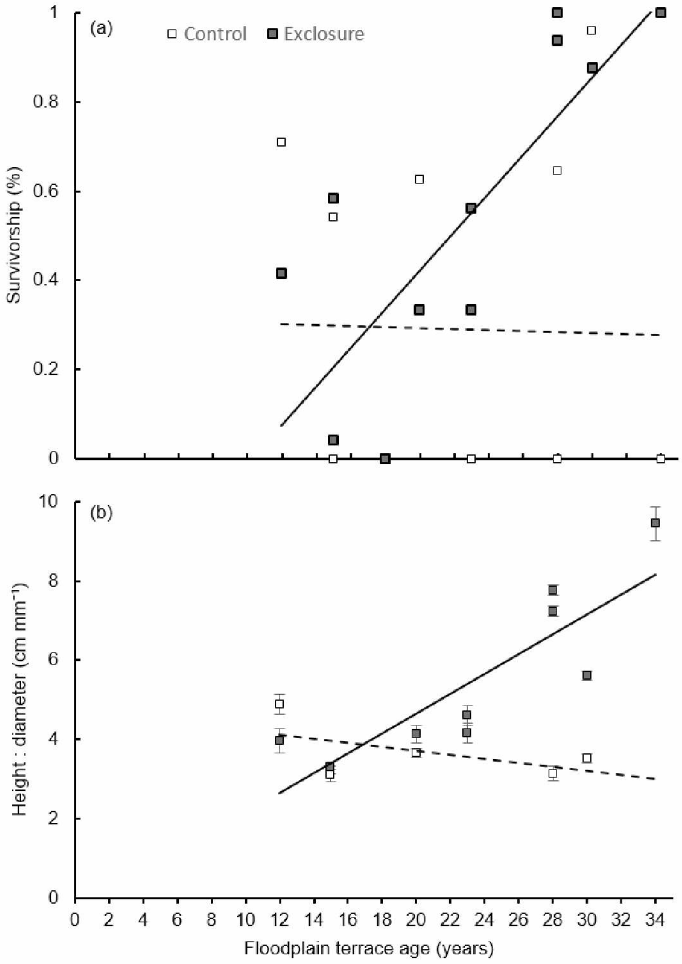

Figure 1.3. Survival and height growth of white spruce seedlings in 2014 for the AP exclosures (filled squares) and control plots (open squares) across a floodplain terrace age gradient. (a) Survivorship (%) of white spruce seedlings (n = 48) twelve years following planting (adj. r^2 = 0.27, $F_{3,20}$ = 3.85, p = 0.02). A positive correlation was found between survival and terrace age for seedlings within exclosures (β_1 = 0.04, solid trendline), however the relationship was negative for seedlings within control plots (β_2= -0.04 (change in slope), dashed trendline). (b) Height-to-diameter ratios (cm mm^{-1}, Mean ± SE) of exclosures and control plots revealed a similar pattern (adj. r^2 = 0.72, $F_{3,11}$ = 13.14, p < 0.01), where height related positively with terrace age within exclosures (β_1 = 0.25, solid trendline), but negatively within control plots (β_2 = -0.30 (change in slope), dashed trendline).

Figure 1.4. A severely browsed white spruce seedling at BNZ-LTER.

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Chapter 2. Asynchronous recruitment dynamics of snowshoe hares and white spruce in a boreal forest[1]

Abstract

Herbivores have the capacity to modify plant community composition and ecosystem structure and function via browsing. For example, moose (*Alces alces*) and snowshoe hare (*Alces alces*) facilitate succession in Alaska's boreal forest by preferentially browsing early successional species over late successional conifers. Snowshoe hares also eat conifers, including white spruce, and this browsing may affect the pattern of spruce establishment over time. We measured over 800 spruce at 18 locations along the Tanana River floodplain in Interior Alaska, USA and demonstrated that the proportion of spruce browsed annually positively correlates with annual hare abundance. Nearly all seedlings sampled had been browsed. Further, we modeled the pattern of spruce establishment over the last 40 years and found that hare abundance, growing season temperature, early season snow depth, and flooding explain the majority of this pattern. This model demonstrated that less spruce established during periods of high hare abundance than during periods of low hare abundance. The extensive browsing of white spruce that occurs during periods of high hare abundance may further compound the negative effects of climate warming on spruce recruitment in these floodplain forests.

Introduction

Herbivores have the capacity to modify plant community composition and ecosystem structure and function via browsing (Bryant and Chapin 1986; McNaughton et al. 1988; Brandner et al. 1990; Davidson 1993). For example, in the boreal forests of North America,

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[1] Olnes, J. and K. Kielland. 2017. Asynchronous recruitment dynamics of snowshoe hares and white spruce in a boreal forest. Forest Ecology and Management 384: 83 – 91.

moose (*Alces alces*) and snowshoe hare (*Lepus americanus*) facilitate succession by preferentially browsing early over late successional species. Exclosure studies have demonstrated that browsing decreases the time required for thin-leaf alder (*Alnus incana* subsp. *tenuifolia*) to replace willows (*Salix* sp.) in Interior Alaska (Kielland and Bryant 1998) and for conifers, mainly white spruce (*Picea glauca* (Moench) Voss), to replace more palatable tree species at Isle Royal National Park, Michigan (McInnes et al. 1992). These transitions, facilitated by browsing, further alter forest dynamics by affecting soil biogeochemical properties (Pastor et al. 1992; Kielland et al. 1997). The browsing preferences of hares differ from that of moose, however, in that hares also browse the seedlings of late successional conifers, including many species valued as timber resources and for use in reforestation (Bergeron and Tardiff 1988; Milakovksy et al. 2011). Despite an extensive record noting the capacity of hares to browse and even eliminate conifers (see Cook and Robeson 1945; Peterson et al. 2005; Olnes and Kielland 2016), few studies have sought to understand this effect in a natural setting and how this browsing may influence forest dynamics over longer time scales.

White spruce is a dominant boreal tree species in North America, and in Alaska, an indicator of a rapidly changing landscape as its distribution is shifting in response to climate warming (Jorgenson et al. 2014; Juday et al. 2015). The floodplains of Alaska's Yukon and Tanana Rivers represent the most productive landscape for white spruce and are the most important timber regions for Interior Alaska (Wurtz et al. 2006; Juday et al. 2015). Presently, however, reduced annual growth has been documented and this phenomenon is projected to continue in the future, along with reduced viable seed production (Lloyd et al. 2013; Roland et al. 2014; Juday et al. 2015). Over time, reduced white spruce establishment will likely contribute to the projected shift in Interior Alaska from a conifer dominant ecosystem to mixed-wood boreal forest, altering successional processes and community composition (Hollingsworth et al. 2010), as well as forest productivity (Barber et al. 2000). Consequently, areas sufficiently productive for sustainable forestry are shifting westward into regions previously below the climate envelope of white spruce (Juday et al. 2015). Properly managing these shifting forests requires better understanding of the rate and extent of change that may occur, and what factors may influence future regeneration patterns.

Patterns of white spruce establishment are likely affected by snowshoe hare herbivory. Both hares and white spruce are present throughout boreal North America, however, differences in plant community composition (McInnes et al. 1992; Hollingsworth et al. 2010), hare population patterns (Krebs et al. 2014) and plant defensive chemistry (Bryant et al. 1994), imply this interaction varies throughout their range. Previous studies in the Yukon (Smith et al. 1988) and Saskatchewan (Milakovsky et al. 2011), Canada, have noted minimal effects of hare browsing on spruce, while elsewhere, such as in New York, USA (Cooke and Robeson 1945), studies detail more significant impacts. Observations in Interior Alaska have noted that browsing of white spruce seedlings by snowshoe hares can be extensive (Walker et al. 1986; Angell and Kielland 2009; Olnes and Kielland 2016), despite spruce being well defended chemically (Sinclair et al. 1988). Most of this browsing likely occurs during the winter, when hares rely on the twigs of willows, birch (*Betula sp.*), and spruce (Wolff 1978; Bryant 2003). During the summer months, hares are able to shift their diet toward more herbaceous and leafy forage (Bryant 2003; Seccombe-Hett and Turkington 2008). Spruce are also more likely browsed during periods of high hare abundance when more preferable food sources, mainly willows and birch (Fox and Bryant 1984; Smith et al. 1988), are depleted. Given the unique periodicity of the hare population cycle at high latitudes, where populations fluctuate on a roughly decadal basis

(Kielland et al. 2010; Krebs et al. 2013), spruce is subject to a temporal variation in browsing pressure. Because white spruce exhibit synchronized cone production (masting), severe browsing by hares has the potential to eliminate entire cohorts of seedlings if a large cone crop aligns with the peak of the hare cycle. This outcome could delay spruce dominance by years to decades, given the periodic nature of viable seed production in spruce (Roland et al. 2013). Thus, browsing by hares may compound the effect of climate change on the shifting distribution of productive lowland white spruce.

Several environmental variables may influence the effect of hare browsing on spruce establishment. Previous studies have demonstrated the susceptibility of spruce seedlings recruiting along the Tanana River to heat stress and desiccation (Angell and Kielland 2009), as well as to damage from flood events (Yarie et al. 1998). However, flood events that occur prior to seedling establishment may benefit seedlings by providing open mineral beds for recruitment (Walker et al. 1986). Thus, growing season temperature and fluvial dynamics may interact in ways that either benefit or stress establishing seedlings. For example, years with a high flood stage would indicate an elevated water table that spruce can more easily access with their shallow root systems, reducing the risk of desiccation (Yarie 2008). Because hares primarily browse spruce during the winter months, early season snow depth may also affect the vulnerability of seedlings to browsing (Telfer 1974).

We sampled white spruce seedlings along the Tanana River, near Fairbanks, Alaska, to understand spruce-hare interactions in a landscape that may see reduced white spruce establishment in the future. Our first objective was to quantify the level of browsing by hares on white spruce seedlings over the last four decades. We hypothesized that browse frequency would positively correlate with hare abundance across years, and that browsed spruce seedlings would have significantly reduced height growth. Our second objective was to reconstruct the pattern of yearly spruce establishment since 1970 and examine this distribution in relation to historical and simulated data of white spruce seed production and the snowshoe hare cycle. We hypothesized that the relative number of trees established in a given year positively varies in proportion to viable seed production of the two years prior, and negatively correlates with snowshoe hare density for the years following establishment. We further hypothesized that fewer white spruce would establish during hotter and drier summers, and that an early snowpack would benefit seedlings by insulating them from colder temperatures and browsing hares. If so, then the unique periodicity of the hare cycle may act as a demographic filter where spruce most successfully recruit during periods of low hare abundance.

Methods

Study area - The Bonanza Creek Long Term Ecological Research site (BNZ-LTER, 64°43'N, 148°12'W) is located along the Tanana River approximately 30 km southwest of Fairbanks, Alaska, USA. The floodplain is approximately 120 m a.s.l. and exhibits a mosaic of successional stands dominated by willows, thin-leaf alder, balsam poplar (*Populus balsamifera*) and white spruce. Eighteen square, 625 m^2 sampling plots were selected along a 50 km stretch of the Tanana River that encompassed the BNZ-LTER (Figure 2.1). Because our focus was on sampling younger spruce, we primarily selected early-to-mid-successional sites with a mixed canopy of thin-leaf alder and balsam poplar, as these stands represent the successional stage at which spruce becomes abundant in the understory (Walker et al. 1986). Plot selection was based on field observations and then points selected via satellite imagery prior to sampling in the field, which included six previously established LTER research plots.

Sampling design - All field sampling took place during the months of June - August of 2014. We started at the southeast corner of each plot and measured between 50 and 100 individual white spruce. We measured all white spruce individuals encountered; however, because we focused on sampling early and mid-successional forest stands, most spruce measured were either seedlings (< 1.37 m tall) or saplings (> 1.37 m tall, < 12 cm diameter at breast height (d.b.h.)). We measured the height and basal diameter, and recorded browsing history for all white spruce individuals by noting the presence of browse scars along the apical meristem. Estimating browsing history for larger saplings and trees (> 12 cm d.b.h.) was not always possible as browse scars may no longer be visible. We determined the age of most individual spruce trees from whorl counting (counting the number of apical annual growth segments). For older spruce with growth whorls that were too obscured to accurately age in this manner, we collected basal core samples using standard techniques (Grissino-Mayer 2003). From these age estimates, we reconstructed the age structure of young spruce since 1970 by averaging the proportion of sampled spruce established each year across sampling plots.

We additionally back-counted current annual growth segments to estimate the year when the apical meristem was browsed for each browse event (year of browsing) on a subset of 52 individuals measured at four separate locations within the floodplain, consisting of alder-poplar, poplar, and poplar-spruce dominant canopies. For an additional 114 trees we also estimated the age via whorl-counting and by collecting a core or disc from the base to compare age estimates using both methodologies.

Historical and simulated datasets - We collected additional datasets that spanned 1970 until present (year) in order to model the pattern of yearly spruce establishment during this period. Hare abundance (hares ha^{-1}) at BNZ-LTER has been estimated via mark-recapture surveys that have taken place from 1998 to present (Kielland et al. 2010, Feierabend and Kielland 2015, Fig. 2a), and known hare peaks occurred around 1971, 1981, 1990, 1999, and 2009 (Rexstad and Kielland 2006, Kielland et al. 2010, Feierabend and Kielland 2015). For years prior to 1998, we modeled annual hare abundance using a modified sine curve to reflect these known periods of high and low abundance (Figure 2.2a). Hare abundance for the year t was calculated as: $hare\ abundance_t \sim 4 + 6.5 * \sin((t+1)\ /1.5)$. We compiled additional data on viable seed production from BNZ-LTER (viable seeds m^{-2}, http://www.lter.uaf.edu/data_detail.cfm ?datafile_pkey=14, Figure 2.2b), and climate data from the Western Regional Climate Center (http://www.wrcc.dri.edu/summary/Climsmak.html); specifically, the total sum of growing degree days (GDD, base 5°C) from May to September (Figure 2.2c) and the average snow depth between September and December (cm) for each year (Figure 2.2d). We also obtained the maximum flood stage achieved by the Tanana River (m) for each year (USGS, http://water.weather.gov/, Figure 2.2e).

Analysis - We performed all statistical analyses in R statistical software version 3.2.3 (R Core Team 2015). To compare changes in browsing frequency with changes in snowshoe hare abundance, we calculated the percentage of sampled spruce browsed for each year from our estimates of the year of browsing. We pooled data from all sampling locations to generate a pattern at the regional scale. We then calculated the Pearson's correlation coefficient between these data and the record of annual hare abundance (function: cor).

We used linear mixed models to test the effects of browsing on spruce height growth for spruce seedlings (function: lmer). We focused on seedlings to ensure that all spruce included were within the browsing range of hares (< 200 cm, Telfer 1974), and because apical browse events were clearly identifiable among seedlings. Our fixed effects were spruce age, browse history, and their interaction, while sampling plot was a random effect. We log-transformed the response variable of height to improve model fit and meet model assumptions. We determined the significance of each fixed effect using F tests (function: lmerTest), and assessed the overall fit by calculating R-squared values for mixed models (function: r.squaredGLMM, Nakagawa and Schielzeth 2013). We calculated both the marginal (R_m^2) and conditional (R_c^2) R-squared values, which give the amount of variation explained by the fixed effects alone and by the fixed effects plus the random effect of plot, respectively. We then compared the marginal R-squared values for models with and without browsing as a fixed effect to determine how much the browsing parameter improved model fit.

We first calculated the proportion of sampled spruce that germinated each year at the plot level. We then tested for significant relationships between historical and modeled data of seed production, annual hare abundance and patterns in yearly spruce establishment using multiple linear regression. To accomplish this, we averaged the proportion of spruce established in each year (t) across plots and used this as our response variable. Our fixed effects were the number of viable seeds produced in the two years prior to spruce establishment, $t - 1$ and $t - 2$, and the relative abundance of hares for the year of establishment and three years following, t to $t + 3$. We also included the total sum of GDD from May to September and the average snow depth between September and December for the years t to $t + 3$, and the maximum flood stage achieved by the Tanana River for the years $t - 1$ to $t + 1$ as additional model covariates. All fixed effects variables were standardized to have a mean of zero and a standard deviation of 1 in order to improve model fitting.

Given zeroes in our dataset, we first added 0.01 to each datum of our response variable in order perform a log-transformation. This transformation allowed us to fit a full model using all covariates that met the assumptions of homoscedasticity and normality of the residuals for multiple regression. After fitting the full model, we then used an automated sampling routine to determine the top five models with the highest R^2 values (library: leaps, function: regsubsets). To reduce the risk of selecting an over fitted model, we used two criteria to select the best model from the top five models chosen by R^2 values. First, we calculated the Bayesian Information Criterion (BIC) for each model, where the best model is that with the lowest BIC value. We used BIC values rather than the Akaike's Information Criterion (AIC) because BIC tends to select more parsimonious models. We considered models with a difference in BIC (ΔBIC) greater than 2 to be less informative than the top model. Secondly, to further assess model fit and predictive ability, we performed a ten-fold cross validation on each model and calculated the overall mean square error (MSE) from each iteration (library: DAAG, function: CVlm). Models with lower average MSE values had better predictive power. For our final models, we checked for any temporal autocorrelation by plotting an autocorrelation function of the residuals (function: acf).

Results

Summary - Substantial browsing of white spruce occurred throughout our study area. We measured a total of 871 individual white spruce that varied widely in height (11 cm - > 1000 cm) and age (9 – 72 years old). 54%, 40% and 6% of sampled spruce were either seedlings, saplings, or trees, respectively. For all spruce, 80% had their apical meristem browsed at least once by hares. Browsing frequency and hare abundance were correlated at BNZ-LTER ($r = 0.60$, Figure 2.3) and most browse events occurred during periods of high hare abundance, whereas almost no browsing occurred during periods of low abundance (< 5% browsed, Figure 2.3).

The effect of herbivory on spruce seedling height growth - Browsing had a minimal, positive effect on the relationship between spruce seedling height and age. Specifically, browsing increased the intercept of the regression line but had no effect on the slope (Table 2.1). Browsing explained 3% (1% total) of the remaining variation in height of white spruce seedlings after accounting for age (Table 2.1). Including the random effect of plot increased the total amount of variation in height explained to 75% (Table 2.1). Browsed spruce were significantly older (median age difference: 5 years, ANOVA, $F_{1,466} = 20.01$, $p < 0.001$, Figure 2.4a) and taller (median height difference: 25 cm, $F_{1,466} = 19.71$, $p < 0.001$, Figure 2.4b) than spruce that had not been browsed.

The pattern of yearly spruce establishment - Our estimates of spruce age using whorl counts closely approximated spruce age determined by counting annual growth rings ($Age_{ring} \sim 2.63 + 0.93Age_{whorl}$, $F_{1,112} = 292$, $p < 0.001$, $R^2 = 0.72$). This near 1:1 relationship affirmed whorl counting as a suitable method for estimating spruce age and reconstructing the pattern of yearly establishment across our sampling area. We found that spruce recruited continuously throughout 1970 – 2011, although the number of established spruce varied greatly from year to year. The periods of greatest successful spruce establishment were 1987-1989, 1993, 1994, and 1998 (Figure 2.5).

The top five models of spruce establishment, chosen by our automated model selection routine, ranged in R^2 values from 0.41 to 0.64 (Table 2.2). Of these, only one model had ΔBIC less than 2 from that of our top model. For each model the average MSE following ten-fold cross validation ranged from 0.25 – 0.31 given a range of -4.61 to -2.50 for the response variable of the log-transformed proportion of sampled spruce established. The top two models with the lowest BIC scores also had the lowest average MSE values. Of these two models, we selected the most parsimonious model (Tables 2.2 and 2.3).

Our model explained 61% of the total variation in spruce establishment from 1970 – 2011 ($F_{7,34} = 7.43$, $p < 0.001$, Tables 2.2 and 2.3, Figure 2.5). In general, our model of spruce establishment revealed a negative effect of both hare abundance (years t and $t + 2$) and GDD (years $t + 2$ and $t + 3$). We found a positive relationship between spruce establishment and both snow depth (years $t + 1$ and $t + 2$) and flood stage (year $t - 1$). Interestingly, none of our models showed any significant relationships between viable seed production and the pattern of yearly spruce establishment.

Discussion

Summary - We have demonstrated that snowshoe hares extensively browse white spruce at BNZ-LTER and that this browsing likely reduces spruce establishment throughout this portion of the Tanana River floodplain. Over the last four decades, nearly all spruce sampled have had their apical growth segments removed at least once by hares, particularly during periods of high hare abundance. Browsing is likely a source of direct mortality for spruce, which is reflected by the negative relationship between hare abundance and spruce establishment over time.

The response of spruce to herbivory is complex because spruce has many strategies to deter browsers, including low palatability and high concentrations of toxins, such as camphor

(Sinclair et al. 1988). Moreover, its reproductive strategy of masting can overwhelm both granivores and herbivores with an abundance of seeds and then seedlings (Janzen 1971), creating dense patches of spruce cohorts that largely escape browsing. Hares are formidable browsers during periods of high abundance, however, and are capable of eliminating nearly all available woody vegetation, including spruce (Cooke and Robeson 1945; Peterson et al. 2005). This unique and dynamic plant-herbivore interaction leads to high temporal and spatial variability in spruce recruitment, where spruce may remain untouched by hares in some locations, but in others browsing can result in 100% seedling mortality (Olnes and Kielland 2016).

The effect of herbivory on spruce height growth - We argue that the apparent positive effect of hare browsing on spruce height growth is a byproduct of age differences between each browse category. Spruce trees that were not browsed tended to be the youngest individuals, whereas spruce that were browsed tended to be the oldest (Figure 2.4a). It is likely that the increase in intercept with browsing is a reflection of age differences, rather than a browse effect. The median age for spruce seedlings that had not been browsed was 7 years, and given that 75% of this group were under nine years old in 2014 (3rd quartile = 9 years, Figure 2.4a), most individuals were under five years old at the time of the last hare peak (2009, Figure 2.3). Using our regression relationship for spruce seedling height and age (Table 2.1), we estimate that five-year-old seedlings should be approximately 18 cm tall (mean height of all five-year-old seedlings sampled (n = 10): 17.6 ± 1.54 cm). This is nearly equal to the average early snow depth from 1970 to the present year of 15.04 ± 1.12 cm (Figure 2.2d). Therefore, most seedlings that have not been browsed were still short enough to be buried by early season snow during the last hare peak. Exclosure studies may demonstrate more accurately the true effect of browsing by hares on spruce height growth by allowing for more even sample sizes of browsed and unbrowsed spruce. For example, previous exclosure studies we conducted on the floodplain demonstrated a significant negative effect of hare browsing on spruce height growth (Olnes and Kielland 2016). Our results likely differed from those of the exclosure studies because very few seedlings avoid being browsed in a natural setting. Further, we defined our browsing effect as a binary categorical variable (browsed or not browsed). We may have found a more significant negative effect of browsing if we had defined our browse effect as a continuous variable (number of apical browse events or percent current annual growth browsed).

The pattern of yearly spruce establishment - Spruce trees browsed in the first few years of establishment are most vulnerable to mortality because a single browse event may suffice to remove all meristematic tissue. In the autumn, newly recruited spruce may appeal to hares as the only green browse available. Our model reflected this vulnerability as hare abundance for the year of establishment and two years following establishment were significant negative terms (Table 2.2). Other lag years for hare abundance may not have been significant because of multicollinearity, where hare abundance for a specific year was sufficient to represent abundance for multiple surrounding years. An early snow pack can benefit seedling survival, likely by burying seedlings and reducing the amount of time they are vulnerable to hares during the onset of winter each year.

Although it is known that flood events can damage or kill spruce seedlings along the floodplain (Angell and Kielland 2009), our model results suggest that recruiting spruce mainly benefit from flooding as this produces mineral beds optimal for seedling establishment. This effect may in part explain the lack of correlation between viable seed production and spruce establishment. Many seeds are deposited along the floodplain during a masting event, but the number that actually germinates may also depend on the extent of suitable recruitment sites (Walker et al. 1986). Therefore, the timing of flood events that lead to more suitable microhabitats for spruce establishment may mask the relationship between seed production and spruce establishment along the floodplain. It is likely that spruce establishment in upland environments would more strongly reflect the pattern in viable seed production over time (G.P. Juday, *unpublished data*).

Implications for management - Forest and plantation managers should promote spruce regeneration during the low in the hare cycle. Our model for the pattern of spruce establishment along the Tanana River floodplain suggests that seedlings establishing immediately following a hare peak (when hare abundance is low) can have twice the survival rate of seedlings establishing during peak years (Table 2.3). In areas with abundant snowfall, seedlings established during periods of low hare abundance will likely be short enough to be insulated by the snowpack during the subsequent hare peak. Although the timing of establishment appears to affect survival rates, managers in areas that see significant hare peaks should expect that all seedlings will eventually be browsed, including those that established during periods of low hare abundance. Many seedlings were able to withstand browsing during the most recent peak of 2009, however, we observed very few individuals with browse scars corresponding to the prior peak year of 1999, despite a similar abundance of hares and seedlings at the time of both peaks. This may reflect a ‘missing record’ of seedlings that survived the 1999 hare peak, but succumbed to browsing during the 2009 peak.

Spruce seedlings in the boreal forest will likely encounter two hare peaks before they are released from hare herbivory (~200 cm in height, Telfer 1974; Drew 1988). Forest managers in the boreal region should be cognizant of the stage of the hare cycle and consider more intensive herbivore management practices during peak years (Drew 1988). Methods for deterring hares from establishing spruce include the use of repelling odors (Sullivan and Crump 1984; Sullivan et al. 1992) and protective plastic covers (Zimmerling and Zimmerling 1998), or reducing the amount of vegetative cover available to hares around seedlings (Parker 1984). Manipulating cover presents a trade-off for managers, however, as reduced cover may negatively affect seedling growth (Angell and Kielland 2009; Milakovsky et al. 2011; Olnes and Kielland 2016).

Homage to Aldo Leopold - The potential for asynchrony between herbivores and seedling recruitment did not escape the attention of the observant Aldo Leopold. In his famous book, *A Sand County Almanac*, he details the life history of an oak (*Quercus sp.*) he has recently harvested from his property in Wisconsin (Leopold 1949). Within this passage he writes:

“Indeed, it is all too clear that every surviving oak is the product either of rabbit negligence or rabbit scarcity. Some day some patient botanist will draw a frequency curve of oak birth years, and show that the curve humps every ten years, each hump originating from a low in the ten-year rabbit cycle”

As Leopold postulated for oaks in Wisconsin, we have demonstrated for white spruce in Alaska. Other studies have also noted this asynchronous plant-herbivore interaction (Brandner et al. 1990), however, our study is the first to demonstrate an inverse relationship between conifer recruitment and the hare population cycle over time. It is likely that browsing by hares influences the pattern of establishment for other boreal species in a similar manner (Fox and Bryant 1984, Smith et al. 1988).

Conclusion

Northern ecosystems have received recent attention regarding climate change because of polar amplification (Coumou et al. 2015). In response to climate change, the distribution of white spruce is shifting dramatically, with increased growth and seed viability leading to expansion in some locations, but decreased growth and seed viability resulting in contraction at others (Roland et al. 2013, 2014; Juday et al. 2015). This contributes to changing Alaskan landscapes characterized by increasingly deciduous forests where conifers once dominated, and coniferous forests expanding into former tundra landscapes (Mann et al. 2012; Lloyd et al. 2013; Jorgenson et al. 2014).

Across this region, we posit that snowshoe hares act as a demographic filter to white spruce establishment as we have demonstrated at BNZ-LTER. Here, browsing appears to be as important a predictor of spruce success, if not greater, than growing season temperatures or early season snowfall during the first few years of establishment. Spruce that recruit during a high in the hare cycle are less likely to successfully establish than spruce recruiting during periods of low hare abundance. The large geographic extent over which spruce-hare interactions occur emphasizes the potential significance of browsing by snowshoe hares in modifying the shifting distribution of this important conifer in the boreal forest.

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Figures

Figure 2.1. Locations of 18 study plots along the Tanana River floodplain (white dots). The Bonanza Creek Long Term Ecological Research (BNZ-LTER) site is outlined in white.

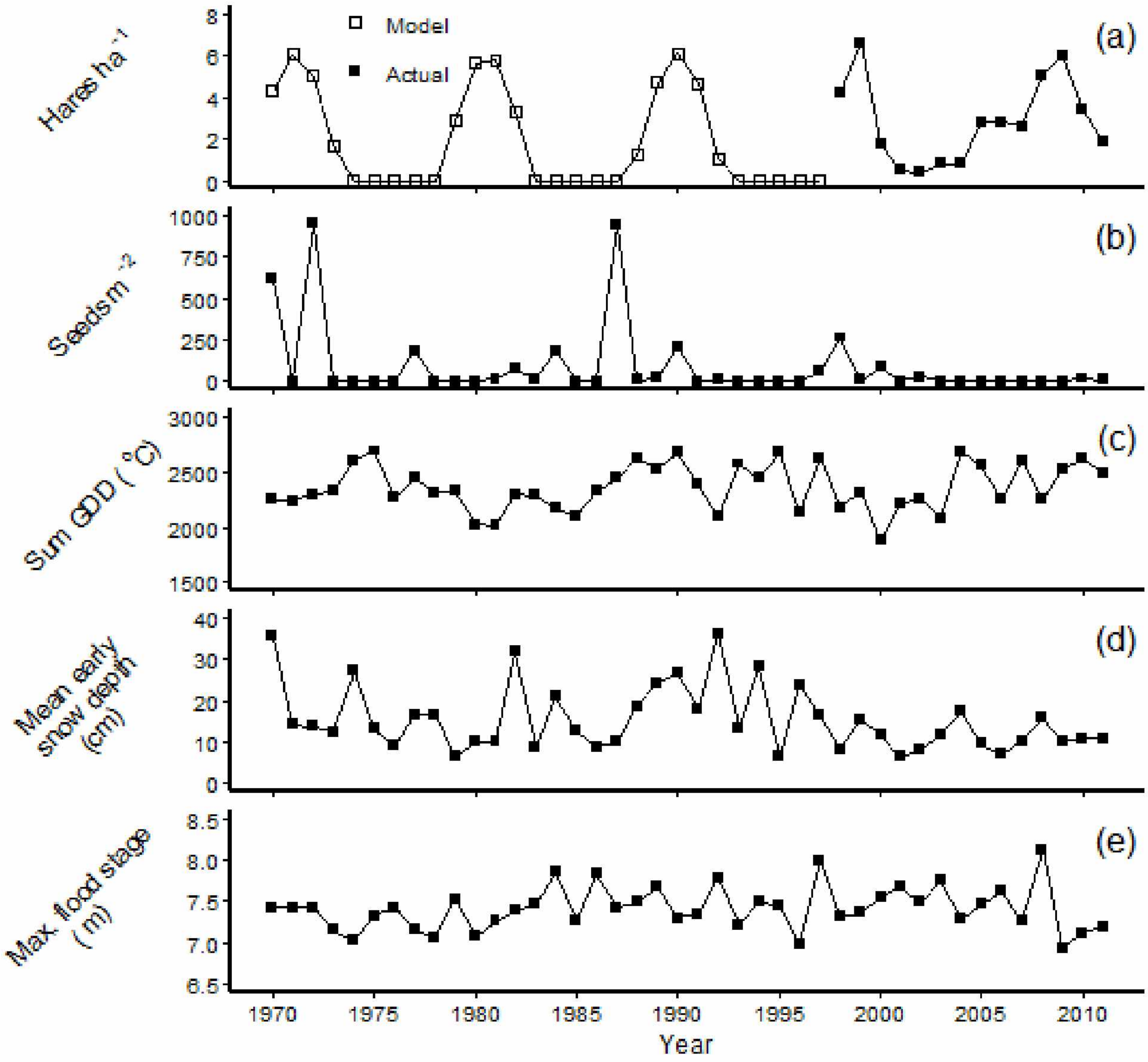

Figure 2.2. Model parameters used to explain the pattern in yearly establishment of white spruce from 1970 – 2011. (a) is the annual snowshoe hare abundance at BNZ – LTER. (b) is the average number of viable spruce seeds m^{-2} produced at BNZ-LTER. (c) is the sum Growing Degree Days (base 5°C) from May – September. (d) is the average monthly snow depth from September – December (cm). (e) is the maximum flood stage achieved by the Tanana River for each year (m).

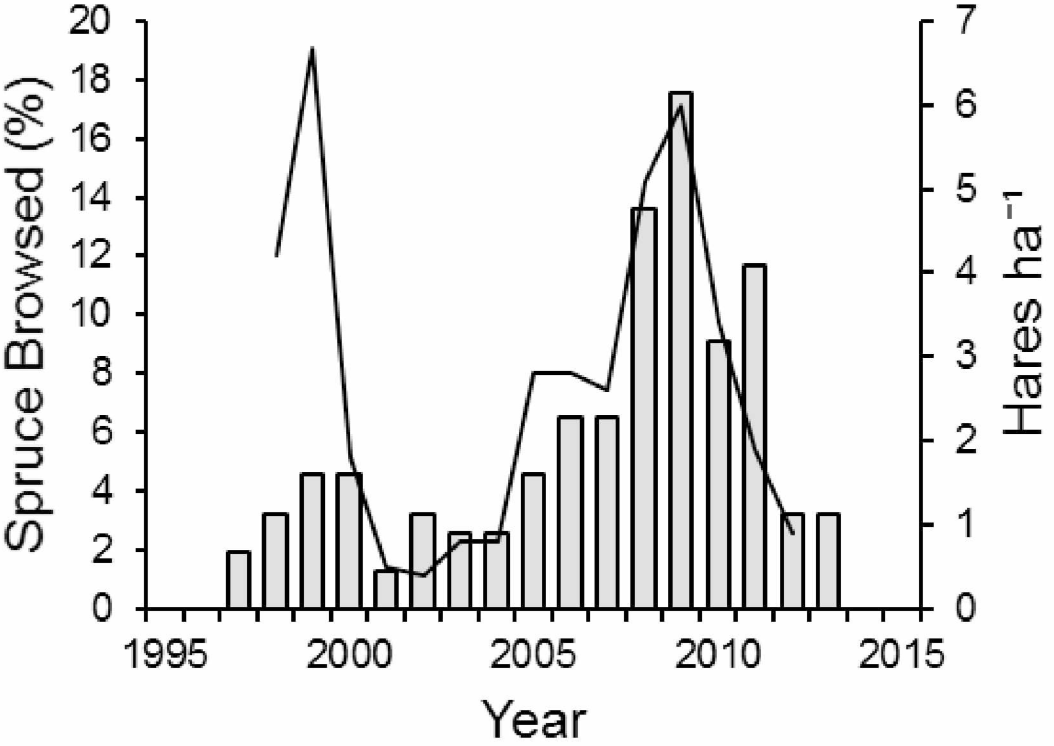

Figure 2.3. The proportion (%) of white spruce browsed annually (shaded bars) in relation to the snowshoe hare population cycle (line) at the Bonanza Creek LTER sites located along the Tanana River, Interior Alaska. n = 52.

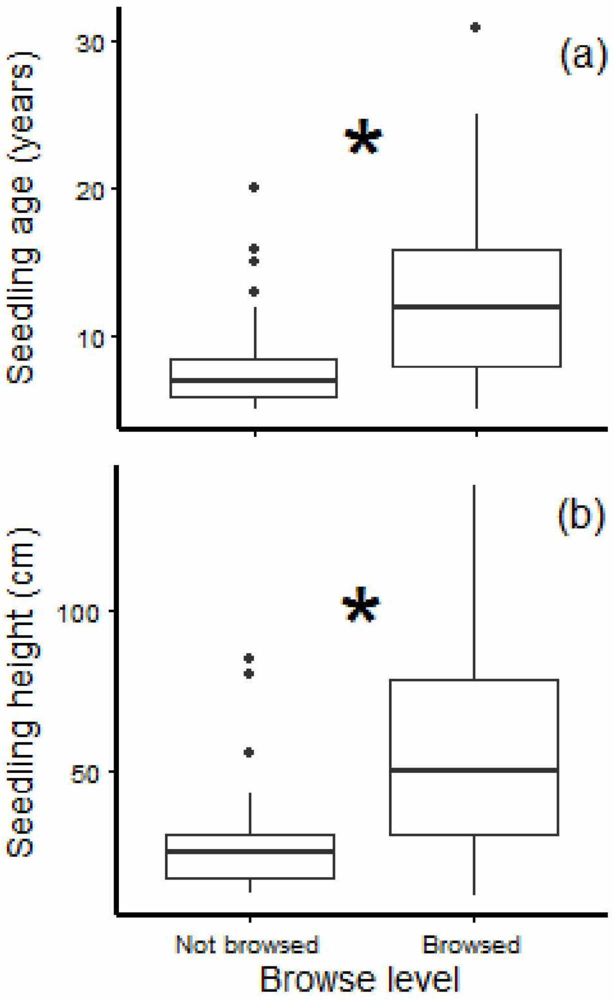

Figure 2.4. Box and whisker plots of age (a) and height (b) distributions among spruce seedlings that were not browsed (n = 27) and browsed seedlings (n = 441). Thick lines represent the median value and the rectangles represent the interquartile range. Whiskers are equal to the minimum and maximum values of the sample, and dots reflect outliers in the data. Significant difference indicated by *.

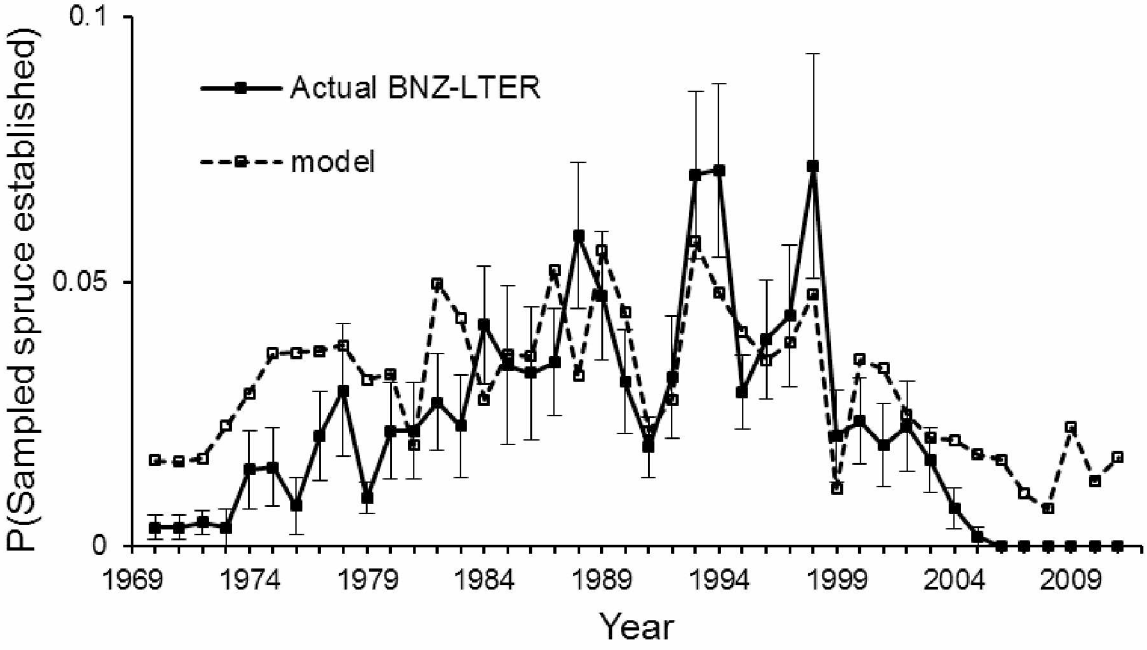

Figure 2.5. Pattern in yearly spruce establishment along the Tanana River, Interior Alaska. Actual BNZ-LTER data represent the mean proportion of sampled spruce established each year across plots (n = 18). Error bars represent standard error around the mean. Model coefficients are presented in Table 3

Tables

Table 2.1. Results of linear mixed model for white spruce seedling height, with spruce age, browse history and their interaction terms as fixed effects. Spruce height was log-transformed. Plot was a random effect with varying intercept. $\beta_{0,0}$ = the intercept when spruce is not browsed, $\beta_{0,1}$ = added intercept for browsing, β_1 = slope for fixed effect of spruce age, β_2 = slope for spruce age and browsing interaction term. Significant model parameters are indicated with *.

Model	$\beta_{0,0}$	$\beta_{0,1}$	β_1	β_2	R^2_m Age	$R^2_{m,}$ Age x Browse	$R^2_{c,}$ Age x Browse
Age	2.40±0.15*	0.10±0.01*	0.30±0.14*	-0.01±0.01	0.70	0.71	0.75

Notes. Marginal R^2 (R^2_m) is the amount of variation explained by the fixed effects alone. Conditional R^2 (R^2_c) is that amount of variation explained by both fixed and random effects.

Table 2.2. Top five models chosen by an automated routine to select for highest R^2 value. Also presented are the results for the full model. BIC is the Bayesian Information Criterion, and $\overline{MSE}$ is the averaged mean square error after performing a ten-fold cross validation for each model. Model in bold indicates the final model selected. Model parameters are defined in Table 3.

Model	Parameters	*BIC*	R^2	$\overline{MSE}$
1	$Hare_t + Hare_{t+2} + GDD_{t+2} + GDD_{t+3} + Snow_{t+1} + Snow_{t+2} + Flood_{t-1} + Flood_t$	74.92	0.64	0.25
2	$\boldsymbol{Hare_t + Hare_{t+2} + GDD_{t+2} + GDD_{t+3} + Snow_{t+1} + Snow_{t+2} + Flood_{t-1}}$	**75.61**	**0.61**	**0.26**
3	$Hare_t + GDD_{t+2} + GDD_{t+3} + Snow_{t+1} + Snow_{t+2} + Flood_{t-1}$	77.05	0.56	0.26
4	$Hare_t + GDD_{t+3} + Snow_{t+1} + Snow_{t+2} + Flood_{t-1}$	79.99	0.48	0.30
5	$Hare_t + GDD_{t+3} + Snow_{t+1} + Flood_{t-1}$	81.43	0.41	0.31
Full	$Seed_{t-2} + Seed_{t-1} + Hare_t + Hare_{t+1} + Hare_{t+2} + Hare_{t+3} + GDD_t + GDD_{t+1} + GDD_{t+2} + GDD_{t+3} + Snow_t + Snow_{t+1} + Snow_{t+2} + Snow_{t+3} + Flood_{t-1} + Flood_t + Flood_{t+1}$	93.97	0.75	0.40

Table 2.3. Parameters used in full model to explain the pattern in yearly spruce establishment. Parameters in bold were included in final model. The response variable, the proportion of sampled spruce established each year, was log-transformed. All model parameters were standardized to have a mean of 0 and a standard deviation of 1. 'NS' means parameter was not significant in final model.

Parameter	Description	β value	p
Intercept	**-**	**-3.59**	**<0.001**
$Hare_t$	**Relative hare abundance in year *t***	**-0.34**	**<0.001**
$Hare_{t+1}$	Relative hare abundance in year $t + 1$	NS	
$Hare_{t+2}$	**Relative hare abundance in year *t* + *2***	**-0.15**	**0.04**
$Hare_{t+3}$	Relative hare abundance in year $t + 3$	NS	
$Seed_{t-1}$	Viable seeds m^{-2} produced in year $t - 1$	NS	
$Seed_{t-2}$	Viable seeds m^{-2} produced in year $t - 2$	NS	
$GDD_t^\dagger$	Sum GDD May – September for year *t*	NS	
GDD_{t+1}	Sum GDD May – September for year $t + 1$	NS	
GDD_{t+2}	**Sum GDD May – September for year *t* + *2***	**-0.20**	**0.009**
GDD_{t+3}	**Sum GDD May – September for year *t* + *3***	**-0.30**	**<0.001**
$Snow_t$	Average snow depth (cm) September – December for year *t*	NS	
$Snow_{t+1}$	**Average snow depth (cm) September – December for year *t* + *1***	**0.30**	**<0.001**
$Snow_{t+2}$	**Average snow depth (cm) September – December for year *t* + *2***	**0.24**	**0.002**
$Snow_{t+3}$	Average snow depth (cm) September – December for year $t + 3$	NS	
$Flood_{t-1}$	**Maximum flood stage (m) achieved for year *t* – *1***	**0.21**	**0.006**
$Flood_t$	Maximum flood stage (m) achieved for year *t*	NS	
$Flood_{t+1}$	Maximum flood stage (m) achieved for year $t + 1$	NS	

†GDD is the growing degree days (base 5° C)

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Chapter 3: Can snowshoe hares control treeline expansions?[1]

Abstract

Treelines in Alaska are advancing in elevation and latitude because of climate warming, which is expanding the habitat available for boreal wildlife species, including snowshoe hares (*Lepus americanus*). Snowshoe hares are already present in tall shrub communities beyond treeline and are the main browser of white spruce (*Picea glauca*), the dominant tree species at treeline in Alaska. We investigated the processes involved in a 'snowshoe hare filter' to white spruce establishment near treeline in Denali National Park. We modeled the pattern of spruce establishment from 1970 to 2009 and found that fewer spruce established during periods of high hare abundance. Multiple factors interact to influence browsing of spruce, including the hare cycle, snow depth and the characteristics of surrounding vegetation. Hares are abundant at treeline and may exclude spruce from otherwise optimal establishment sites, particularly floodplain locations with closed shrub canopies. The expansion of white spruce treeline in response to warming climate will be strongly modified by the spatial and temporal dynamics of the snowshoe hare filter.

Introduction

When herbivores browse dominant plant species, they can influence the composition and distribution of plant communities, or even biomes (Rutherford et al. 2012; Bryant et al. 2014). As climate change perturbs the current range of certain biomes (Jorgenson et al. 2014; Juday et al. 2015), it is critical to understand the role of herbivores in shaping the new distributions of

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[1] Olnes, J., Kielland, K., Juday, G.P., Mann, D.H., Genet, H., and R.W. Ruess. 2017. Can snowshoe hares control treeline expansions? Ecology, 98: 2506–2512. doi:10.1002/ecy.1968

plant communities (Bryant et al. 2014). For example, white spruce, *Picea glauca* (Moench) Voss, is a dominant boreal tree species in North America, and its distribution is shifting both upward in elevation and northward in latitude because of climate change (Jorgenson et al. 2014; Nicklen et al. 2016). This range expansion may cause a transition from tundra to boreal forest communities across much of Interior Alaska (Juday et al. 2015). A change in the distribution of white spruce also represents a shift in occurrence of available habitat for a suite of boreal wildlife species, such as the snowshoe hare (*Lepus americanus* L.). Snowshoe hares are boreal forest residents that have expanded their range in response to increased shrubification in the Arctic (Tape et al. 2015) and expansion of tree distribution beyond previous treelines (Ewacha et al. 2014). Such changes in plant structure and community composition benefit hares by providing increased cover and food resources in what were previously graminoid-dominated tundra environments (Ewacha et al. 2014; Tape et al. 2015). Observations in Interior Alaska have noted extensive browsing of white spruce seedlings by snowshoe hares, which has been shown to exert significant control over spruce establishment in low-elevation floodplain habitats (Olnes and Kielland 2017). Because both snowshoe hares and white spruce are responding to climate warming in a similar manner, browsing of white spruce by hares provides a unique opportunity to study the effects of herbivory on expanding vegetation when range expansion of herbivores and plant communities is coupled across trophic levels.

Many of the habitat requirements for snowshoe hares overlap with those most conducive to white spruce seedling establishment. Suitable hare habitat is defined by the quality of available winter browse and by dense cover that provides protection from predators (Feierabend and Kielland 2014). Spruce establish successfully under areas of similarly dense cover that reduces the risk of desiccation and heat stress (Angell and Kielland 2009; Milakovsky et al.

2011); however, the presence of a high hare population can negate the suitability of these otherwise optimal sites for spruce establishment. Exclosure experiments show that when hares are excluded, spruce experience higher survival and faster height growth with increasing shrub cover. By contrast, spruce exposed to browsing hares do not indirectly benefit from increased shrub cover because of the direct effect of increased browsing on spruce (Olnes and Kielland 2016). Spruce is rarely browsed when it is establishing at locations with insufficient cover for hares.

This study focused on white spruce because it is the dominant tree species at treelines in Alaska. Our overall goal was to assess the effect of joint range expansions between different trophic levels on the dynamics of expanding vegetation. We addressed this question by exploring the presence of a 'snowshoe hare filter' to white spruce recruitment near the limit of its range, where successful spruce seedling establishment is influenced by the abundance of hares across time and space. To examine how snowshoe hares modify spruce seedling establishment at this climatically sensitive ecotone, we measured the browsing history and surrounding site characteristics of white spruce seedlings along an elevational gradient in Denali National Park and Preserve. We first examined how browsing by hares may influence the pattern of spruce seedling establishment over time, hypothesizing that browse frequency would positively correlate with changing hare abundance across annual time scales. We then reconstructed the age structure for young white spruce since 1970, and examined this distribution in relation to historical and simulated data of the snowshoe hare cycle. We hypothesized that the relative number of trees established negatively correlates with snowshoe hare density for the year of establishment and the following year. We also predicted that warmer growing seasons would benefit seedling establishment at treeline (Nicklen et al. 2016), as would early-season snow depth by burying seedlings, thus protecting them from browsing hares. For our second objective, we compared changes in site characteristics with changes in seedling and hare density (via fecal pellets), and browse intensity. We hypothesized that site characteristics associated with high browsing frequency would reflect site preferences of both hares and spruce seedlings. Specifically, we expected both hares and spruce to be most abundant in areas with tall shrub cover (Tape et al. 2015; Olnes and Kielland 2016).

Methods

Study location and sampling design - Denali National Park and Preserve (hereafter "Denali") is located in the Alaska Range approximately 130 km southwest of Fairbanks (63°43'N, 148°57'W) and represents the elevational limit of white spruce in Alaska. Snowshoe hares are present and periodically achieve very high abundance (Krebs et al. 2013). Lower elevations are dominated by white and black spruce (*Picea mariana* (Mill.) Britton, Sterns and Poggenb.) forests, which transition to shrub tundra at higher elevations (Roland et al. 2013). Nine sites were accessed along the 143-km park road corridor via hiking. For each location, we established 1.5 – 5 km transects perpendicular to the hillslope. Along these transects, we established 25 m^2 plots at 75 m elevation intervals between 500 - 1175 m a.s.l. These transects encompassed the elevational range of white spruce, including treeline (~1100 m a.s.l.), as determined by Roland et al. (2013). Because of the distinct variation in vegetation communities between floodplains and uplands, and that floodplains represent high-quality hare habitat and optimal conditions for spruce establishment (Olnes and Kielland 2016), additional plots were positioned along major stream or river drainages near each elevational transect (500 – 945 m a.s.l.). Total plot number varied between 4 and 12 plots per transect site (n = 81 total), based on the range of elevations present at each location and the accessibility of each plot.

In the summer of 2015, we sampled individual white spruce within each 25 m^2 plot, and used four 1 m^2 subplots to measure the density of deciduous shrub species (ramets m^{-2}) and to count hare pellets (pellets m^{-2}). We recorded browsing history for all white spruce individuals and back-counted current annual growth segments to estimate the year when the apical meristem was browsed. Hare browse events were identified by the sharp 45° angle of the bite. Browse scars can persist for several decades, while the spruce individual may continue height growth from a new apical leader. We also measured white spruce density by three classes: seedling (< 1.37 m tall), sapling (> 1.37 m tall and < 12 cm diameter at breast height (1.37 m, d.b.h)), or tree (> 1.37 m tall and > 12 cm d.b.h.) (Roland et al. 2013). We determined the age of most individual spruce trees using whorl counts (the number of apical annual growth segments, Olnes and Kielland 2017). For trees with annual growth segments that were too obscured to accurately age in this manner, we collected basal core samples and determined tree age using standard techniques of tree ring counting (Grissino-Mayer 2003). For each tree, we subtracted our age estimate from 2015 to estimate the year of establishment.

Reconstruction of historical patterns in hare abundance - We obtained estimates of historical hare abundance from existing survey data collected by the National Park Service (NPS). Hare data were collected by annual road surveys in which the total number of hares observed from the Denali park road was counted during a single trip each year from 1991 to 2013 (McIntyre and Schmidt 2012).

One of our goals was to examine the temporal pattern of seedling establishment in relation to the pattern in hare abundance from 1970 – 2009 to test our hypothesis that hares mainly affect seedling establishment during peak years. But because quantitative hare data did not exist for all years prior to 1991, we simulated hare abundance for missing years using a sine curve with peaks matching known periods of high hare abundance for the Alaska region (Rexstad and Kielland 2006, Krebs et al. 2013). Hare abundance for the year *t* was calculated as: $hare\ abundance_t \sim -0.4 + 8.5 * \sin((t+1)/1.5)$ (Appendix 3.1, Figure 3.S1). This sine curve approximates the ten-year hare cycle with peaks in 1971, 1981 and 1989 (Rexstad and Kielland 2006, Krebs et al. 2013). Each modeled hare peak was equal in amplitude to the known 1999 hare peak. The coarse pattern in hare abundance represented by our sine curve was sufficient to model changes in hare browsing pressure across years.

We obtained additional climate variables from the Western Regional Climate Center (WRCC, http://www.wrcc.dri.edu/summary/Climsmak.html) to inform further our model of seedling establishment. Specifically, we calculated the total sum of Growing Degree Days (GDD, base 5°C) for the months of May to September for the years 1970 to 2015 (Appendix 3.1, Figure 3.S1). For this same set of years, we also calculated the average snow depth (cm) for the months September to December (Appendix 3.1, Figure 3.S1). We have previously demonstrated that these variables are important factors influencing the pattern of spruce establishment at low elevation floodplains (Olnes and Kielland 2017).

Analysis - We performed all statistical analyses using the R statistical software version 3.2.3 (R Core Team 2015). Model selection consisted of comparing the Akaike's Information Criterion (AIC) for competing models, and selecting models with the lowest AIC value. When top models differed by less than 2, we selected the most parsimonious model. Assumptions of equal variance and normality of the residuals were confirmed graphically for all linear models. For significant models involving time series, we assessed for possible temporal autocorrelation by viewing autocorrelation functions of the model residuals (function: acf). Alpha was set at 0.05.

To assess the change in browsing pressure with annual changes in hare abundance, we calculated the proportion of sampled spruce in each plot that were browsed for each year using our estimates of the year of browsing. We averaged these values across all our sampling plots to generate a single time series for the years 1988 to 2015. We then used linear regression to test the strength of the relationship between the proportion of spruce browsed and the record of hare abundance (function: lm).

We then tested for a significant relationship between relative hare abundance and patterns in yearly spruce establishment. To accomplish this, we reconstructed establishment dates for surviving spruce by binning plots based on elevation (500 – 700 m, 701 – 900 m, 901 – 1100 m a.s.l.), and used the number of sampled spruce established for each year (t) within each elevational bin as the response variable. Our fixed effects were the relative abundance of hares, the average snow depth for the months of September to December, and the sum of GDD from May to September for the year of establishment and the following year. All fixed effects variables were standardized to have a mean of zero and a standard deviation of 1 to improve model fitting. We modeled the pattern of spruce establishment for the years 1970 – 2009 using a generalized linear mixed model (function: glmer). Because our response variable was overdispersed, we used a negative binomial distribution with a log-link function and confirmed this was a better fit over a Poisson distribution via likelihood ratio tests (function: anova). We proposed six different *a priori* models using varying combinations of our fixed effects and our elevational bin as a random effect for all models (Appendix 3.2, Table 3.S1). We estimated the goodness of fit for our top model by calculating the Pearson's correlation coefficient (R) between the actual response values and fitted values from the model for each year, and then squared this value to obtain a $Pseudo\text{-}R^2$ for each model.

We used generalized linear mixed models for seedling density and linear mixed models for hare (pellet) density, to test how these variables changed with changes in site characteristics at the plot level. We hypothesized competing models based on four explanatory variables for seedling density (elevation, hare pellet density, landscape type (floodplain or upland) and total density of ramets, Appendix 3.2, Table 3.S2) and three explanatory variables for pellet density (elevation, landscape type and total density of ramets, Appendix 3.2, Table 3.S3). For seedling density, we used a Poisson error structure with a log-link function. For hare pellet density, we square-root transformed the response variable to meet model assumptions. For all models, sample transect was a random effect. We calculated the conditional R^2 (R_c^2) for mixed effect models, which estimates the combined amount of variation explained by the model's fixed and random effects (Nakagawa and Schielzeth 2013).

To determine if surrounding vegetation characteristics could affect the likelihood of being browsed, and to assess how plant community composition affects seedling density and the presence of hares, we also conducted a canonical correspondence analysis (CCA, library: vegan, function: cca) using our deciduous species density data in relation to three browse-related variables: seedling density, pellet density, and the density of seedlings browsed by hares. For each plot, we averaged the density of ramets for each deciduous species within each subplot. We also included the density of white spruce saplings and trees in our analysis to better understand how seedling-hare dynamics are affected by older spruce cohorts. With CCA, orthogonal latent variables are generated that maximize correlation between plant community composition and our browsing variables, which may reveal underlying patterns in the data. Plant species and browse variables that are similarly correlated with a latent variable are also correlated with each other, and appear near one another in ordination space.

Results

We observed widespread browsing of white spruce seedlings and saplings by hares. A total of 796 individual white spruce trees were measured that varied widely in height (4 cm to > 800 cm) and age (5 to 135 years old). Of these, 41% had their apical meristem browsed at least once by hares.

Browsing frequency and hare abundance were strongly correlated (Figure 3.1, $R^2 = 0.82$, $p < 0.001$). Most browse events occurred during periods of high hare abundance, whereas almost no browsing occurred during periods of low abundance (< 5% browsed). Browsing was greatest in the years surrounding the 2009 hare peak.

We related hare abundance to the pattern of spruce establishment between 1970 and 2009. All models performed better than an intercept-only model (Appendix 3.2, Table 3.S1). The best performing model included all covariates for the year of establishment (Fig. 1, $Pseudo\text{-}R^2 = 0.21$). Spruce establishment was negatively related to annual hare abundance ($\beta = -0.31$, $p < 0.01$). We ran an additional model, with all hare peaks set as equal, that also resulted in a negative relationship between spruce establishment and hare abundance ($\beta = -0.17$, $p = 0.048$), ensuring that the large 2009 hare peak was not driving our primary model's result. Both growing season GDD ($\beta = 0.38$, $p < 0.001$) and early-season snow depth ($\beta = 0.16$, $p = 0.03$) were positively related to spruce establishment.

Variation in seedling density across plots was best explained by the full model (R^2_c = 0.35); however, the density of total deciduous ramets was not a significant explanatory variable (Appendix 3.2, Tables 3.S2 and 3.S4). Elevation ($\beta = -0.77$, $p < 0.001$) and hare pellet density ($\beta = -0.29$, $p < 0.001$) both had a negative effect on seedling density (Figure 3.2 b and c). Landscape type also influenced seedling density, with more seedlings found in floodplains than at upland sites ($\beta = -0.51$, $p < 0.001$). The best model for hare pellet density ($R^2_c = 0.31$, Appendix 3.2, Tables 3.S3 and 3.S5) showed an increase in density with elevation (Figure 3.2a, $\beta = 0.73$, $p < 0.01$) and greater densities in floodplain versus upland sites ($\beta = -0.98$, $p = 0.02$).

The CCA revealed significant underlying patterns in vegetation composition that related to browsing intensity (permutation test for CCA, $F_{3,77} = 2.08$, $p = 0.001$, Appendix 3.2, Table 3.S6). Two latent variables, or components (CCA 1 and CCA 2), explained 8% of the pattern in deciduous woody vegetation across our sites. Component 1 represents a floodplain to upland gradient and component 2 represents a gradient of canopy openness (Figure 3.3). Our CCA analysis also distinctly separated commonly occurring plant communities into separate quadrats in the ordination space (Figure 3.3). The top left quadrat (quadrat 1, Figure 3.3), represents open upland sites dominated by dwarf birch (*Betula nana*, 'BetNan'), red currant (*Ribes triste*, 'RibTri'), Alaska spirea (*Spirea stevenii*, 'SpiSte'), and bog blueberry (*Vaccinium uliginosum*, 'VacUli'). Neither seedlings nor hares were common at these sites. Quadrat 2 (top right, Figure 3.3), depicts floodplain locations with open canopy structure that were dominated by trembling aspen seedlings (*Populus tremuloides*, 'PopTre'), Alaska rose (*Rosa acicularis*, 'RosAci'), willows (*Salix* sp.,'Salix'), and soapberry (*Shepherdia canadensis*, 'SheCan'). Seedlings were most abundant within these plots; however, the lack of cover deterred hares and little browsing of spruce was observed. Upland locations dominated by mature spruce forests ('Tree') had the closed canopies preferred by hares, but spruce seedling abundance tended to be low (quadrat 3, Figure 3.3). The presence of hares meant that browsing of seedlings occurred despite low seedling densities. Quadrat 4 (Figure 3.3) represented plant communities where both hares and seedlings were abundant and thus where the greatest amount of browsing was observed. These sites were floodplain locations with closed canopies dominated by shrubby cinquefoil (*Dasiphora fruticose*, 'DasFru'), alders (*Alnus viridis* ssp. *fruticosa* and *Alnus incana* ssp. *tenuifolia*, 'Alnus'), and balsam poplar (*Populus balsamifera*, 'PopBal').

Discussion

Factors affecting spruce establishment and range expansion are numerous, interacting and complex. Among these factors is browsing by hares, which thins the forests of recruiting spruce, and, consequently, changes stand structure, stand composition, successional trajectory, and the rate of treeline advance. At some sites, hares can eliminate entire spruce cohorts, while at other sites entire spruce cohorts largely escape hare herbivory (Olnes and Kielland 2016). This 'snowshoe hare filter' strongly influences spruce establishment across space and time near the tree limit at Denali.

Most browsing occurs during hare population peaks (Figure 3.1), and in areas of preferred hare habitat, specifically floodplains with closed canopies (Figure 3.3). We also observed greater seedling densities in floodplain environments located near treeline (Figure 3.3), suggesting that spruce expansion at these locations will likely precede expanding forests in the uplands. However, treeline advance may be slowed in the presence of hares, and their abundance at floodplain sites with closed canopies restricts spruce establishment to suboptimal locations with more open canopies (Figure 3.3, Angell and Kielland 2009; Milakovsky et al. 2011).

Our first objective was to explore how changes in snowshoe hare abundance over time may affect the temporal pattern in spruce establishment. Spruce are particularly vulnerable during the first year of establishment because a single browse event can kill the seedling. In particular, the 2009 hare peak in Denali was substantially higher than the two prior hare peaks (Figure 3.1). Most browse events we measured occurred during the 2009 hare peak, and we found relatively few seedlings successfully established around this time (Figure 3.1). Because browsing of spruce increases with increasing hare abundance, the amplitude of a given hare peak should be inversely proportional to the number of seedlings that establish over that time. The mechanisms that determine the amplitude of a hare peak are not fully understood, however, and both bottom-up (winter food availability) and top-down (predation) controls are likely interacting to influence the duration and size of a peak (Krebs et al. 2014).

Hare cycles are regionally synchronized across North America's western boreal forest, but significant variation in amplitude occurs across the region for any given peak (Krebs et al. 2014). For example, the 1999 hare peak was substantially smaller compared to the 2009 hare peak in Denali (Figure 3.1), whereas both peaks were equally large 120 km to the north at the Bonanza Creek Long Term Ecological Research (LTER) site near Fairbanks (Krebs et al. 2013). Because of significant variation in amplitude across time and space, some locations may experience negligible browsing by hares for decades, while elsewhere, the consecutive occurrence of two large hare peaks may lead to widespread, severe browsing of spruce seedlings (Olnes and Kielland 2017).

In addition to hare abundance, environmental factors further influence the capacity of hares to limit spruce recruitment. Seedlings that are quickly covered by snow are shielded from browsing hares, which consume greater quantities of spruce during the winter months when herbaceous material is unavailable (Smith et al. 1988). During the 2009 hare peak, average early-season snow depth was only 9 ± 2 cm, indicating that many young seedlings would have been vulnerable to browsing given the minimal snow accumulation. This interaction between biotic and abiotic factors highlights the complexity of spruce establishment at landscape scales.

Growing season temperature (sum GDD May – September) had a positive effect on spruce establishment. As we hypothesized, warmer growing seasons benefit spruce at its range limit, reflecting the fact that summer temperature is a primary climatic factor limiting treeline advance in the Alaska Range (Lloyd and Fastie 2003). Warmer temperatures may promote establishment and growth (Nicklen et al. 2016); however, the restriction of spruce to primarily open floodplain sites by hares puts them at greater risk of desiccation as summers become warmer and drier (Fig. 3), a trend already occurring at lower elevations (Angell and Kielland 2009; Juday et al. 2015).

Although warmer growing seasons will allow spruce to advance in elevation at Denali, the rate of treeline advance will more likely be determined by the dispersal ability of spruce. Prior research in Denali has suggested that the proximity to reproductive individuals is a primary factor influencing treeline advance, with nearly zero recruitment occurring 50 m beyond reproductive stands (Stueve et al. 2011). Thus, spruce dispersal ability most likely explains why seedling abundance decreases with elevation (Figure 3.2 b). Conversely, tall shrubs respond more rapidly to climate warming and are thus able to advance in elevation more quickly than spruce (Dial et al. 2016). The presence of extensive shrub communities beyond treeline has allowed hares to occupy habitats at higher elevations than the present limit of spruce (Figure 3.2 a).

At both broad and fine scales, the range and habitat preferences of hares and white spruce overlap. The distribution of the boreal forest is changing as spruce responds to a warming Subarctic, and the snowshoe hare has responded by colonizing increasingly shrubby habitats far beyond treelines (Figure 3.2 a, Tape et al. 2015). Thus, all spruce range expansion is likely to take place through the snowshoe hare filter, which will increase the heterogeneity of recruitment patterns within this transition zone (Herrero et al. 2016).

Another complicating factor that is not well understood is how the snowshoe hare cycle in boreal North America will be affected by ongoing climate change (Krebs et al. 2013). Given the strength of the snowshoe hare filter on white spruce establishment, the shifting distribution of the boreal forest will likely be affected by changes to the 10-year hare cycle. As tundra gives way to tall shrubs and, eventually, to forest, scientists and resource managers must continue paying attention to those shy and small herbivores occupying the undergrowth.

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Figures

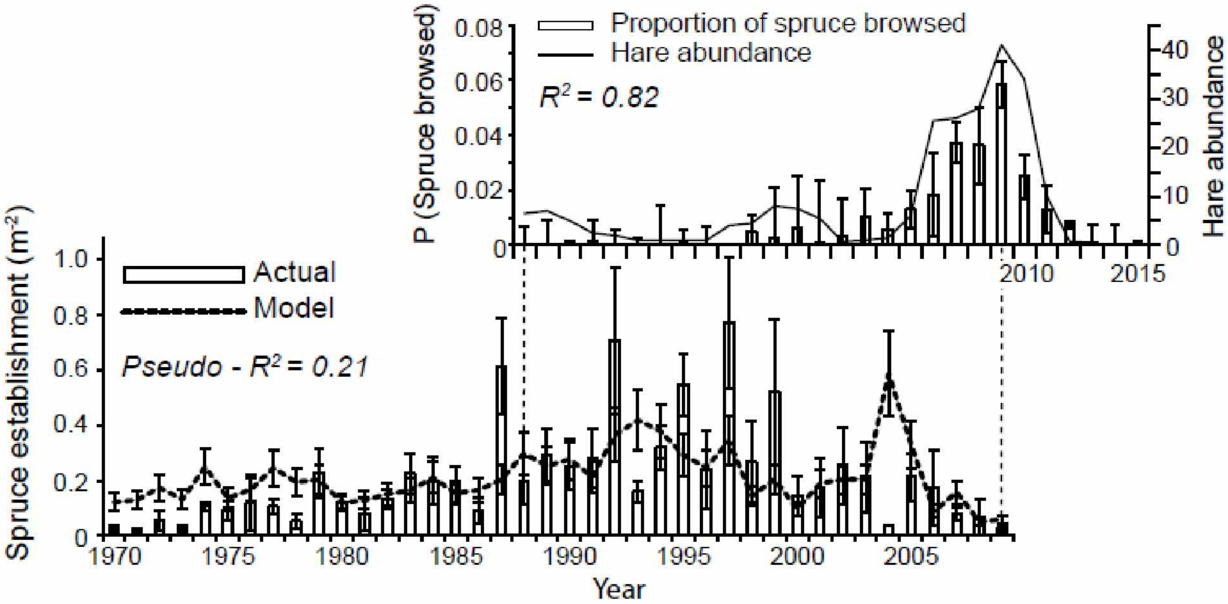

Figure 3.1. Pattern of yearly spruce establishment (modeled and actual) based on the number of sampled white spruce (m^{-2}) that established each year from 1970 to 2009, summed within elevational bins. The pseudo-R^2 is the squared Pearson's correlation between actual values and values predicted by the model. Upper right: the proportion of white spruce browsed annually from 1988 to 2015 compared to estimates of annual hare abundance (hares on road). Error bars represent the standard error around the mean.

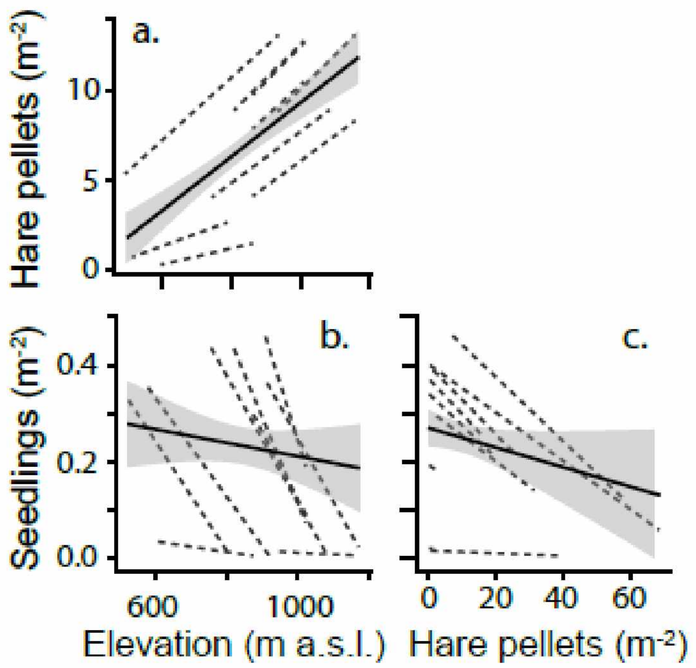

Figure 3.2. Patterns of seedling and hare pellet density (m^{-2}) across Denali. Hare pellet density increased with elevation (a.). Seedling density declined with elevation (b.) and hare pellet density (c.). Dotted lines are regression trends for each transect site (n = 9). Solid line is the overall trend across transect sites. Gray shading represents the standard error around the regression line.

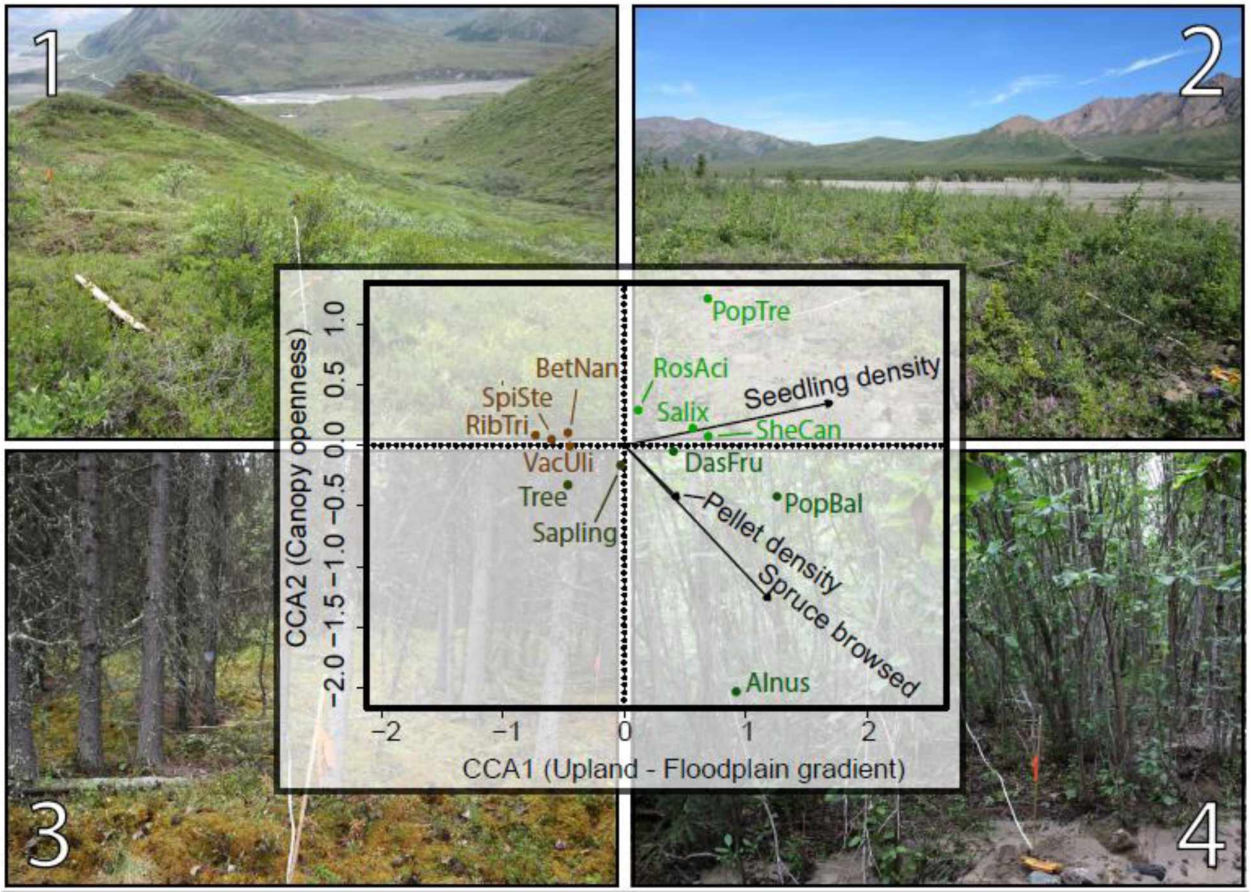

Figure 3.3. Results of Canonical Correspondence Analysis (CCA) for Denali. Photos in the background reflect plant communities described in each quadrat of the ordination space. Species labels are defined in the text.

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Appendices

Appendix 3.1. Supplementary figures

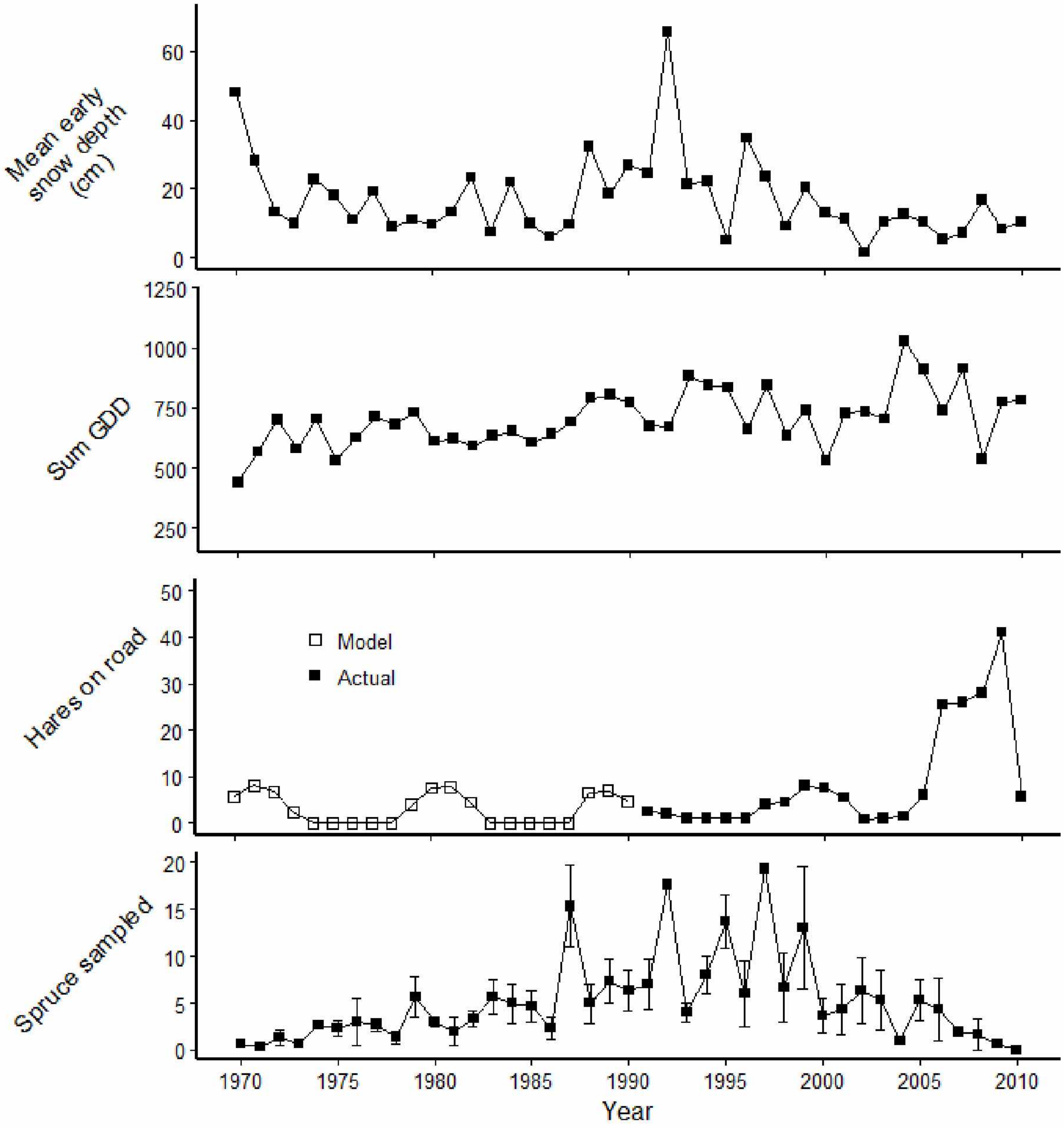

Figure 3.S1. Explanatory variables used to describe the pattern in white spruce establishment over time (Spruce sampled) for Denali. Error bars represent standard error.

Appendix 3.2. Supplementary tables

Table 3.S1. Competing models to explain the pattern of seedling establishment from 1970 - 2009 in Denali. All models had negative binomial error structure, and elevation (500 – 700 m, 701-900 m, 900 – 1100 m) was a random effect. All parameters were standardized to have a mean of zero and a standard deviation of one. Final model AIC value is indicated in bold.

Model	Parameters	AIC
Full	$Hare_t$† + $snow_t$‡ + GDD_t†† + $Hare_{t+1}$ + $snow_{t+1}$ + GDD_{t+1}	638.19
1	$Hare_t + snow_t + GDD_t$	**635.87**
2	$Hare_t + snow_t$	648.57
3	$Hare_t + GDD_t$	638.67
4	$Hare_t$	649.30
I	*Intercept only*	655.88

†Relative hare abundance in year *t*, based on available data and simulated data using the modified sine curve: $hare\ abundance_t \sim -0.4 + 8.5 * \sin((t+1)/1.5)$

‡Average snow depth (cm) September – December for year *t*.

††Sum GDD May – September for year *t*.

Table 3.S2. Competing models to explain seedling density in Denali. All models had Poisson error structure and transect was a random effect. All parameters were standardized to have a mean of zero and a standard deviation of one. Final model AIC value is indicated in bold.

Model	Parameters	AIC
Full	*Elevation* + Pellet density*† + *Total ramets*†† + *Landscape type*‡	**850.13**
1	*Elevation + Pellet density*	862.49
2	*Elevation + Total ramets + Landscape type*	875.25
3	*Pellet density + Total ramets + Landscape type*	877.79
4	*Elevation*	880.01
5	*Pellet density*	983.59
I	*Intercept only*	1014.53

**Elevation* is the elevation of each plot at Denali (500 - 1175 m a.s.l.)
†*Pellet density* is the mean hare pellets m^{-2} for each plot
††*Total ramets* is the mean number of ramets m^{-2} of all woody vegetation (excluding spruce) for each plot
‡*Landscape type* is a categorical variable designating each plot as either floodplain or upland

Table 3.S3. Competing models to explain hare pellet density in Denali. Transect was a random effect. The response variable of hare pellet density was square-root transformed. All parameters were standardized to have a mean of zero and a standard deviation of one. Model parameters are defined in Table S2. Final model AIC value is highlighted in bold.

Model	Parameters	AIC
Full	*Elevation + Total ramets + Landscape type*	327.08
1	*Elevation*	326.87
2	*Elevation + Landscape type*	**323.73**
3	*Landscape type*	328.00
I	*Intercept only*	327.02

Table 3.S4. Model results for final model of seedling density at Denali. Model parameters are defined in Table S2.

Final Model			R^2_c
	β	*p*	0.35
Intercept	1.43	<0.01	
Elevation	-0.77	<0.001	
Pellet density	-0.29	<0.001	
Total ramets	-0.03	NS	
Landscape type (upland)	-0.51	<0.001	

Table 3.S5. Model results for final model of hare pellet density at Denali. Model parameters are defined in Table S2.

Final Model			R^2_c
	β	p	0.31
Intercept	2.90	<0.001	
Elevation	0.73	<0.01	
Landscape type (upland)	-0.98	0.02	

Table 3.S6. Results of canonical correspondence analysis (CCA) for Denali ($F_{3,77} = 2.08$, p = 0.001). CCA 1 and CCA2 are latent variables that relate variation in browsing variables to variation in species occurrence. For each species, the name provided in parentheses was used to label the location of that species within the ordination plot depicted in Figure 3.

	CCA 1 (upland – floodplain gradient)	CCA 2 (canopy openness)
Proportion explained	0.78 (0.06)	0.19 (0.02)
Scores		
Browsing variables		
Pellet density (Pellet)	0.24	-0.23
Seedling density (Seedling)	**0.93**	0.19
Seedlings browsed (Browse)	**0.65**	**-0.69**
Spruce size class		
Sapling (Sapling)	-0.03	-0.16
Tree (Tree)	-0.47	-0.33
Associated species		
Alnus sp. (Alnus)	0.92	-2.03
Betula nana (BetNan)	-0.47	0.10
Populus balsamifera (PopBal)	1.26	-0.42
Populus tremuloides (PopTre)	0.68	1.21

Dasiphora fruticose (DasFru)	0.40	-0.05
Ribes triste (RibTri)	-0.73	0.08
Rosa acicularis (RosAci)	0.11	0.28
Salix sp. (Salix)	0.56	0.14
Shepherdia canadensis (SheCan)	0.69	0.07
Spirea stevenii (SpiSte)	-0.60	0.05
Vaccinium uliginosum (VacUli)	-0.45	-0.01

Chapter 4. Functional responses of white spruce to snowshoe hare herbivory at treeline[1]

Abstract

Herbivores modify the rate of shrub and treeline advance and both direct and indirect effects of herbivory may simultaneously interact to affect the growth rates of plants at this ecotone. We investigated the effect of snowshoe hare (*Lepus americanus*) herbivory on the height of white spruce (*Picea glauca*) at two treeline locations in Alaska, USA. White spruce is expanding its distribution both upwards in elevation and northward in latitude because of climate warming, and snowshoe hares are already present in areas likely to be colonized by spruce. We hypothesized that herbivory would result in browsed individuals having reduced height, suggesting herbivory is a direct, negative effect on spruce treeline advance. Our results suggest browsing does reduce spruce height at treeline. We found an interactive effect between browsing history and spruce age; when young (under 30 years old), individuals that were browsed tended to be taller than unbrowsed individuals, however, older seedlings (over 30 years old) that had been browsed were shorter than unbrowsed individuals of the same age. Hares suppress faster growing individuals that are initially taller by preferentially browsing them as they emerge above the winter snowpack. This reduced height, in combination with increased mortality associated with browsing, is predicted to slow the advance of both latitudinal and altitudinal treeline expansions and alter the structure of treeline forests.

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[1] In revision at PLoS One as Olnes, J., Kielland, K., Genet, H., Juday, G.P., and R.W. Ruess. Functional responses of white spruce to snowshoe hare herbivory at the treeline.

Introduction

Herbivory has direct and indirect effects on the rate of shrub expansion and treeline advance [1, 2]. Directly, herbivory may reduce growth rates via biomass consumption and meristem removal [3, 4] that may lead to plant mortality. By contrast, the presence of herbivores may benefit the growth of less palatable species by reducing competition from neighbors [5,6], but also benefit the growth of palatable species by inducing compensatory growth [7, 8]. Predicting the response of vegetation is complicated when direct (i.e. alteration of growth rate) and indirect (i.e. change in of species competition) effects act simultaneously.

In Alaska, white spruce (*Picea glauca* (Moench) Voss) is gradually advancing upward in elevation and northward in latitude, replacing tundra landscapes with boreal forest [9, 10]. Preceding treeline advance is the expansion of tall deciduous shrubs, which provides suitable habitat for snowshoe hares (*Lepus americanus* L.) to occupy landscapes currently, or soon to be, colonized by white spruce [11, 12]. Snowshoe hares are dominant boreal herbivores that have the capacity to modify vegetation dynamics, including the establishment of white spruce via their browsing of seedlings during winter [13]. Whereas treeline spruce typically experience the negative consequences of direct herbivory by hares, they may also accrue benefits when hares browse the surrounding, more palatable vegetation. Thus, the functional responses of white spruce to herbivory, in terms of growth, seed production, and establishment, reflect the outcome of these negative and positive effects.

In light of previous studies demonstrating the capacity for hares to significantly reduce spruce height in lowland floodplains [4, 14], we investigated whether treeline spruce would also experience reduced height as a result of snowshoe hare herbivory. We addressed this question by measuring the height, age, and browsing history of white spruce seedlings at two treeline locations in Alaska: at the altitudinal limit of white spruce in Denali National Park, and at the latitudinal limit of the species near the Middle Fork of the Koyukuk River. We hypothesized that browsed individuals would have reduced height growth compared to individuals that had not been browsed, as indicated by changes in the slope of the relationship between spruce height and age. To further understand the role of associated deciduous vegetation in altering spruce height at treelines, we additionally hypothesized that the proportion of surrounding deciduous vegetation browsed would positively relate to spruce height, reflecting an indirect benefit of hare browsing.

Methods

Study locations and sampling design. Denali National Park and Preserve (Denali), and the Middle Fork of the Koyukuk River (Koyukuk) include extensive areas representative of the altitudinal and latitudinal limits of white spruce in Alaska, respectively (Fig 1). Snowshoe hares are present in both areas and periodically achieve very high abundances [15].

Denali (63°43'N, 148°57'W) is located within the Alaska Range, approximately 130 km southwest of Fairbanks. Lower elevations are dominated by white and black spruce (*P. mariana* (Mill.) B.S.P.) forests, which transition to alpine shrub tundra at higher elevations [16]. Nine sites were accessed along the 143-km park road corridor via hiking. For each site, we established a transect 1.5 – 5 km long, oriented perpendicular to the hillslope. Along these transects, we established 25 m^2 plots at 75 m elevation intervals between 500 - 1175 m a.s.l. These plots encompassed the elevational range of white spruce as determined by Roland et al. [16]. Because floodplain and upland vegetation communities are distinct, and floodplains represent high-quality hare habitat and optimal conditions for spruce establishment [12], additional plots (n = 38 floodplain plots total) were positioned along major stream or river drainages near each elevational transect (500 – 945 m a.s.l.). Plot number varied between 4 and 12 plots per transect site (n = 81 plots total), based on the range of elevations present at each location and the accessibility of each plot. We specifically addressed variation in spruce establishment and snowshoe hare herbivory along elevational gradients and between habitat types in a separate study [12].

Located on the southern flanks of the Brooks Range, the Koyukuk study area (67°25'N, 150°07'W) is approximately 310 km north of Fairbanks. Sites were located between 365 and 790 m a.s.l. and were accessed from the Dalton Highway. Ten sites were selected along a latitudinal gradient in which the most northerly site represented the farthest north white spruce trees along the highway corridor. At each of the 10 sites, we sampled three 25 m^2 plots (n = 30 plots total). Plot locations were chosen randomly using satellite images prior to field sampling and included both floodplain (n = 18 plots) and upland (n = 12 plots) locations. All plots were located below the local altitudinal tree limit.

In the summer of 2015, we sampled all individual white spruce within each 25 m^2 plot at both Denali and Koyukuk, and measured the height and basal diameter, and recorded browsing history for each individual as either "no browsing", "moderate browsing", or "severe browsing". Moderate browsing was defined as 1 – 2 apical browsing events, and severe browsing was defined as > 2 apical browsing events or more than half of all lateral branches being browsed. This is a conservative estimate of browsing history as older browse scars may no longer be apparent, however, we consider this hidden browse history rare for spruce seedlings and saplings as browse scars often remain visible for several decades [12,13]. Hare browse events were identified by the sharp 45° angle of the bite and we back-counted current annual growth segments to estimate the year when the apical meristem was browsed. Similarly, we determined the age of most individual spruce trees using whorl counts (the number of apical annual growth segments [13]). For trees with annual growth segments that were too obscured to accurately age in this manner, we collected basal core samples and determined tree age using standard techniques of tree ring counting [17]. To estimate the age of each tree when browsed, we subtracted the year of browsing from the year of establishment for each tree. Within each plot, we also used four 1 m^2 subplots to estimate the density of deciduous woody vegetation (ramets m^{-2}) and associated browsing by hares (browsed ramets m^{-2}). We did not sample browsing of herbaceous vegetation because our study focused on winter browsing, when hares primarily eat woody vegetation [18, 19]. Individual deciduous ramets were defined as a single stem rooted in the ground within the 1 m^2 subplot and counted as being browsed if any subsequent branches off this ramet had apical growth points removed by hares. We then calculated the proportion of deciduous woody ramets browsed from these values. Values were averaged across each subplot to obtain a single proportion of ramets browsed per plot for each species.

Analysis. We performed all statistical analyses using the R statistical software version 3.4.3 [20]. Assumptions of equal variance and normality of the residuals were confirmed graphically for all linear models. Statistical significance (α) was set at 0.05.

We used a linear mixed effect model to test the effects of browse history on spruce height for all spruce < 200 cm tall (function: lmer), encompassing the height range for which spruce are vulnerable to browsing by hares [21]. Our response variable was spruce height, and our fixed effects were spruce age, browsing history and their interaction term, the proportion of associated deciduous vegetation browsed, and habitat type (floodplain or upland). We included the proportion of associated deciduous vegetation browsed to test our hypothesis that indirect browsing by hares may have a positive influence on spruce height. Although our primary goal was to assess the direct and indirect effects of hare browsing specifically, we included the habitat type term because we suspected that floodplain spruce would have significantly greater height than upland spruce for both Denali and Koyukuk as floodplain habitats tend to be more productive. Because our analysis was conducted at the level of individual tree, we avoided pseudoreplication by including sampling region (Denali or Koyukuk) and plot nested within region as random effects. We log-transformed the response variable to improve model fit and meet model assumptions for our full model. We then developed competing models that incrementally excluded our fixed effects and selected the best model based on Bayesian Information Criterion scores (BIC). BIC is a parsimonious method of model selection that accounts for model fit while penalizing for the number of parameters included in the model. We selected the model with the lowest BIC score as our final model for spruce height (function: bic), and only considered additional models if their BIC score differed by less than 2 from the lowest BIC score. We determined the significance of each fixed effect within our final model using F tests (function: anova) and compared the means among browsing categories using pairwise comparisons for mixed effects models (function: lsmeans). We determined whether model coefficients significantly differed from zero using t tests (function: lmer). We calculated both the marginal (R_m^2) and conditional (R_c^2) R-squared values for our model (function: r.squaredGLMM), which give the amount of variation explained by the fixed effects alone and by the fixed and the random effects, respectively [22]. To estimate the amount of variation in spruce height explained by browsing, we also calculated the marginal R-squared for our final model without hare browsing and compared this to the R_m^2 of the model that included the browsing by age interaction.

Results

A total of 1,294 white spruce trees were measured (796 at Denali and 498 at Koyukuk) that varied in height (from 4 cm to > 800 cm) and age (from 5 to 135 years old). Widespread browsing of white spruce seedlings and saplings by hares occurred at both study locations; 40% (36% moderate browsing, 4% severe browsing) and 53% (34% moderate browsing, 19% severe browsing) of the measured white spruce had their apical meristem browsed at least once by hares at Denali and at Koyukuk, respectively. Most browsing events occurred when spruce were 10 to 20 years old for both Denali (mean age when browsed ± S.D., 15.8 ± 5.9 years) and Koyukuk (15.1 ± 8.1 years; Fig 2A). There was no significant difference in the age of browsed spruce between the study locations (paired t test, t = 0.07, d.f. = 51, $P = 0.94$).

A total of 988 spruce (76%) across both study regions were < 200 cm tall and this sample was used to analyze changes in height with changes in browsing history. Our model that included only the browsing by age interaction produced the lowest BIC score (Table 1). The interactive effect of spruce age and browsing history was significant (F = 45.34, d.f. = 2, 972.43, $P < 0.001$; Fig 2B). Moderately browsed (pairwise comparison of Least Squares Means, $P < 0.001$) and severely browsed ($P < 0.001$) individuals had significantly different relationships between height and age than individuals that had not been browsed but did not differ from each other in their height-age relationship ($P = 0.12$). Both browse categories had reduced positive slopes for height with increasing spruce age than for individuals that were not browsed, but increases in the intercept for each browse category show that browsed young spruce (< 30 years of age) tended to be *taller* than unbrowsed individuals (Table 2). Our fixed effects explained 61% of the variation in spruce height ($R_m^2 = 0.61$). Removing browse history from the model reduced the amount of variation explained to 55% (R_m^2= 0.55), suggesting browsing history explains a significant amount of variation in spruce height after accounting for spruce age. Plot and region explained an additional 18% of the variation in spruce height (R_c^2 = 0.78), suggesting that environmental conditions, not surprisingly, have a large effect on spruce growth.

Discussion

Treeline white spruce trees are frequently browsed by snowshoe hares in Alaska. For newly recruiting individuals their fate is clear; a single browsing event can remove all meristematic tissue, resulting in death [4, 12]. For older seedlings with multiple growth points, browsing appears to have variable effects on spruce height, depending on the age of the individual. Although height growth occurs at a slower rate for browsed individuals as indicated by a reduced slope between spruce height and age, browsed spruce under approximately 30 years old tend to be *taller* than individuals that have not been browsed (Fig. 2B). By contrast, after approximately 30 years of age, unbrowsed individuals surpass browsed individuals in height as a result of their faster height growth rate (greater slope), allowing them to reach 200 cm and escape hare browsing 5 – 10 years earlier than browsed spruce (Fig. 2B).

The pattern of browsed spruce initially being taller than unbrowsed individuals could either reflect a response to herbivory or be the result of selective preferences of hares. Many deciduous species exhibit compensatory growth when browsed, and it is theoretically possible that spruce respond similarly to moderate levels of browsing [23]. Recent experiments using herbivore exclosures or clipping to simulate browsing, however, suggest white spruce does not exhibit a compensatory growth response [4, 24]. Browsed spruce may also benefit from the indirect effects of hare browsing on surrounding vegetation, but we found no support for the indirect effect of browsing on spruce height in our mixed effects model (Table 1).

Rather than being a response to herbivory, we surmise that greater initial height in browsed individuals reflects the browse preferences of hares. Hares are selecting to browse faster growing individuals that are taller [25, 26], whose faster growth may be a simple change in carbon allocation to biomass rather than defense (at a cost of greater vulnerability to herbivores). Because snow depth greatly influences the accessibility of spruce to browsing hares, faster growing seedlings that are taller will be exposed above the snowpack earlier than slower growing seedlings, increasing their likelihood of being browsed. In this study, 84% of browsed spruce were taller than the mean winter snow depth for Denali and the Koyukuk (~40cm, Western Regional Climate Center), whereas 55% of all unbrowsed spruce were below this height (Fig. 2B). The expected advantages of growing faster at treeline are negated by increased vulnerability to browsing, which reduces spruce height, eventually reversing pre-existing height differences among browse categories (Fig. 2B). Variable growth rates may also affect palatability and digestibility, where, as noted, trees allocating carbon to growth may produce less defensive compounds [24]. Conversely, slower growing spruce are likely to be more heavily defended chemically given reduced allocation of carbon to growth, and thus, avoided by hares. Suppression of faster-growing spruce will further slowdown treeline establishment in the presence of hares, as the time for populations of spruce to reach maturity and form a canopy (given sparse or less than spatially complete recruitment) will be determined by the slowest growing individuals in the population.

At both treeline locations, more browsing occurred in floodplain habitat than in upland habitat [12], suggesting that spruce growing in floodplain habitats are more likely to have reduced height because of browsing hares. This may partly explain why habitat type was not a significant variable in our final height model. Hare browsing may negate some of the expected increases in height for floodplain spruce. Exclosure studies have shown spruce growing under deciduous vegetation characteristic of floodplain habitats are shorter when exposed to hare herbivory than when excluded from herbivory [4]. At floodplain sites that are too open, spruce are known to be vulnerable to desiccation, resulting in reduced height growth at these locations [4, 27]. Thus, the potential for greater growth of spruce growing in productive floodplain habitats may be negated by hare browsing in areas with sufficient cover, and by physiological stress in open areas.

One component our study could not capture was the missing record of spruce seedlings that die because of hare browsing. At both locations we observed sites where seedlings had been killed due to browsing but remained standing (Fig 3). In the 7 plots (6 at Denali, 1 at Koyukuk) where we recorded spruce killed by hares, dead spruce made up to 53% (± 10%) of all standing spruce. This mortality estimate is conservative for these locations because many dead spruce, especially young seedlings, do not remain standing, as demonstrated in controlled experiments with planted spruce and herbivore exclosures [4]. The paucity of browsed spruce under ten years of age may partly reflect this missing record.

Our results also reinforce other findings that white spruce is an important component of the snowshoe hare winter diet [18, 19]. Whereas white spruce occurs at lower densities than most other potential woody forage plants, the proportion of individual spruce browsed (50%) was among the highest for any forage species (Table 3). Hares may actively select to browse spruce seedlings in the winter to help them to diversify their toxin load (albeit accruing additional toxins in the process). The importance of spruce as a winter diet item to hares should be emphasized, particularly in the context of the shifting growth performance of spruce across the Alaskan landscape in response to climate warming [28].

Understanding constraints on height growth is critical to understanding rates of treeline advance and the structure of the advancing forests. The effects of browsing by hares on spruce height have diverse functional consequences. Individual trees may appear to be initially benefitting from the presence of hares, either through compensatory growth following browse events or via indirect benefits of hares browsing surrounding vegetation. However, our results suggest that hares are selecting for taller, faster-growing individuals. Thus, the apparent positive effect may actually be an additional negative consequence, where the fastest-growing individuals in a population are suppressed by hares, causing the slower-growing individuals to determine the rate at which populations escape herbivory. Simultaneously, many young seedlings, as well as older individuals, succumb to severe hare browsing. Quantifying this missing record is key to understanding the capacity of herbivores to limit tree establishment, and for understanding the true potential of spruce to advance in the presence or absence of hares.

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Figures

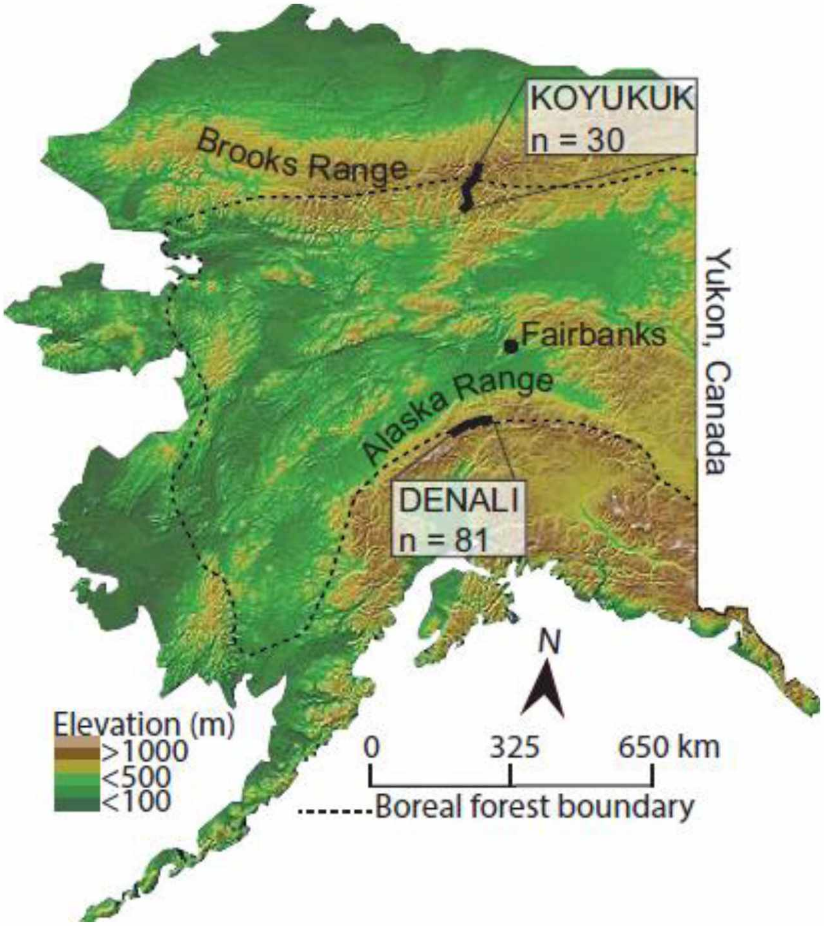

Figure 4.1. Locations of sampling regions, Denali and Koyukuk, in Alaska, USA.

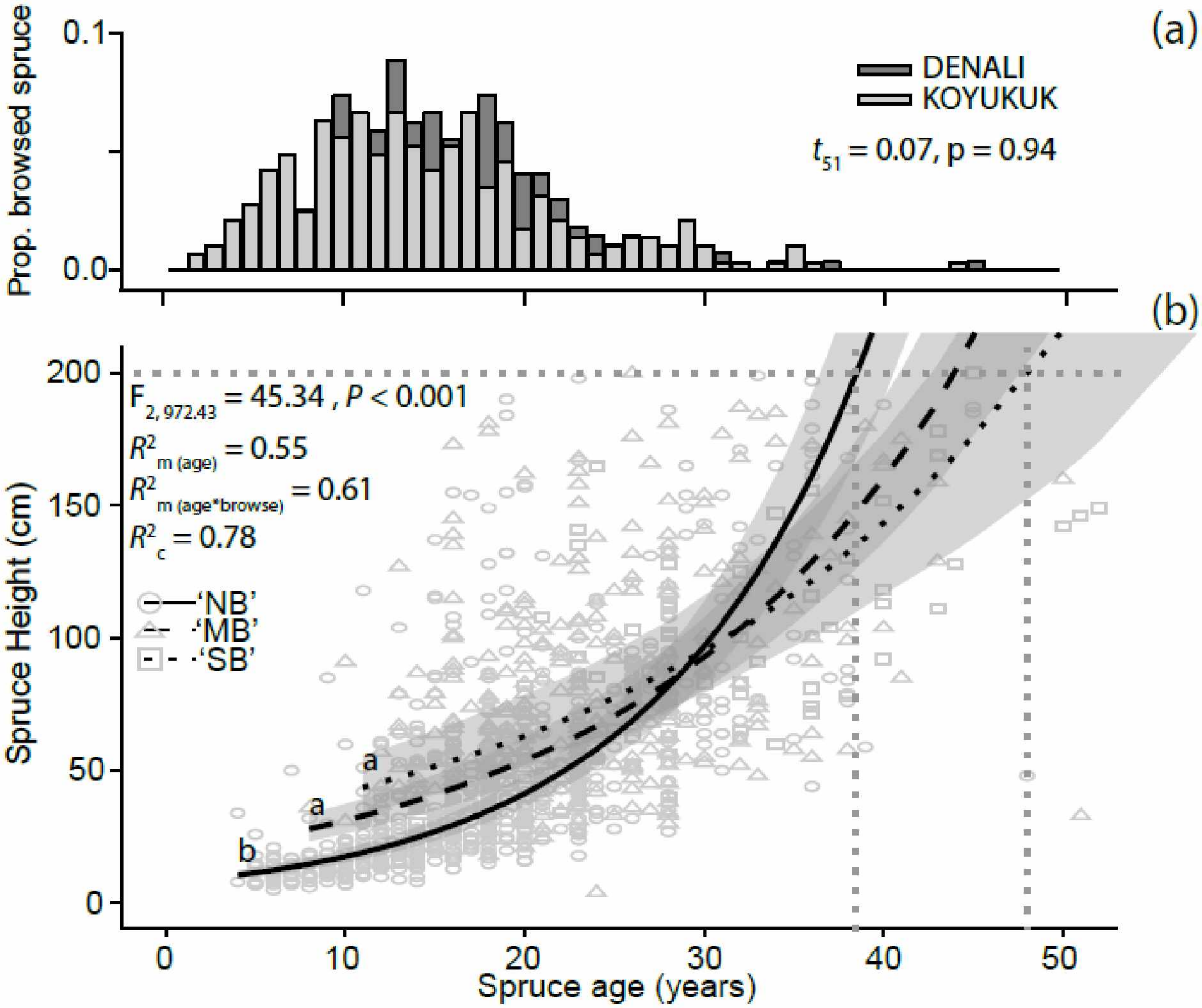

Figure 4.2. (a) Most spruce were 10 – 20 years of age when browsed at both Denali and Koyukuk. (b) Browsing history (no browsing (NB), moderate browse (MB), severe browse (SB)) alters the relationship between spruce height (cm) and age (years). Stippled gray lines indicate age difference of escaping herbivory (height = 200 cm) for browsed or not browsed spruce. Letters denote significant differences among browse categories. Shaded regions reflect the 95% confidence interval around each regression line

Figure 4.3. An unknown is the missing record of spruce that die because of hare browsing, as exemplified in the photograph of individuals likely to soon die by browsing hares at Koyukuk.

Tables

Table 4.1. Six models were hypothesized to explain variation in spruce height at treeline (log-transformed). Final model selection was determined by calculating the Bayesian Information Criterion (BIC) for each model. Fixed effects included were spruce age (Age), browsing history (Browse), the proportion of associated deciduous woody vegetation browsed (pDeciduous), and habitat type (Habitat, upland or floodplain). Final model is indicated in bold.

Model	Fixed effects within model	BIC
Full	Age*Browse + pDeciduous + Habitat	1298.14
1	Age*Browse + pDeciduous	1292.41
2	Age*Browse + Habitat	1290.82
3	**Age*Browse**	**1285.83**
4	Age + Browse	1338.58
5	Age	1359.73

Table 4.2. Results of linear mixed effects model for white spruce seedling height at treeline in Alaska. The response variable, spruce height, was log-transformed.

Parameter	Estimate (± S.E.)	D.F.	t	*P*
Intercept (No browse)	2.020±0.089	2.50	22.72	<0.001
Added intercept (Moderate browse)	0.873±0.092	964.00	9.49	<0.001
Added intercept (Severe browse)	1.304±0.165	981.80	7.89	<0.001
Slope (Age x No browse)	0.085±0.002	980.30	31.14	<0.001
Slope change (Moderate browse)	-0.030±0.004	966.20	-7.71	<0.001
Slope change (Severe browse)	-0.044±0.005	966.20	-7.96	<0.001

Table 4.3. The density of woody vegetation near treeline

Species	Total Density, m^{-2}	Browsed (%)
DENALI		
Salix sp.	3.93 ± 0.52*	47 ± 7 %
Betula nana	1.66 ± 0.34	21 ± 3 %
Picea glauca	**0.44 ± 0.05**	**40 ± 5 %**
Alnus sp.	0.14 ± 0.07	30 ± 4 %
Shepherdia canadensis	0.95 ± 0.25	10 ± 2 %
Populus balsamifera	0.27 ± 0.08	35 ± 4 %
Rosa acicularis	0.80 ± 0.22	15 ± 2 %
KOYUKUK		
Salix sp.	3.63 ± 0.69	38 ± 5 %
Betula nana	1.31 ± 0.49	23 ± 6 %
Picea glauca	**0.59 ± 0.07**	**53 ± 6 %**
Alnus sp.	0.70 ± 0.24	36 ± 7 %
Shepherdia canadensis	1.45 ± 0.44	11 ± 3 %
Populus balsamifera	0.27 ± 0.11	38 ± 7 %
Rosa acicularis	0.04 ± 0.03	25 ± 3 %

‘Total Density’ refers to the density of ramets or main stems for each species, including both browsed and unbrowsed individuals.

*Mean ± S.E

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Chapter 5. Herbivory by snowshoe hares on regenerating black spruce foreshadows future capacity to influence postfire succession

Abstract

The future boreal forests of Alaska will likely consist of more stands dominated by deciduous trees because changes to the fire regime have resulted in larger and more severe fires, which facilitate the establishment of trembling aspen (*Populus tremuloides*) and Alaska birch (*Betula neoalaskana*). Areas that burned with high severity are shifting from a landscape of black spruce (*Picea mariana*) self-replacement towards a dominance relay landscape, where deciduous trees make up the canopy for many decades before black spruce becomes the canopy dominant. Whether stands completely transition to a deciduous-dominant system or return to black spruce dominance depends on the capacity of regenerating black spruce to grow and produce seed before the next fire. Herbivory by snowshoe hares (*Lepus americanus*) can alter the ability of black spruce to succeed under deciduous canopies. We hypothesize that hare herbivory reinforces deciduous dominance by suppressing black spruce. We address this question by measuring changes in spruce height and herbivory across 54 sites within the Regional Site Network, long-term monitoring plots maintained by the Bonanza Creek Long- Term Ecological Research program. We found that herbivory by snowshoe hares reduces spruce height growth, indicating hares are selectively browsing the oldest and/or fastest growing individuals. The likelihood of spruce being browsed is increased by dense deciduous canopies where hares tend to be more abundant. Snowshoe hares reinforce deciduous dominance by suppressing black spruce under deciduous canopies; however, the magnitude of the effect was smaller than we expected.

Introduction

Alaska's boreal forest of tomorrow will likely differ from the boreal forest of today as a greater proportion of the landscape will likely be dominated by deciduous or mixed wood forests (Shenoy et al. 2011; Pastick et al. 2017). A primary driver of this shift in forest composition is changes to the fire regime (Mann et al. 2012; Kelly et al. 2013). Fire scientists have documented a significant increase in the annual extent of area burned (Kasichke et al. 2010), and in the severity of fires (Turetsky et al. 2011), both of which can facilitate the postfire establishment of deciduous trees in moderately to well-drained areas once dominated by the conifer black spruce (*Picea mariana* (Mill.) B.S.P.).

Severe fires largely eliminate the thick organic soil layer prevalent in black spruce stands prior to burning (Turetsky et al. 2011). Deciduous trees, primarily aspen (*Populus tremuloides* Michx.) and Alaska birch (*Betula neoalaskana* Sarg.), benefit from the absence of an organic layer because their smaller seeds have better germination success in the exposed mineral soil (Johnstone and Chapin 2006; Shenoy et al. 2011). By gaining an initial foothold following a severe burn, the presence of aspen and birch reflects a shift away from black spruce self-replacement thought to most commonly occur (Johnstone et al. 2010). Rather than black spruce self-replacement, a deciduous canopy may persist for half a century or more before spruce could emerge as the canopy dominant by way of relay succession (Kurkowski et al. 2008).

Several studies suggest that the fire return interval in boreal Alaska is often too short to allow for relay succession (Kurkowski et al. 2008; Johnstone et al. 2010; Shenoy et al. 2011). However, historical fire return intervals are based on wildfires occurring in spruce dominated landscapes and fire records are not long/old enough to assess the reburn potential of these novel, postfire deciduous stands that are less flammable than stands dominated by black spruce (Bernier et al. 2016; Alexander and Mack 2017). For example, the Bonanza Creek Long Term Ecological Research (BNZ LTER) program maintains a Regional Site Network (RSN) of 94 plots within fire scars of varying age and burn severity (described in more detail below). Nearly all young- and intermediate-aged sites classified as deciduous forest contain regenerating black spruce growing slowly beneath the deciduous canopy. Whether boreal landscapes transition more permanently to a deciduous-dominated state, mixed-wood forest, or return to a black spruce dominant system, will depend on the capacity of black spruce to survive and produce seed while outlasting birch and aspen before the next fire. Thus, factors affecting the rate of black spruce growth and mortality under deciduous canopies ultimately can influence the likelihood of relay succession and whether black spruce can produce seed prior to reburning (Chapin et al. 2004).

Herbivory by snowshoe hares (*Lepus americanus*) is one mechanism that could alter the likelihood of relay succession occurring. Although black spruce is considered among the least palatable of boreal tree species (Bryant and Kuropat 1980), it is known to be an important component of the snowshoe hare's winter diet (Wolff 1978). Studies from Canada's boreal forest have shown that herbivory can reduce black spruce seedling growth and survival in collapse scar bogs (Camill et al. 2010) and at elevational treeline (Munier et al. 2010). In Alaska, snowshoe hares are known to similarly affect the establishment of white spruce (*Picea glauca* (Moench) Voss) during floodplain succession (Olnes and Kielland 2017) and at both elevational and latitudinal treelines, particularly during peak population periods (Olnes et al. 2017, Olnes et al. *in review*). Although we have observed evidence of snowshoe hares browsing regenerating black spruce following fire at several RSN sites, their capacity to influence postfire vegetation dynamics is not well understood.

Here we address the question of whether herbivory by snowshoe hares on black spruce influences postfire succession in the boreal forest of Interior Alaska. We hypothesize that herbivory by snowshoe hares can reinforce deciduous dominance by suppressing regenerating black spruce under deciduous canopies. By suppressing black spruce, hare browsing can potentially increase the likelihood that a stand burns prior to spruce seed production and emergence into the canopy, reducing the possibility of relay succession.

Methods

The Regional Site Network

The Bonanza Creek Long Term Ecological Research program (BNZ-LTER) maintains research plots (n = 94) throughout Interior Alaska that vary in site drainage conditions, topography, disturbance history (time since fire and burn severity), and conifer and deciduous tree densities, known as the Regional Site Network (RSN). A description of the RSN can be found at the BNZ-LTER website (http://www.lter.uaf.edu/research/study-sites-regional). We sampled fifty-four RSN plots across all fourteen fire scars within the network, capturing the range of variability representative of the entire RSN. Twenty plots were at young sites (<20 years since fire), twenty-four plots were at intermediate-age sites (45 – 75 years since fire), and ten plots were at mature sites (>80 years since fire). All sites had been dominated by black spruce prior to burning.

By sampling plots within the RSN, we were able to use BNZ-LTER forest inventory data to inform our analysis of hare herbivory and postfire succession. For each plot, we obtained data on seedling, sapling, and tree densities for Alaska birch, trembling aspen and black spruce (individuals ha^{-1}), and calculated tree basal area by species ($m^2 ha^{-1}$). We also gathered data on drainage conditions (categorical variable), aspect (degrees), and elevation (meters). All data are available online via the BNZ-LTER database (http://www.lter.uaf.edu/data/data-catalog) and summarized in Supplementary Table 1. From the inventory data, we calculated the proportion of live trees (diameter >2.5 cm at height of 1.37 m) that were deciduous as the sum of all aspen and birch divided by total tree density (stems ha^{-1}). We carried out the same calculation to also derive the proportion of seedlings and saplings that were deciduous and the proportion of stand basal area that was deciduous.

Field Sampling

We collected additional site variables for each plot in the summer of 2017. Each RSN plot is 50 m by 60 m, and is subdivided into thirty, 10 m by 10 m subplots, delineated by plot markers every 10 m (Appendix 5.1, Figure 5.S1). We sampled within the perimeter subplots to limit our effect on the core subplots, where long-term monitoring of tree growth and mortality takes place. At each plot, we began sampling at the northwest corner, and sampled along the center (5 m from the edge) of each perimeter subplot (Appendix 5.1, Figure 5.S1). We sampled every black spruce seedling or sapling (<1.4 m tall or < 2.5 cm diameter at height 1.37 m) nearest to a transect running through the center of the perimeter subplots at 5 m intervals (~36 individuals per plot). Within each corner subplot, as well as at the center point (30 m) of transects running along the 60 m sides of the plot, we measured canopy cover from a height of 1.4 meters above the ground using a spherical densiometer and facing towards the center of the plot (n = 4 – 6 subsampling points per plot). At each location where we measured canopy cover, we also counted the number of hare pellets within a 1-m^2 quadrat. Canopy cover readings and hare pellet densities were averaged to obtain a single value for each plot. We additionally counted the total number of standing dead black spruce with visible hare browse scars within a random selection of subplots (n = 3 - 5 subplots per plot).

We made a series of measurements to inform our understanding of snowshoe hare herbivory and its effect on black spruce height growth. For each individual spruce sampled, we measured the height (cm), basal diameter (mm), and counted the total number of apical browse scars. Hares most commonly browse the apical leader of spruce and their bite marks are easily distinguished as a sharp, 45°-angle browse scar. We additionally estimated the year of browsing for the three most recent browse scars on each black spruce by counting annual growth segments from the current annual growth to the browse scar and then subtracting this value from the year of sampling (2017) (Olnes et al. 2017). We also measured the height of the tallest browse scar on each spruce. For a subset of 77 individuals across 10 plots, we estimated spruce age by counting annual growth segments along the bole of the seedling or sapling to determine the relationship between spruce age and basal diameter.

Analysis

All analyses were conducted using R statistical software version 3.4.3 (R Core Team 2017). Assumptions of all linear models (i.e. normality and homoscedasticity) were confirmed graphically, and the significance of fixed effects was determined by F-tests for mixed-effect models unless otherwise stated (function: anova). We examined the amount of variation explained by our models using estimates of R-squared for mixed-effects models (library: MuMIn, function: r.squaredGLMM). We calculated both the marginal R-squared (R^2_{m}) and the conditional R-squared (R^2_{c}), which explain the amount of variation due to the fixed effects and the fixed effects plus the random effects, respectively (Nakagawa and Schielzeth 2013). Significance was determined by an alpha value of 0.05 for all statistical tests ($\alpha = 0.05$).

To estimate the probability of an individual spruce being browsed, we used a generalized linear mixed effects model that included the percentage of stand basal area that was deciduous for a given site, individual spruce height (0 – 200 cm), and their interaction term as our fixed effects (library: lme4, function: glmer). We included the percentage of stand basal area that was deciduous as a fixed effect because we hypothesized that browsing would be positively associated with denser, deciduous-dominant canopies (Olnes and Kielland 2016). We further assumed that spruce height would positively relate to the probability of being browsed because of interactions between winter browsing and snow depth (Olnes et al. 2017), as well as the fact that taller spruce have likely been exposed to browsing hares for a greater amount of time than shorter spruce. We used a binomial distribution with a logit-link function, and sampling plot was a random effect. We graphically tested the assumption of equal variance of the residuals for generalized linear models using a binned residual plot (library: arm, function: binnedplot). We estimated the significance of fixed effects by calculating z scores to determine whether coefficient values were significantly different from zero.

We investigated the effect of snowshoe hare herbivory on individual black spruce height using linear mixed-effects models (library: lme4, function: lmer). To specifically capture the effect of hare browsing, we only included seedlings and saplings with apical growth points below 200 cm, within the browsing range of snowshoe hares (Appendix 5.1, Figure 5.S2). We ran three similar models addressing the effect of browsing intensity on spruce height, basal diameter and the height-to-diameter ratio for each site age group (young, intermediate, mature). Our browsing intensity variable was categorical and defined by the number of apical browse events. Spruce were either not browsed, moderately browsed (1 – 2 apical browse events), or severely browsed (3 or more apical browse events). We used spruce basal diameter as a proxy for spruce age because estimating the age of black spruce seedlings and saplings can be challenging in the field. Further, by assessing the relationship between height and basal diameter, we gained insight into how browsing may influence individual spruce structure (tall-thin versus short-wide). For our models at young sites, we included the proportion of seedlings and saplings that were deciduous and an interaction term with browsing as additional fixed effects. For models of spruce height at intermediate and mature sites, we included the proportion of stand basal area that was deciduous rather than the proportion of seedlings and saplings that were deciduous. After fitting a full model for each response variable within each site age group, we incrementally removed our fixed effects and used likelihood ratio tests to select the most parsimonious final model (function: anova). All models included the random effects of fire scar and plot within fire scar. To assess where significant differences in our response variables occurred between browsing categories, we performed pairwise comparisons for mixed-effects models (library: lsmeans, function: lsmeans). Lastly, if deciduous dominance was a significant fixed effect, we assessed whether the effect was positive or negative by reviewing the beta coefficient and tested if it was significantly different from zero using a t-test (function: lmer)

To further test our hypothesis that browsing by hares reinforces deciduous dominance, we built structural equation models (SEM) detailing the pathway with which deciduous dominance promotes browsing and thus leads to reduced height in black spruce (library: lavaan, function: sem). This analysis was performed at the plot level and browse intensity was a continuous variable defined as the average number of apical browse events per individual spruce. Because hare browsing appeared minimal in mature sites (fire scars ≥ 80 years old), we built our

SEM using only young and intermediate age plots ($n = 42$). We hypothesized that browsing intensity is directly related to spruce seedling and sapling density, and hare abundance that is spatially driven by habitat suitability. Therefore, we predicted that canopy cover will positively influence browsing intensity on black spruce, and that canopy cover is influenced by time since fire, the proportion of stand basal area that is deciduous, and the density of deciduous (aspen and birch) seedlings and saplings. We then predicted that spruce height would be positively influenced by canopy cover that reduces drought stress (Angell and Kielland 2009) and time since fire, and negatively affected by hare browsing intensity and competition with deciduous trees. We built a second SEM that was identical to the first; however, we substituted spruce height with the spruce height-to-diameter ratio because we suspected some variation in height may be masked by spruce age effects or hare browse selectivity. All variables within the models were standardized and centered around a mean of zero and a standard deviation of one to allow for direct comparison of effect size among variables.

We used three methods to assess the quality of our SEM models (Hu and Bentler 1999). We first performed a chi-square test to assess how well our theorized models fit the observed data, where no significant difference between the observed and expected covariance matrices indicates a suitable model ($p > 0.05$). We then calculated the comparative fit index (CFI) for SEM, which tests how well our models fit the data compared to an independence model (no correlation among parameters). For CFI, values approaching 1 (>0.95) are considered suitable. Lastly, we calculated the root mean square error of approximation (RMSEA), which compares model fit with the model degrees of freedom. Values close to zero indicate a potentially suitable model ($\text{RMSEA} < 0.06$).

To connect our SEM models with fire severity, we compared changes in aspen, birch and black spruce seedling and sapling densities across a gradient of burn severity (low, medium, high) only available for the young sites (n = 20). We developed linear mixed-effects models for each species, where seedling and sapling density was the response variable, square-root- or log-transformed to meet normality assumptions for the model residuals. Model parameters were burn severity as the fixed effect and fire scar as the random effect. We assessed significant differences across burn severity levels by pairwise comparisons for mixed effect models.

Results

We sampled 1411 black spruce individuals at 54 sites. 40% of all sampled spruce had evidence of past apical browse events (33% moderately browsed (1 – 2 events), 7% severely browsed (> 2 events)). Most browsing occurred during periods of high hare abundance (2009 and 2015 to 2017), particularly within intermediate sites (Figure 5.1). For young sites, browsing has only occurred within the recent rise in hare abundance across the region (2015 to 2017). Browsing was minimal across the mature sites.

Individual effects of browsing

The probability of an individual spruce being browsed is a function of stand-level vegetation characteristics as well as spruce height. Our logistic mixed-effects model demonstrated that the probability of being browsed increases with increasing deciduous dominance (Figure 5.2, $z = 2.81$, $p = 0.004$) and that spruce height positively interacts to further increase the probability of being browsed (Figure 5.2, $z = 2.71$, $p = 0.007$). Nearly all black spruce individuals recruiting under pure deciduous canopies are likely to be browsed at least once before escaping the browse range of hares, which is around 200 cm (Appendix 5.1, Figure 5.S2).

The most parsimonious model for spruce height at young sites (n = 555 black spruce) included only the term for browsing history ($F_{2,544.35} = 7.23$, $p < 0.001$) and explained 2.6% of the variation in height ($R^2_m = 0.026$). The random effects of plot and plot within fire scar explained an additional 34.4% of the variation in spruce height ($R^2_c = 0.37$). Interestingly, moderately browsed spruce were significantly taller than spruce that had not been browsed (Figure 5.3, mean difference ± S.E.: 10.91 ± 3.10 cm, $t_{551.98} = -3.52$, $p = 0.001$). Severely browsed spruce did not vary in height from spruce that had not been browsed. Similarly, browsing history was the only term included in our final model of spruce basal diameter at young sites ($F_{2,543.35} = 13.18$, $p < 0.001$), and explained 5.1% of the variation in basal diameter ($R^2_m = 0.051$). The random effects of plot and plot within fire scar explained an additional 30% of the variation in spruce basal diameter ($R^2_c = 0.35$). Again, basal diameter only significantly differed between moderately browsed spruce and spruce that have not been browsed (Figure 5.3, 2.66 ± 0.52 mm, $t_{548.47} = -5.10$, $p < 0.001$). Browsing intensity was also the only fixed effect to be included in the final model for the spruce height-to-diameter ratio ($F_{2,526.23} = 19.07$, $p < 0.001$), explaining 7.6% of the variation ($R^2_m = 0.076$) and the random effects explained an additional 20% of the variation in spruce height-to-diameter ($R^2_c = 0.28$). For spruce at young sites, the height-to-diameter ratio decreased with browsing intensity as moderately browsed spruce had significantly lower height-to-diameter ratios than spruce that had not been browsed (Figure 5.3, -1.03 ± 0.20 cm mm^{-1}, $t_{516.12} = 5.11$, $p < 0.001$) and severely browsed spruce had significantly reduced height-to-diameters ratios than moderately browsed spruce (-1.44 ± 0.55 cm mm^{-1}, $t_{532.81}$

$= 2.60$, $p = 0.02$). Severely browsed spruce also had significantly different height-to-diameter ratios than spruce that had not been browsed (-2.47 ± 0.56 cm mm^{-1}, $t_{540.97} = 4.43$, $p < 0.001$).

We found a different pattern for the effect of browsing intensity and deciduous dominance for our models on spruce structure at our intermediate sites ($n = 521$ black spruce). For spruce height, our final model included both browsing intensity and deciduous dominance (measured as the proportion of stand basal area made up of deciduous trees), however only deciduous dominance was a significant effect ($F_{1,17.26} = 4.68$, $p = 0.04$). Deciduous dominance negatively related to spruce height at intermediate sites ($\beta = -28.82$, $t_{17.3} = -2.16$, $p < 0.04$) and explained 4.5% of the variation in spruce height ($R^2_m = 0.045$). Plot and plot within fire scar explained an additional 17.5% of the variation in spruce height ($R^2_c = 0.22$). For spruce basal diameter, both browsing history ($F_{2,514.77} = 20.45$, $p < 0.001$) and deciduous dominance ($F_{1,14.30} = 7.78$, $p = 0.01$) were included in the model as significant effects. Deciduous dominance was also negatively related to spruce basal diameter ($\beta = -5.65$, $t_{14.30} = -2.79$, $p = 0.01$), but both moderately (mean difference ± S.E.: 1.69 ± 0.63 cm mm^{-1}, $t_{514.63} = 2.68$, $p < 0.02$) and severely (5.54 ± 0.87 cm mm^{-1}, $t_{510.38} = 6.37$, $p < 0.001$) browsed spruce had greater basal diameters than spruce that had not been browsed (Figure 5.3). Our fixed effects explained 11% of the variation in spruce basal diameters ($R^2_m = 0.11$) and the random effects explained an additional 14% of the variation ($R^2_c = 0.25$). For our model of spruce height-to-diameter ratios at intermediate sites, only browse intensity was included in our final model ($F_{2,515.76} = 24.26$, $p < 0.001$). Similar to the pattern for younger sites, the height-to-diameter ratio for spruce at intermediate sites declined with increasing browse intensity. Moderately browsed (-0.70 ± 0.18 cm mm^{-1}, $t_{517.94} = 3.88$, $p < 0.001$) and severely browsed (-1.74 ± 0.25 cm mm^{-1}, $t_{517.22} = 6.94$, $p < 0.001$) spruce had lower height-to-diameter ratios than spruce that had not been browsed (Figure 5.3). Severely browsed individuals also had lower height-to-diameter ratios than moderately browsed spruce (-1.04 ± 0.22 cm mm^{-1}, $t_{507.48} = 4.58$, $p < 0.001$). 8% of the variation in spruce height-to-diameter ratios was explained by spruce browsing history ($R^2_m = 0.08$) and the random effects of plot and plot within fire scar explained an additional 28% of the variation ($R^2_c = 0.36$).

We found no effect of hare browsing or deciduous dominance on spruce structure in our models for mature sites (n = 182 black spruce) as no model performed better than an intercept-only model. By examining spruce structure within each stand age group, we've identified varying patterns in the way hares alter spruce structure that appear dependent on environmental conditions pertinent to stand age.

Browsing effects at the site level

Our SEM models revealed the most likely pathway in which browsing by hares may influence postfire successional dynamics (Figure 5.4). For our SEM that focused on spruce height, the chi-square test was not significant ($\chi^2_7 = 4.07$, $p = 0.67$) and the comparative fit index was 1.00, thus both indicating that we had constructed a suitable model. The root mean square error of approximation was not significantly different from zero (RMSEA = 0.00, $p = 0.72$). The proportion of deciduous trees ($\beta = 0.52$, $z = 5.73$, $p < 0.001$) and time since fire ($\beta = 0.82$, $z = 6.03$, $p < 0.001$) both positively influenced percent canopy cover ($R^2 = 0.75$). Birch seedling and sapling density also had a positive effect on canopy cover ($\beta = 0.23$, $z = 2.80$, $p = 0.005$), however, there was no significant effect of aspen seedling and sapling density. In turn, canopy cover positively influenced hare browsing intensity ($R^2 = 0.54$, $\beta = 0.71$, $z = 6.7$, $p < 0.001$), but spruce seedling and sapling density had no effect on browsing intensity. Spruce height ($R^2 = 0.71$) was positively affected by canopy cover ($\beta = 0.89$, $z = 4.45$, $p < 0.001$), as well as by time since fire ($\beta = 0.51$, $z = 2.38$, $p = 0.02$), but negatively affected by hare browse intensity ($\beta = -0.51$, $z = -4.01$, $p < 0.001$) and the proportion of stand basal area that was deciduous ($\beta = -0.32$, $z = -2.31$, $p = 0.02$). Birch seedling and sapling density also was negatively related to spruce height ($\beta = -0.22$, $z = -2.06$, $p = 0.04$). The positive, direct benefit of canopy cover to spruce height ($\beta = 0.89$) is largely offset by the effect of increased hare browsing ($\beta = -0.51$) and competition from deciduous trees ($\beta = -0.32$) or seedlings and saplings ($\beta = -0.22$) in these areas.

Substituting the height-to-diameter ratio for absolute height produced a similar fitting model according model diagnostics. Again, the chi-square test was not significant ($\chi^2_7 = 4.68$, $p = 0.58$), and the CFI value (CFI = 1.00) and low RMSEA (0.00) indicated a well-fit model (Figure 5.4). Spruce height-to-diameter ($R^2 = 0.41$) was more positively influenced by percent canopy ($\beta = 1.18$, $z = 4.76$, $p < 0.001$) than height alone, and as well as more negatively influenced by browsing intensity ($\beta = -0.57$, $z = -3.60$, $p < 0.001$). The proportion of stand basal area that was deciduous also negatively affected spruce height-to-diameter ratios ($\beta = -0.36$, $z = -2.09$, $p < 0.04$). Time since fire and deciduous seedlings and sapling densities had no effect on the height-to-diameter ratio.

We related our pathway depicted in the SEM models to burn severity through its effect on seedling and sapling density of hardwoods and black spruce at the young sites. Seedling and sapling density varied across burn severity levels for aspen ($F_{2,17} = 6.86$, $p = 0.001$), but not for birch ($F_{2,17} = 1.24$, $p = 0.31$) or black spruce ($F_{2,15} = 1.12$, $p = 0.35$). Within aspen, only densities between low and high severity burns were significantly different ($t_{17} = 3.70$, $p = 0.005$). Although differences were lacking statistical significance for spruce and birch, all three species show an increase in density with increasing burn severity (Figure 5.5)

Discussion

Snowshoe hares are browsing regenerating black spruce at a high rate (40% seedlings and saplings browsed when averaged across all stands), resulting in reduced height-to-diameter ratios for browsed individuals. Because browsed individuals also have larger basal diameters than unbrowsed spruce, smaller height-to-diameter ratios likely reflects reduced height growth as a result of browsing. This negative effect of browsing by snowshoe hares is strongly influenced by site conditions, particularly canopy cover. The positive influence of deciduous dominance on canopy cover and of canopy cover on hare browsing, implies that snowshoe hare herbivory does interfere with relay succession by suppressing recruiting black spruce under deciduous canopies specifically. Although the response of black spruce to browsing is negative, the magnitude of this effect is less than we expected (low amount of variation in height growth explained by browsing, no changes in density), indicating that black spruce may be resilient to the observed levels of browsing.

The magnitude of the browse effect observed at any time is influenced by the timing of the hare cycle because browsing frequency and intensity track fluctuations in hare abundance (Figure 5.1, Olnes and Kielland 2017). Spruce that recruit during a low in hare abundance have a lower probability of being browsed. On the other hand, if the window for early recruitment following fire aligns with a hare population peak, then hares have the potential to reduce the regeneration of spruce (Sinclair 2003). Interacting with the hare cycle is time-since-last-fire and the stage of postfire succession, because habitat suitability changes over time and only some successional stages provide suitable cover and sufficient forage for hares (Feierabend and Kielland 2014). There is a narrow time window following fire when there is both sufficient cover to attract hares and when spruce are within browsing range, and the capacity of hares to limit spruce regeneration is dependent on the timing of this narrow time window with that of the hare population cycle.

Browsing was minimal in most mature black spruce stands, most likely due to insufficient cover and low availability of suitable forage deterring hares from using these habitats. For example, our hare pellet density data (m^{-2}) suggests that hares prefer denser canopies than typically found at more open mature black spruce sites. Average canopy cover (± S.E.) for mature black spruce stands was 44 ± 8%, whereas plots with higher pellet densities (>10 pellets m^{-2}) tended to have estimates of canopy cover greater than 75% (Appendix 5.1, Figure 5.S3). Snowshoe hares are known to use dense stands of black spruce as refugia (Wolff 1980; Feierabend and Kielland 2014), but such stands seem to be represented by only a small number of spruce-dominant intermediate and mature sites. The only mature site with pellet densities > 10 pellets m^{-2} also had the greatest spruce seedling and sapling density (77,590 spruce ha^{-1}).

For any given black spruce, the probability of being browsed by hares increases with increasing deciduous canopy cover. As spruce grow into the browsing range of hares under these denser canopies, their likelihood of being browsed approaches 1.0 by the time they will escape herbivory at ~200 cm in height (Figure 5.2), demonstrating that taller spruce have a greater likelihood of having been browsed (Olnes et al. *in review*).

The response of black spruce to browsing is consistent with the hypothesis that fast growth resulting in a taller plant reaching above the snow surface increases the risk of being browsed. We interpret this phenomenon as a plant vigor effect (Price 1991), similar to what we've observed for treeline white spruce (Olnes et al. *in review*). Browsed spruce at young and intermediate sites do marginally vary in height from unbrowsed individuals; however, they have significantly greater basal diameters (Figure 5.3). This results in reduced height-to-diameter ratios with increasing browsing. The likely explanation for this is that hare browsing suppresses either older or more vigorous spruce that would otherwise be taller. For example, severely browsed individuals at intermediate sites with the mean basal diameter of 20 mm are ~24% shorter (122 cm) than they would be if not browsed (160 cm), when estimating height using the mean height-to-diameter ratio for unbrowsed (7.8 cm mm^{-1}) and severely browsed (6.0 cm mm^{-1}) individuals. Moderately browsed individuals with a mean basal diameter of 17 mm are ~9% shorter than unbrowsed individuals when calculating height based on the height-to-diameter ratio for unbrowsed individuals (131 cm versus 119 cm). Spruce that are not browsed tend to be shorter because they are still shielded from hares under the snowpack, too young (so less time exposed to hares), or hares may be selecting against slower growing individuals (Olnes et al. *in review*). If so, browsing by hares suppresses the fastest growing individuals following fire, causing slower growing spruce to determine the rate of emergence into the canopy. Although we observed these patterns as significant, browsing intensity as a variable explained very little of the variation in spruce height and the height-to-diameter ratio (< 10%), making it important to note that browsing is likely a minor influence on black spruce growth *per se*.

However, browsing is just beginning to occur within the young sites corresponding to the recent, slow increase in hare densities (Figure 5.1). Many of these sites present an opportunity to observe the true potential for hares to affect postfire succession because they represent good hare habitat and experience increasing hare abundance coinciding with regenerating spruce within the browse range of hares. It is likely that browsing will significantly affect spruce densities over time at some of these younger sites where high densities of deciduous seedlings and saplings favor greater hare abundance (Figure 5.6a). We predict that these sites will show more dramatic effects of hare browsing with time as regenerating spruce will likely encounter multiple hare population peaks.

Similarly, many intermediate-aged sites (n = 10) had significant numbers of standing dead spruce seedlings with prevalent hare browse scars (Figure 5.6b, 100 to 10,000 dead spruce ha^{-1}), suggesting herbivory was a contributing factor to mortality in the past for spruce experiencing multiple hare density peaks (Figure 5.1). Although standing dead spruce made up a significant percentage of total standing spruce (living and dead) for three of these sites (30 – 90% of standing spruce), the remaining sites consisted of more than 90% standing spruce as living. It is unlikely that hares can significantly increase mortality at locations where spruce is recruiting at very high densities, because of predator satiation (Figure 5.6c, Crawley and Long 1995). Interestingly, these dense stands of spruce can later become refugia for snowshoe hare (Wolff 1980; Feierabend and Kielland 2014).

Our SEM models clarify these interactions between tree species composition, canopy cover, hare browsing, and spruce height, and support our assumptions regarding herbivory during postfire succession (Figure 5.4). As we hypothesized, time since fire and the proportion of stand basal area made up of deciduous trees explain most of the variation in canopy cover. Subsequently, canopy cover had a strong effect on spruce height, both directly and indirectly via hare browsing. Spruce may benefit from canopy cover which may reduce desiccation risk (Angell and Kielland 2009; Olnes and Kielland 2016) or cause spruce to primarily allocate resources to primary versus secondary growth as a result of a low light regime in the understory (e.g. Burton 1993). The latter possibility is supported in the SEM model that included the height-to-diameter ratio, as the positive effect of canopy cover was even stronger, implying that canopy cover promotes height growth over radial growth. Further, locations with dense deciduous canopies may be correlated with optimal site conditions for tree growth, and thus the positive correlation in spruce height and deciduous canopy cover may actually be a reflection of site productivity. Where hares are present, browsing offsets the benefits associated with increased canopy cover to spruce growth.

Hares reinforce deciduous dominance brought on by more severe fires. Severe burns are likely to allow more deciduous species to establish than in low-severity burns by removing the organic layer (Johnstone and Chapin 2006). This alters the habitat for hares by leading to denser canopies as the deciduous component grows. Hares favor the denser deciduous canopies for cover and food availability (Krebs et al. 2001). As deciduous stands get denser, slower growing spruce may experience a reduction in growth or density due to increased competition for resources, as suggested by the negative effect of increasing deciduous basal area on spruce height in both our height models and SEM. With sparser spruce on the landscape, any given individual is more likely to be browsed by hares when abundances are high. This is especially true for the oldest or fastest-growing individuals, which are the first to emerge above the snowpack. However, many sites possessed high densities of both deciduous species and black spruce, and hares are less likely to significantly suppress spruce at these locations.

Although we illustrated that hare browsing suppresses black spruce seedlings under deciduous canopies following fire, the effect size was smaller than we anticipated across much of the landscape. This suggests black spruce is resilient to the snowshoe hare filter – delayed but not deterred in its push for the canopy. Continued monitoring may reveal a greater capacity for hares to influence postfire succession, particularly at locations with high densities of recruiting deciduous tree species.

Figures

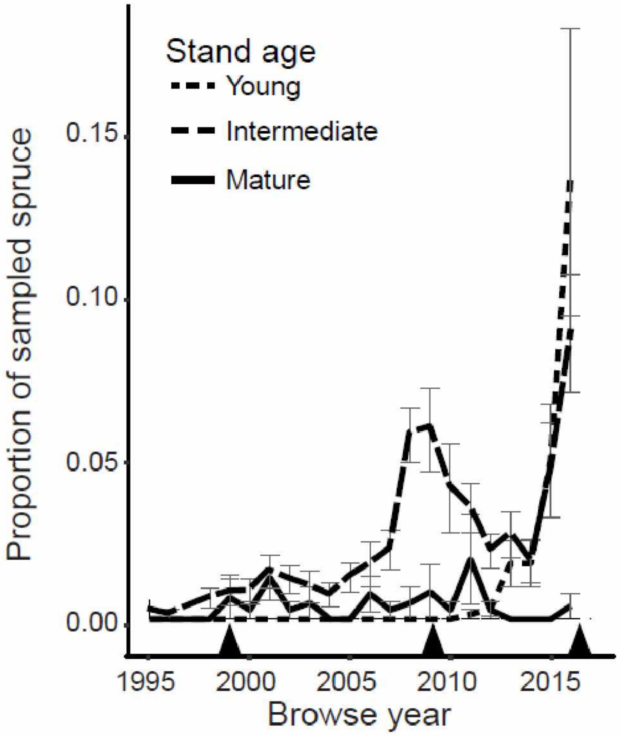

Figure 5.1. The proportion of sampled spruce browsed each year averaged across plots (mean ± S.E.) for each age group of fire scars (young (<15 years), intermediate (45 – 75 years) and mature (> 80 years since fire)). The pattern in browse events demonstrates that most browse events occurred during the hare population peak of 2009 and during the recent two winters (2015-2016, 2016-2017). Periods of peak hare abundance are denoted by arrows along the x-axis (Kielland et al. 2010; Feierabend and Kielland 2015).

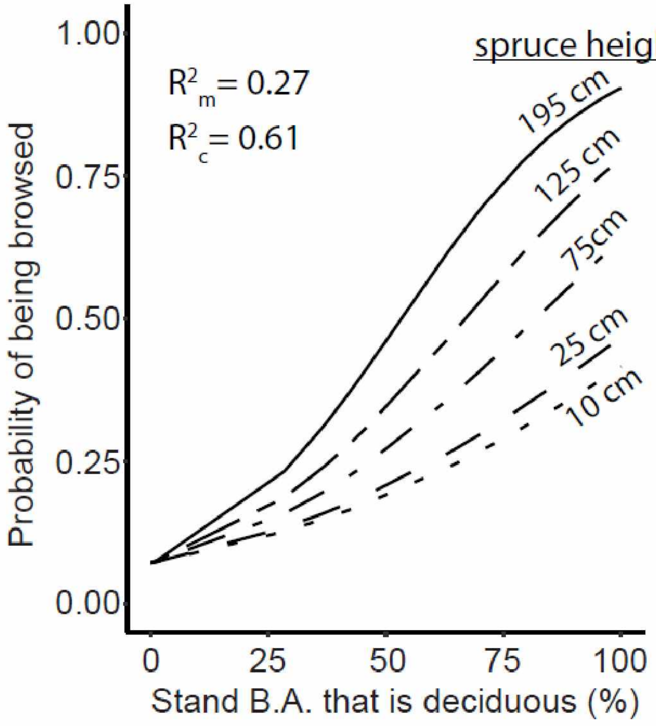

Figure 5.2. The probability of an individual spruce seedling or sapling being browsed increases with increasing deciduous dominance (% stand basal area (B.A.) that is deciduous, z = -4.38, $p < 0.001$) and with increasing spruce height (z = 3.20, p = 0.001). Curves represent how the probability varies for different spruce heights ranging from 10 cm to 195 cm.

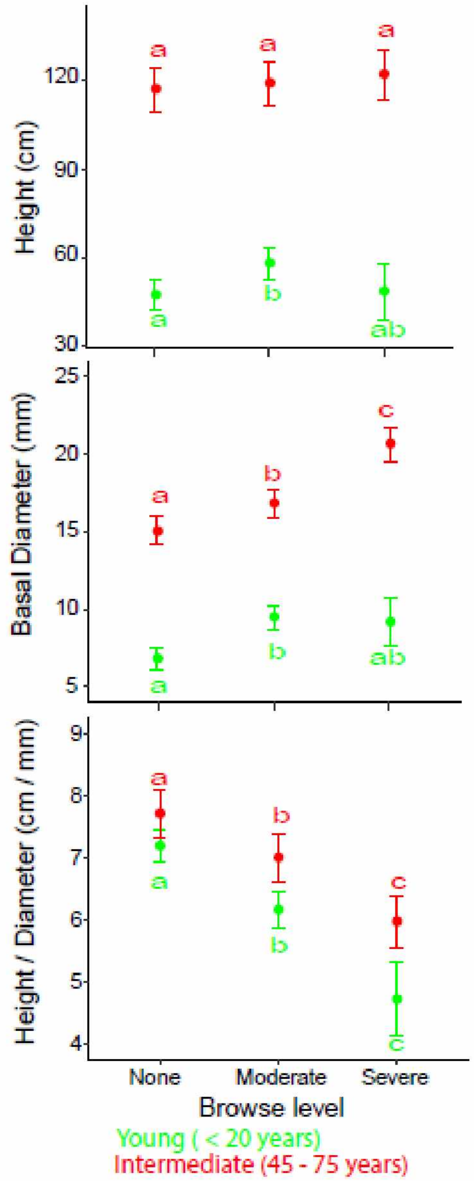

Figure 5.3. Spruce that are browsed vary little in height from unbrowsed spruce at both young (green) and intermediate (red) age sites (a), however, spruce basal diameter tends to increase with increasing browsing intensity (b). Conversely, the height-to-diameter ratio declines with browsing intensity (c). Error bars reflect the standard error around the mean. Letters denote significant differences among browse categories within stand age group.

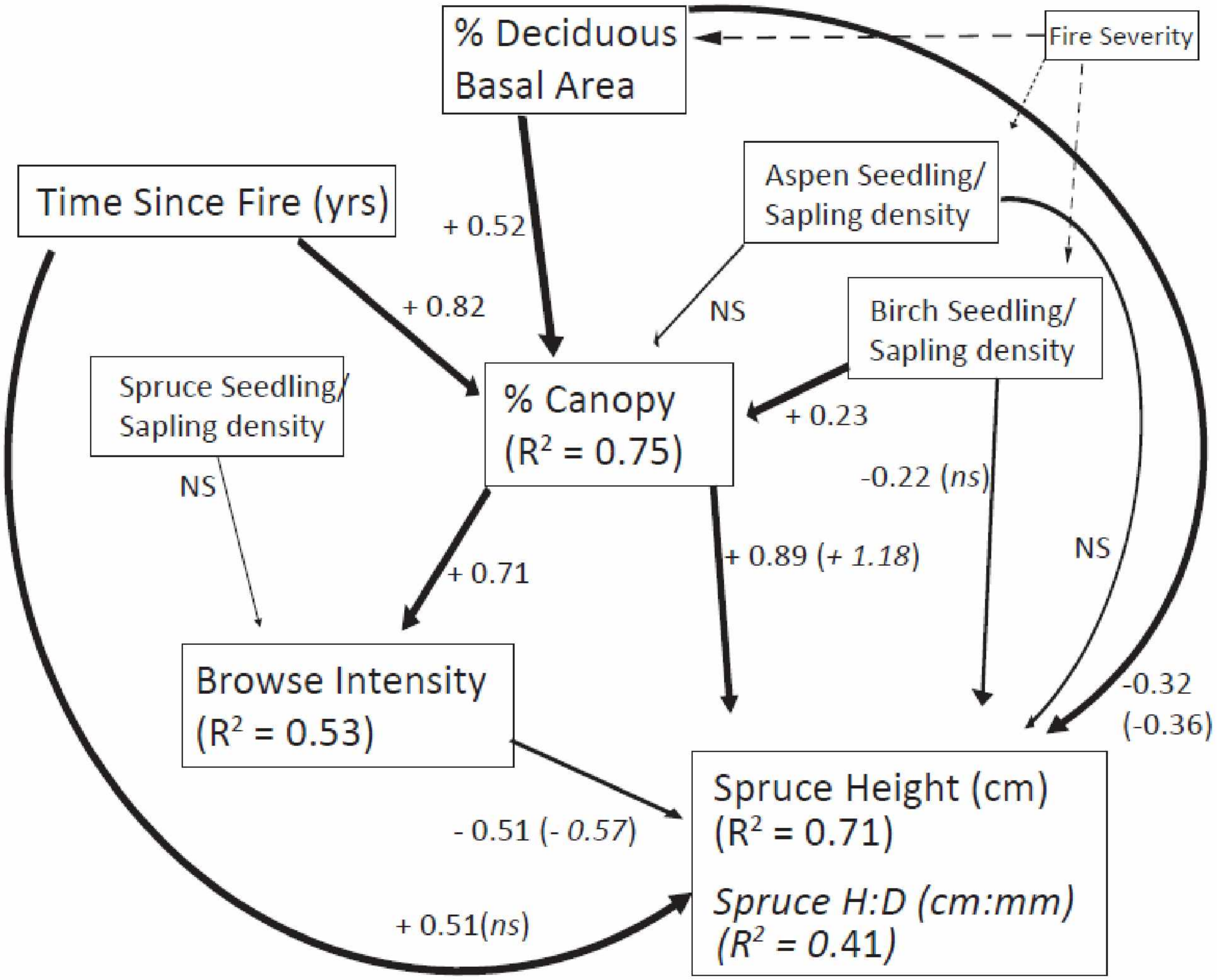

Figure 5.4. SEM model proposing the pathway by which hare browsing can suppress spruce under deciduous canopies. Bold lines reflect significant model parameters. Parameter estimates specific to the height-to-diameter model are italicized. The effect of fire severity on deciduous parameters was not tested in the SEM but is shown to connect changes in fire severity with spruce-hare interactions.

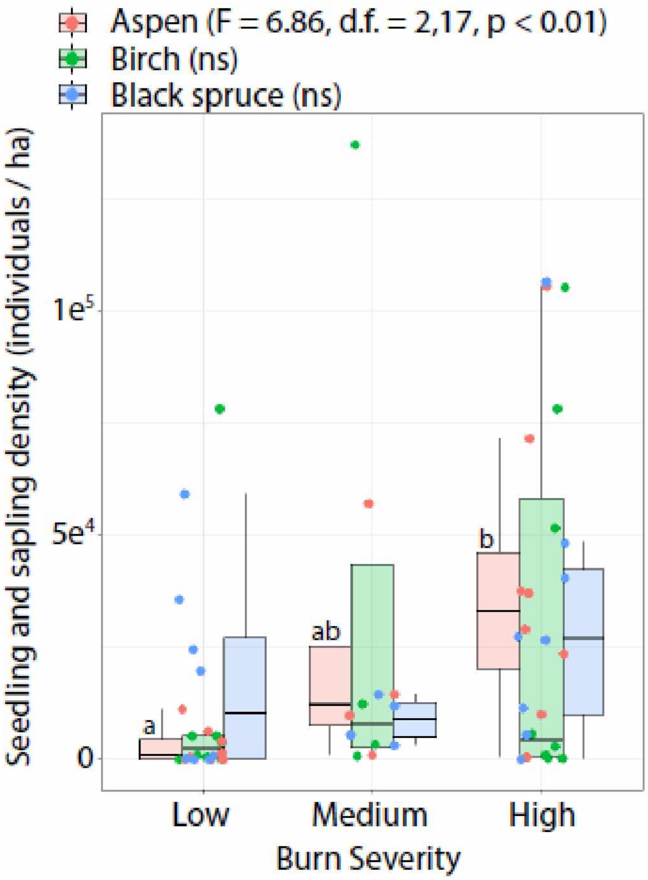

Figure 5.5. Postfire seedling and sapling density for aspen, birch and black spruce across varying levels of burn severity. All sites included in this analysis were young sites (0 – 15 years since burning). Thick lines represent the median value and the rectangles represent the interquartile range. Whiskers are equal to the minimum and maximum values of the sample, and dots reflect outliers in the data. Significant differences across levels of burn severity only occurred for aspen and are denoted by letters.

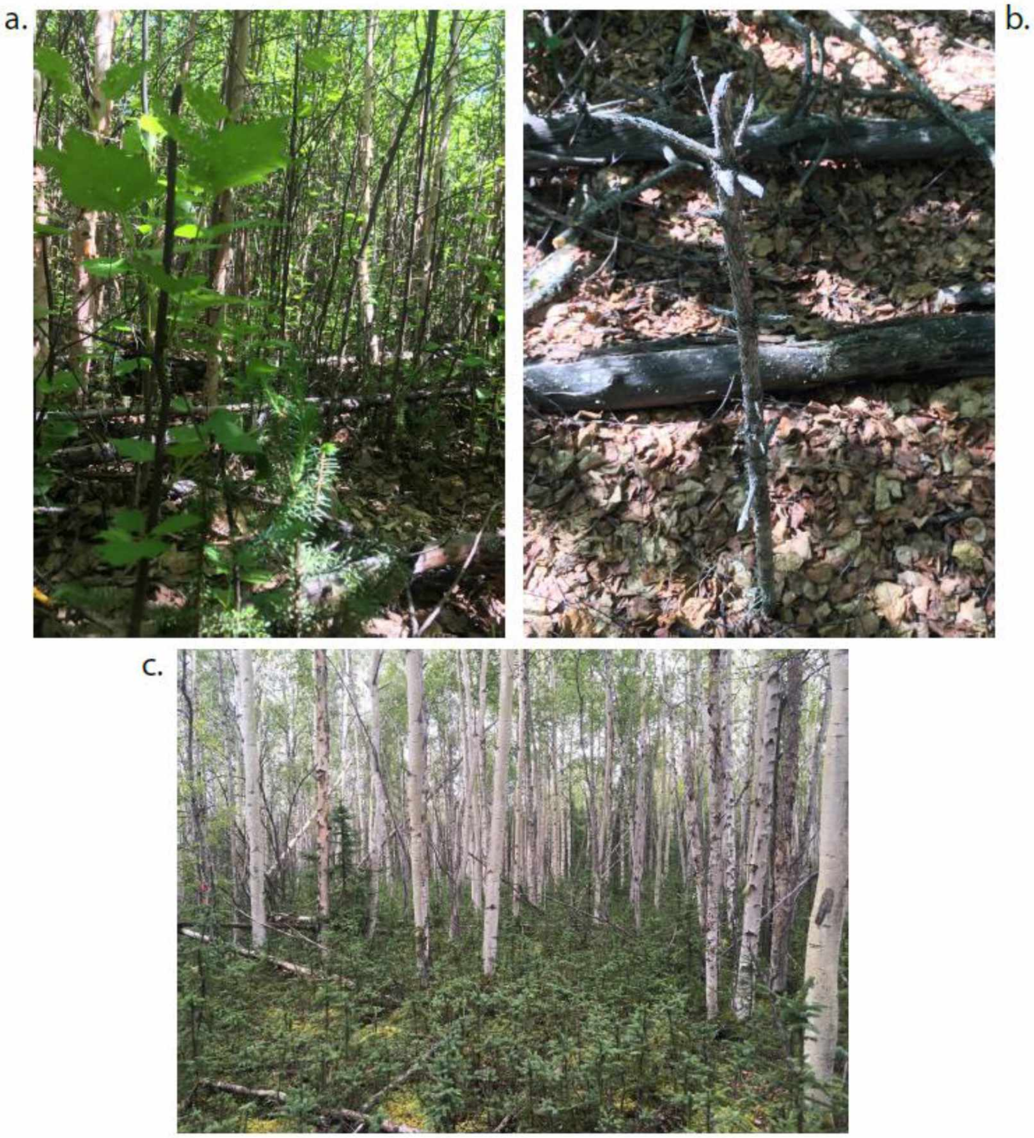

Figure 5.6. In young sites with high levels of deciduous recruitment resulting in suitable cover, hares can suppress spruce that are recruiting at lower densities (a.). These locations may reveal a greater capacity for hares to alter postfire succession in the future, as current spruce regeneration is coinciding with an increase in hare abundance. At many intermediate sites, standing dead spruce with hare browse scars suggests that herbivory has played a role in spruce mortality (b.). However, many fire scars consist of black spruce recruiting at high densities under a fairly open overstory where hares are unlikely to cause significant spruce mortality (c.).

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Appendix 5.1. Supplementary figures.

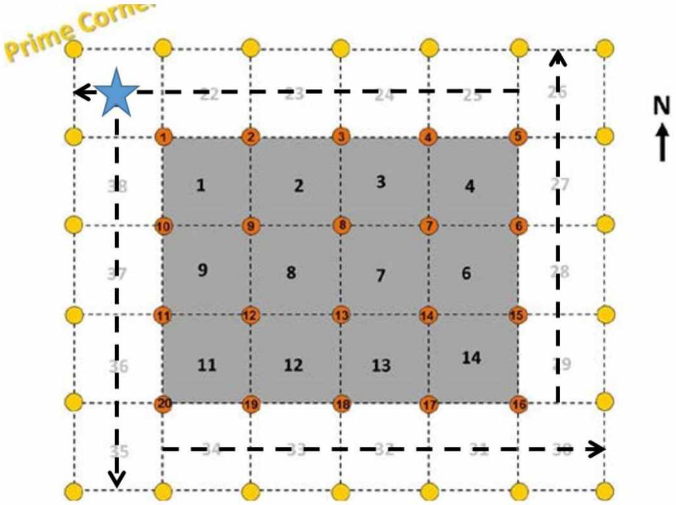

Figure 5.S1. Plot layout for each plot within the Regional Site Network. Plots are 50 m by 60 m and subdivided into thirty, 10 m by 10 m subplots. We sampled along the outer plots (dashed lines) so as to limit our activity within the core center plots.

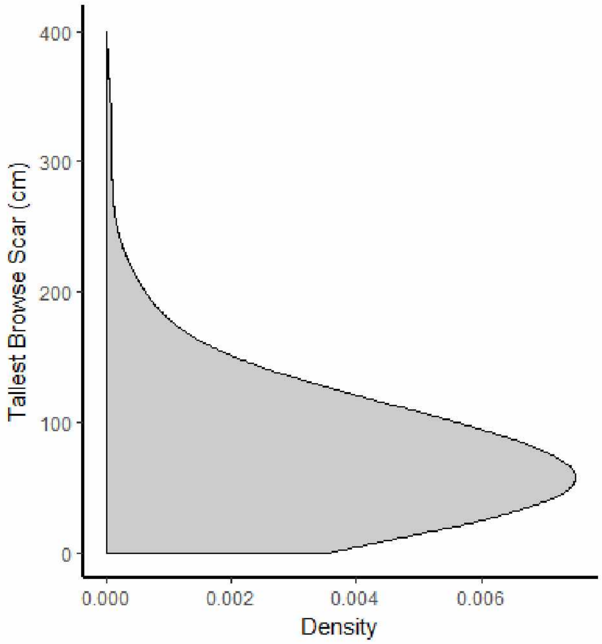

Figure 5.S2. Density plot of tallest browse scar found on all sampled spruce. Density function is a kernel density estimate, which can be interpreted as a smoothed histogram for continuous data (function: geom_density).

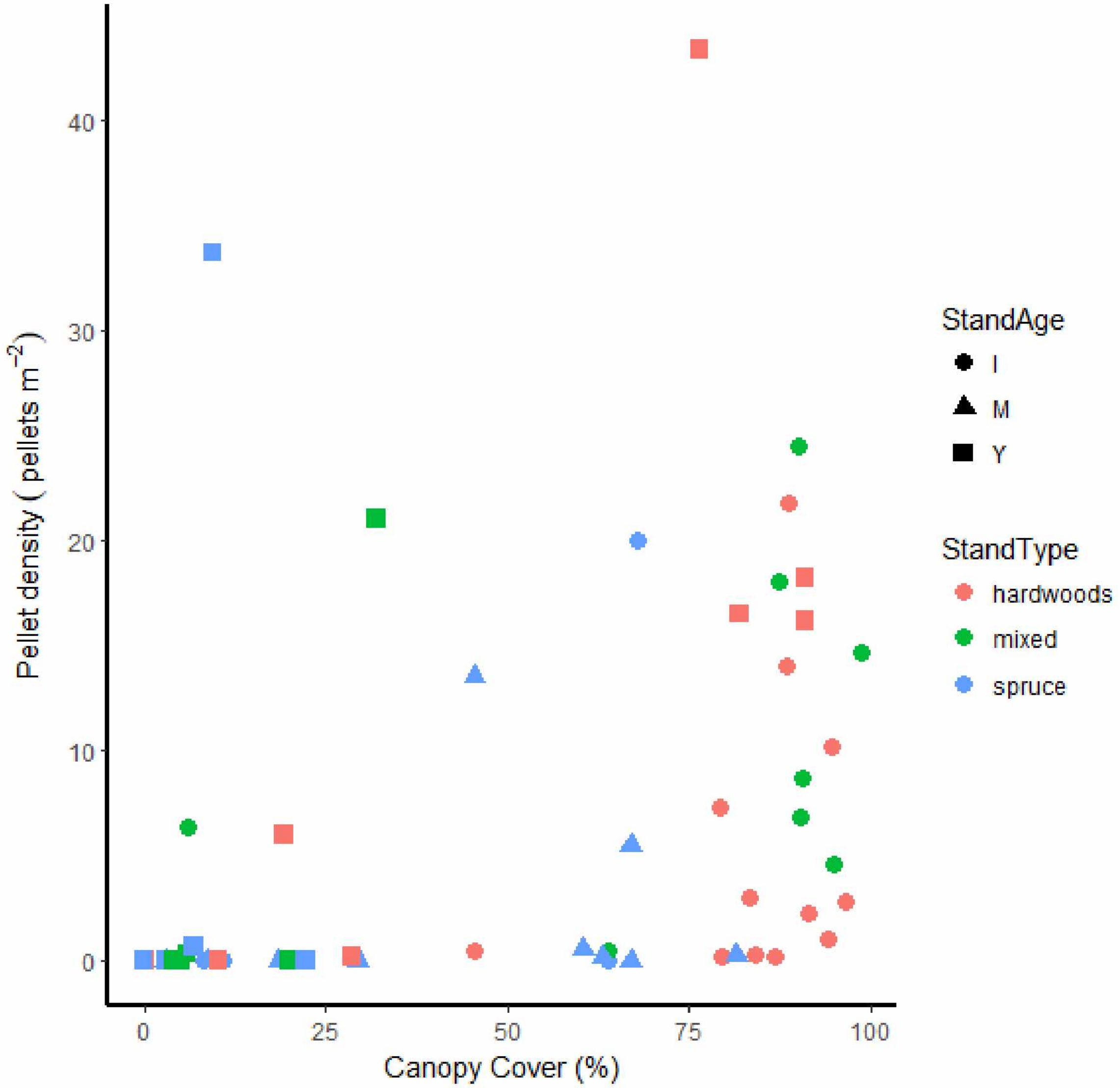

Figure 5.S3. Hare pellet density values were greatest at sites with canopy cover values larger than 75%.

Conclusion

Herbivory of spruce by snowshoe hare – The spatial and temporal patterns of spruce herbivory by snowshoe hares are similar throughout Interior Alaska. Namely, where and when hares are abundant, spruce can be heavily browsed, resulting in suppressed seedling growth and increased seedling mortality. This snowshoe hare filter acts as an additional layer of complexity that further shapes the vegetation mosaic covering the landscapes of Interior Alaska.

Spruce are most vulnerable to browsing when hare abundances are high. During periods of low hare abundance, typically < 5% of spruce are browsed by hares in any given winter. By contrast, during years of peak hare abundance, nearly 50% of all spruce seedlings may have their apical meristem removed at least once by hares. In addition to the timing of the hare cycle, the height of a given spruce individual also influences its vulnerability to browsing over time. Initially, young seedlings are largely protected by the winter snow pack because hares primarily consume spruce seedlings in winter. However, if the snow pack is slow to accumulate, hares may cause substantial mortality of young seedlings (< 10 years old, < 20 cm tall), which are more vulnerable to mortality as a result of browsing. Moreover, spruce seedlings that have grown above the snowpack within the window of a hare peak are also likely to be browsed. Specifically, the earliest seedlings to emerge above the snow are most likely to be browsed severely. These individuals are highly vulnerable because quality browse is limited in the winter, particularly in areas that also provide suitable cover (Wolff 1980; Feierabend and Kielland 2014). By being browsed, this early-emerging cohort is suppressed in the range of hares, and this feeds back to further increase the likelihood of being browsed again (Sinclair 2003). Once spruce reach 2 m (~20 - 50 years old) they are effectively released from the snowshoe hare filter.

These general patterns in spruce-hare interactions vary markedly across the landscape. Specifically, browsing is most intense where dense cover is provided by deciduous shrubs and regenerating trees because hares are most abundant in these areas (> 75% canopy cover in summer, high stem densities in winter). As a result, browsing of spruce by hares reinforces deciduous dominance by suppressing spruce in the understory. Spruce are particularly vulnerable under canopies of alder (*Alnus* sp.) in floodplain habitats (Chapin et al. 2016). The vulnerability of spruce under stands of alder is also prevalent in montane communities near treeline (Olnes et al. 2017). In areas that are too open for hares, spruce is rarely browsed. However, open areas along river floodplains are typically too warm and dry during the growing season for optimal spruce regeneration (Angell and Kielland 2009), whereas seedlings growing in open areas at the treeline are vulnerable to winter desiccation (Stueve et al. 2011). Thus, along floodplains and at treeline, white spruce must contend with herbivory by hares or encounter environmental stressors where hares are absent. Open areas following fire in black spruce stands are often the direct result of low-severity burning leading to poor establishment sites for deciduous species (Johnstone and Chapin 2006), and thus primarily reflect areas where black spruce self-replacement is occurring. Black spruce regenerating at these locations are unlikely to be browsed by hares.

In addition to the spatial and temporal patterns of the snowshoe hare filter to spruce regeneration, variation in spruce seedling recruitment densities also influences the capacity for hares to influence future stand composition and succession. Where spruce has recruited at high densities, hares appear to have little effect on the spruce population, and future thinning will more likely be controlled by intraspecific competition. Once these dense stands of spruce become sufficiently tall, they serve as refugia for snowshoe hare (Wolff 1980; Feierabend and Kielland 2014).

The hare filter and Alaska's changing boreal forest – Alaska's boreal forest is undergoing substantial changes. Shifts in the distribution of productive white spruce (Juday et al. 2015), migrating treeline (Jorgenson et al. 2014; Nicklen et al. 2016), and novel fire regimes (Kelly et al. 2013) are each altering patterns of spruce regeneration on the landscape. Because many regenerating spruce will pass through the snowshoe hare filter as they grow towards the canopy, it is important to consider how this plant-animal interaction contributes to future patterns in the distribution of spruce. Luckily, the extent to which a population of spruce will be affected by the snowshoe hare filter is predictable across time and space. Future ecologists, ecological modelers, and resource managers should remain cognizant of the contributions herbivores make to shaping landscape heterogeneity (Herrero et al. 2016) and strive to incorporate these complex interactions into broad-scale studies (Christie et al. 2015; Conway and Johnstone 2017), landscape models (De Jager et al. 2017), or resource management scenarios (Ranglack et al. 2015).

The future of the snowshoe hare cycle – In Interior Alaska, a pronounced snowshoe hare cycle has influenced vegetation dynamics (Bryant et al. 1994). Although this is most strongly demonstrated for the most preferred browse species like willows (*Salix* spp.) and birch (*Betula* spp.) (Bryant et al. 1983), similar responses have been suggested for white spruce (Sharam and Turkington 2009). In general, regenerating trees and shrubs tend to allocate more resources to chemical defense when growing within the browsing range of hares. This pattern in the response of vegetation highlights the long and tangled evolutionary history of boreal vegetation and snowshoe hares.

Extensive efforts have been made to describe the causal mechanisms of Canada's and Alaska's pronounced hare cycle (Fox 1978; Wolff 1980; Krebs et al. 2014a). Recent work by researchers at Denali National Park demonstrate strong links between weather patterns, primary production, and the amplitude of the snowshoe hare population cycle (Schmidt et al. 2017). By connecting the amplitude of the hare cycle to bottom-up factors (food availability) that stem directly from changes in precipitation, snow depth, and growing season temperatures, a clear link can be drawn between the dynamics of the hare cycle and climate change. Although dampening of the hare cycle has not been observed for Interior Alaska (Krebs et al. 2014b), it is possible that ongoing climate change will alter hare population dynamics over time (Ims et al. 2008). If the hare cycle in Interior Alaska were to disappear, regenerating spruce would likely not encounter the snowshoe hare filter as hare populations would likely be maintained at lower abundances across the landscape.

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