Species-specific responses to herbivore exclusion in post-fire upland forests of Interior Alaska

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# Abstract (265/ 300)

*Questions*:

Environmental changes at high latitudes appear to stimulate large changes in plant communities, such as shifts in tree dominance driven by changing fire severity and frequency. We were interested in whether such changes initiated by disturbance are likely to persist through early succession to generate new patterns of forest dominance. In particular, how strong is the potential for activities of mammal herbivores to alter the patterns of tree dominance initiated by changing fire?

*Location*:

Near Fairbanks, Alaska, USA.

*Methods*:

We set up paired exclosures and control plots to exclude moose (*Acles alces)* and snowshoe hare (*Lepus americanus*) at five sites in early postfire stands across a gradient of fire severity. Within each plot, we tagged 20 individuals of black spruce (*Picea mariana)*, trembling aspen (*Populus tremuloides)*, and Alaskan paper birch (*Betula neoalaskana*) to monitor survival, occurrence of browsing, and growth (height, basal, and crown) over a four-year period. We used linear mixed effect models to determine the proportional change in growth between treatments, using site as the random effect.

*Results*:

We found species-specific responses to mammalian herbivore exclusion after four years. Specifically, birch grew taller inside exclosures and black spruce grew taller and increased more in basal diameter outside exclosures. We found no response of aspen to the exclosure treatment. Survival was high for all three species. We found that relative height structure of tree species best predicted growth responses to herbivore exclusion, not palatability to herbivores.

*Conclusions*:

Although we saw species-specific responses to herbivore exclusion, the impact of mammalian herbivores in Alaskan boreal forests is unlikely to drastically shift the mature canopy composition.

**Key words**: Boreal forest, Alaskan paper birch, black spruce, moose browsing, tree growth, snowshoe hare, forest structure, forest community, disturbance

# 1.0 Introduction

Fire is the dominant landscape-scale disturbance in the boreal forest. In recent decades, fires in boreal Alaska and Canada have increased in severity, size and frequency (Kasischke and Turetsky 2006, Balshi et al. 2009). More severe and frequent fires increase the loss of above and belowground organic material (Keeley 2009), exposing mineral soil that is a more suitable seedbed for recruitment of small-seeded, broadleaf tree species (Johnstone et al. 2010). This loss in suitable seedbed as well as the consumption of seedbank in fire can cause black spruce (*Picea mariana*) forests to shift to dominance by broadleaf species such as trembling aspen (*Populus tremuloides*) and Alaskan paper birch (*Betula neoalaskana*) following frequent or severe fire(Johnstone et al. 2010, Hayes and Buma 2021). Landscape modeling predicts transitions from coniferous to broadleaf stands in early post-fire succession will increase the dominance of mature broadleaf stands across the Alaskan boreal forest (Mann et al. 2012, ). Mammalian herbivores in the boreal browse deciduous species and thus could act as ecosystem engineers, altering forest composition and successional patterns (Côté et al. 2004), subsequently altering the successional outcomes of post-fire stands. Thus, understanding the impacts of mammalian herbivores on early successional, broadleaf forests is crucial for predicting the long-term consequences of changes in fire and climate for Alaskan boreal forests.

Herbivory can be a major driver of forest structure and composition during early and mid-succession following disturbance (Côté et al. 2004, Post and Pedersen 2008). Mammalian browsing on leaves, stems, and twigs have direct negative effects on tree growth that can lead to plant mortality (Côté et al. 2004, Wisdom et al. 2006). Stand structure is most vulnerable to re-organization when herbivore pressure is high (Tremblay et al. 2007, Gosse et al. 2011) through reductions of canopy trees (Chouinard and Filion 2001) or decreases in tree biomass (McLaren 1996). Mammalian herbivores are often selective browsers; several factors determine their diet choice include palatability and nutritive value (Allman et al. 2019, Mathisen et al. 2017), as well as the density and frequency of occurrence of potential diet species (Wolff 1978, Bryant and Kuropat 1980). Species with higher relative growth rates and high palatability to herbivores often dominate early succession (Bryant and Kuropat 1980), which increases the potential for mammal herbivory to shift forest composition towards slower-growing, less palatable species (i.e., black spruce).

Moose (*Alces alces*) and snowshoe hare (*Lepus americanus*) are dominant vertebrate herbivores in boreal forests (Thompson et al. 1992, Olnes and Kielland 2016, Conway and Johnstone 2017). Moose and hare have overlapping diets with preference for broadleaf trees and willows (*Salix* spp.) (Bryant and Kuropat 1980, Seaton et al. 2011). Hares also feed on spruce year-round, with almost 40% of their winter diet consisting of spruce needles (Wolff 1978, Olnes and Hielland 2017). On floodplains of interior Alaska, moose and hare have been found to alter species-specific patterns of tree recruitment and growth significantly (Kielland and Bryant 1998, Kielland et al. 2006, Chapin et al. 2016). However, the influence of mammalian herbivores in upland forests could be different than on floodplains due to differences in successional dynamics, available forage, disturbance, and habitat use, particularly in the context of changing fire regimes.

Fire influences habitat use and selection by mammals by creating heterogeneity in forest composition and structure at both small and large spatial scales. In interior Alaska, recently burned (11-30 years postfire) stands are associated with high moose densities of (Maier et al. 2005). Within a burned area, a mosaic of variable fire severity can increase the distribution and longevity of available moose habitat due to fire effects on species recruitment, composition and growth rates (Kielland and Brown 2015, Conway and Johnstone 2017). Adequate understory cover provides shelter from predators, a key element of habitat quality of snowshoe hares (Carreker 1985). Thus, dense black spruce forests in interior Alaska are associated with high densities and survival of snowshoe hares (Feierabend and Kielland 2015). Differences in forest structure and community due to local contexts of fire severity, prefire cover and topography may influence how the dominant herbivores in Alaskan upland forests drive successional patterns in early forest communities.

Our objective was to test the potential for mammalian herbivory to alter growth and survival of alternative tree species in early succession, thereby shaping patterns of future canopy composition. We evaluated growth responses of three dominant tree species across four years of protection from moose and hare in five paired exclosure and control plots. We established plots across a range of early post-fire vegetation stands that varied in composition and density. Based on palatability, we expected broadleaf species (aspen and birch) to benefit from the exclusion of herbivores (particularly moose) and undergo greater relative growth outside of exclosures. We also expected all individuals to experience a positive short-term response to mammalian exclusion since saplings can demonstrate growth releases shortly after herbivore damage ceases (Chouinard and Filion 2001, Motta 2003, Vila et al. 2003). Finally, we hypothesized that black spruce growth would be lower inside the exclosures compared to control plots, due to increased competition with broadleaf species no longer subject to natural herbivory by moose or hare. This research provides key information on the responses of broadleaf species when safe from mammalian browsing, the indirect effects to conifer-broadleaf species competition and contributes to our understanding of how large herbivores may drive successional patterns and change in Alaskan upland boreal forests.

# 2.0 Methods

## 2.1 Study area

Interior Alaska is characterized by a mosaic of boreal forest types, ranging from deciduous hardwood to conifer-dominated stands, that support populations of dominant herbivores such as moose and hare. The region is bounded by the Brooks Range to the north and the Alaska Range to the south. Mean-annual temperatures at the Fairbanks International Airport, in the center of the region, average -3.1 °C (1917-2000) (Hinzman et al. 2006). Precipitation is generally low and decreases from west to east, with a 50-year average for Fairbanks of 287 mm (Hinzman et al. 2006). Common tree species in interior Alaska are black spruce, white spruce (*Picea glauca* (Moench) Voss), trembling aspen, and Alaskan paper birch. Black spruce forests have dominated interior Alaska for ~5000 years with an approximate fire cycle of ~100 years (Yarie 1981, Lloyd et al. 2006). However, the once stable state of black spruce forests might be shifting, with increases in early dominance of broadleaf species after severe fires (Johnstone et al. 2010).

We conducted this research approximately 50 km northeast of Fairbanks, Alaska within the Carbiou-Poker Creek Research Watershed (CPCRW) in stands that burned in the Boundary Fire in 2004. Early regeneration was influenced by fire severity, from severely burned areas dominated by deciduous species to lightly burned areas dominated by black spruce regeneration (Johnstone et al. 2010). Moose densities have increased in interior Alaska since the 1990s, concurrent with fires creating suitable habitat (DuBois 2010). Local moose density in our study area (Game Management Unit 20A) peaked in 2009 with 0.85 moose/km2 and has since decreased to 0.58 moose/km2 in 2013 (Alaska Department of Fish and Game 2014). The snowshoe hare cycle last peaked in interior Alaska between 2008 and 2010, and roadside counts in 2016 show a recent increase in snowshoe hare populations near Fairbanks during the period of this study (Merizon and Carroll 2016).

## 2.2 Experimental design

Long-term sites along the Steese Highway, which passes through CPCRW into the White Mountains, were established in 2005 to monitor patterns of tree establishment and vegetation succession in response to widespread fire in 2004 (Johnstone et al. 2010, Hollingsworth et al. 2013). In 2013, we established five pairs of plots near a subset of the long-term sites, selecting based on accessibility and variety of deciduous canopy dominance. All sites were located within ~3 kilometers of each other. For reference, we used the same site nomenclature of the initial long-term site established through the Joint Fire Science Program and Bonanza Creek Long-Term Ecological Research Program (Johnstone and Hollingsworth, 2013). At each site, we established two plots approximately ten meters apart that measured 12.19 x 12.19 meters and were visually similar in vegetation composition and density. A one-meter wide buffer was established around the inside edge of each plot where no measurements were taken. One plot was assigned the treatment (exclusion of large herbivores with a fenced exclosure) and the other a paired control (natural herbivory). Each exclosure was 1.82 m tall and constructed of chain-linked fence panels that prevented access by moose and hare throughout the year (Fig. 1).

We measured density of potential canopy tree species (trembling aspen, Alaskan paper birch, and black spruce) as well as willows (*Salix* species) in 2013 in each exclosure and control plot. Density was averaged between the two transects for each plot. In each plot (excluding site BF84), we established two randomly placed parallel belt transects (10 x 1 m) transects spanning the length of the plot. The three closest individuals (one of each species) were then tagged at each one-meter mark along the transect. Due to low density of saplings in BF84, we established four transects in each plot; saplings were selected at every two-meter mark. We measured height, basal diameter, DBH (when present), and the presence/absence of any historical herbivore damage by moose or hare (2005 to winter 2013) for each sapling.

In early June 2014, 2015 and 2017, we recorded any evidence (number of stems browsed) of herbivory on tagged individuals during the preceding winter.

We installed two Thermochron ibuttons (Maxim Integrated Products, San Jose, CA, USA) ~10 cm below the organic layer surface in each plot and recorded soil temperature for one full year beginning in August 2014. In mid-June 2015, we dug three soil pits in each plot and measured organic layer depth, soil pH, and soil moisture. *In situ* organic layer depth (including layers of dead moss and fibric and humic organic material) and soil pH (of mineral soil) were measured once per pit. Soil pH was measured using a pH meter (Hanna Instruments) on a 1:1 dilution with de-ionized water (Roberston et al. 1999). Two soil moisture measurements were taken and averaged using a hand-held moisture probe (Hydro-Sense, Campbell Scientific, Edmonton, AB, Canada) inserted at a 45° angle into the upper 10 cm of mineral soil at each pit. In August of 2014, 2015, and 2017, we measured height, basal diameter, crown width (widest part of the crown and perpendicular to that) and crown depth of all saplings. The average of both crown width measurements was used for analyses. The survival of each individual (live or dead) was recorded; for dead individuals, we noted any evidence of the cause of mortality (e.g., snowshoe hare browsing, broken apical meristem).



Figure 1. Photographs of two exclosures, a lowland tussock area (site BF84, top) and an upslope area with high density and growth of Alaskan paper birch (site BF86, bottom).

## 2.3 Statistical analyses

All analyses were performed using R version 3.5.1 (R Core Team 2018). We used linear mixed effect models in the ‘nlme’ package in R (Pinheiro et al. 2016) to determine the effect of exclosures on growth measurements of all three species. All growth response models included fixed effects of treatment (i.e., exclosure), with site as the random term. We ran models for height, basal diameter, crown width, and crown depth. These growth measurements were transformed to represent the proportional change from either 2013 to 2017 (height and basal diameter) or 2014 to 2017 (crown width and depth). Proportional change was used to account for differences in initial sapling size and, as an example for height, was calculated as: (2017 height – 2013 height) / 2013 height \* 100. Standard error (SE) measurements included in the text (sections 3.2 and 3.4) are at the site level (n = 5).

# 3.0 Results

## 3.1 Site characteristics

The five sites captured a range in post-fire environmental characteristics within the 2004 Boundary Fire (Table 1). Organic layer depth was thinnest at BF76, a south-facing site that also had the tallest trees. The thickest organic layer and coldest summer soil temperatures were at BF84, a moist, flat area in a toe-slope position dominated by tussocks that burned at a low severity. Although sample sizes precluded statistical tests, soil characteristics were similar between paired control and exclosure plots (Table 1) with the exception of lower soil moisture measured in the exclosure in BF76; these apparent differences are confounded with low replication due to hitting near-surface rocks.

## 3.2 Pre-treatment sapling height and density

Alaskan paper birch was consistently the tallest species at all five sites, with an average height of 124.1 ± 4.2 cm (± SE); at one site birch was approaching 200 cm in average height (Table A1). Trembling aspen was on average 61.2 ± 3 cm tall, while black spruce was the shortest (26.5 ± 1 cm (mean ± SE)). Compared to black spruce, density of broadleaf species was higher and more variable across sites. However, black spruce had the highest density (~6 individuals/m2) at one site (BF84), with over three times greater densities than both broadleaf species (Table A2); density of birch and aspen was similar. Over half of all the tagged aspen were below 50 cm and thus likely protected from moose damage by snow in winter. Average density of all *Salix* species was half that of both broadleaf species (4.5 /m2 ± 1.5) and individuals were mostly single-stemmed and short (~50 cm) (personal observation).

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| Table 1. Environmental characteristics (mean ± SE) of each plot in 2015. | | | | | |
| Site | Plot | pH | Organic layer  depth (cm) | Moisture+ | Summer soil temperature (°C)Ψ |
| BF72 | Control | 3.7 ± 0.1 | 6.5 ± 0.8 | 29.91 | 6.7 |
|  | Exclosure | 3.2 ± 0.1 | 9.0 ± 3.0 | 29.61 | 7.2 |
| BF76 | Control | 3.5 ± 0.2 | 2.8 ± 0.4 | 14.72 | 6.2 |
|  | Exclosure | 3.2 ± 0.0 | 5.0 ± 1.3 | 3.03 | 7.3 |
| BF77 | Control | 3.7 ± 0.1 | 9.0 ± 0.8 | 45.91 | 7.8 |
|  | Exclosure | 3.7 ± 0.1 | 8.7 ± 0.4 | 40.71 | 7.4 |
| BF84 | Control | 3.9 ± 0.2 | 12.8 ± 4.2 | 47.11 | 4.0 |
|  | Exclosure | 4.0 ± 0.1 | 16.8 ± 1.0 | 47.11 | 4.8 |
| BF86 | Control | 4.1 ± 0.1 | 5.8 ± 1.4 | 25.21 | 6.8 |
|  | Exclosure | 4.3 ± 0.1 | 8.5 ± 1.2 | 25.81 | 7.4 |
| Notes:  + Sample size for moisture varied from n = 3 (denoted by 1), n = 2 (denoted by 2), n = 1 (denoted by 3) due to surrounding rocks in soil pits.  Ψ Summer soil temperatures are the average of growing season temperatures (May – August). | | | | | |

## 3.3 Browsing on, and survival of, saplings

Birch saplings experienced the highest occurrences of pre-treatment browsing compared to aspen and black spruce. Before exclosures were set-up, approximately double the number of birch saplings were browsed compared to aspen (Fig. 2). Establishment of the fenced plots eliminated signs of new browsing inside exclosures. Browsing on spruce was low, with only two individuals damaged prior pre-treatment and single individuals browsed in control plots in 2015 and 2017; all browsing on spruce was from snowshoe hares. On average, approximately 5% of aspen in control plots were browsed in the winters of 2014 and 2015 and 10% in 2017. Whereas over 30% of birch saplings in control plots were browsed in the winters of 2014 and 2017; only ~10% were browsed during the 2015 winter (Fig. 2). The majority (n = 237; 95%) of winter browsing was from moose.



Figure 2. Average number of trembling aspen (top) and Alaskan paper birch (bottom) (n = 20) that experienced winter browsing (by either moose or snowshoe hare) in either control (grey, n = 5) or exclosure plots (white, n = 5). Bars represent the mean ± SE. Pre-treatment includes all evidence of browsing (2005 – 2013) before exclosures were erected. No evidence of browsing was observed inside the exclosures in 2014, 2015 or 2017.

Survivorship of tagged saplings was high for all three species (Fig. 3). Fewer aspen saplings survived in the control plots compared to exclosures (Fig. 3); however, aspen mortality did occur in both control (n = 4) and exclosure (n = 6) plots. Of the aspen saplings that died, two individuals in control plots had been browsed the previous winter by a snowshoe hare. We also encountered aspen saplings that were recorded as dead in one year, but had resprouted the next year. One birch sapling died within an exclosure plot in between our 2015 and 2017 sampling periods (Fig. 3). A total of three birch in control plots died; two of the dead individuals had been browsed the past winter by a snowshoe hare.



Figure 3. Cumulative survival (%) of trembling aspen (top), Alaskan paper birch (middle), and black spruce (bottom) in control (dashed line) and exclosure (solid line) plots. Error bars represent the minimum and maximum of cumulative survival across sites (n = 5).

## 3.4 Effect of mammalian exclusion

Four years after set-up, exclosures had species-specific effects on proportional sapling growth (i.e., proportional change in height, basal diameter and crown size). We found no significant effect of exclosures on aspen growth (Table 2). Birch saplings were significantly taller inside exclosures, where height increased by 49.6% compared to 29.0% in control plots (Fig. 4). On average, birch saplings were 227.8 ± 41.1 cm tall inside exclosures in 2017, which reflected an increase in height of 107.1 ± 29.1 cm compared to 84.1 ± 27.4 cm in control plots over the four year sampling period. In contrast, black spruce saplings grewgrew more in the control plots than the exclosures (Fig. 4). Black spruce height increased by 50.0% in control plots compared to 40.1% in the exclosures, and spruce stems grew 48.9% thicker in controls while growing only 39.4% thicker inside the exclosures. None of the tree species showed significant changes in crown size in response to the exclosure treatment (Table 2).height, basal diameter, and crown size s

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| Table 2. Parameter estimates from linear mixed effect modelsΨ assessing the effect of the exclosure treatment on proportional height, basal diameter, and crown size responsesϕ of trembling aspen, Alaskan paper birch, and black spruce saplings. | | | | | |
|  | Response variable | Value | Std. Error | t-value | *p*-value |
| Aspen |  |  |  |  |  |
|  | Height | 7.162 | 5.651 | 1.267 | 0.207 |
|  | Basal diameter | −6.618 | 4.181 | −1.583 | 0.115 |
|  | Crown depth | 8.752 | 14.209 | 0.616 | 0.539 |
|  | Crown width | 14.043 | 9.829 | 1.429 | 0.155 |
| Birch |  |  |  |  |  |
|  | Height | 7.967 | 2.473 | 3.222 | **0.002** |
|  | Basal diameter | −2.350 | 3.305 | −0.711 | 0.478 |
|  | Crown depth | 2.577 | 4.327 | 0.595 | 0.552 |
|  | Crown width | −1.254 | 4.769 | −0.263 | 0.793 |
| Spruce |  |  |  |  |  |
|  | Height | −8.630 | 1.845 | −4.677 | **<0.001** |
|  | Basal diameter | −11.500 | 2.978 | −3.861 | **<0.001** |
|  | Crown depth | 0.351 | 2.621 | 0.134 | 0.894 |
|  | Crown width | −0.801 | 3.006 | −0.266 | 0.790 |
| Note: Ψ Linear mixed effect models were run using the ‘nlme’ package in R and the following code: lme(Response Variable ~ Treatment, random = ~1|Site)  ϕ Proportional growth was calculated as: (2017 growth – 2013 growth)/2013 growth \* 100 for height and basal diameter, and (2017 growth – 2014 growth)/2014 growth \* 100 for crown measurements. | | | | | |



Figure 4. Proportional change in height (top) and basal diameter (bottom) after 4 years inside control (grey) and exclosure (white) plots for all three tree species. Bars represent mean ± SE. Significance is noted by \* = *p* < 0.05, \*\* = *p* < 0.01, \*\*\* = *p* < 0.001 and based on results from linear mixed effect models.

# 4.0 Discussion

Alaskan paper birch responded quickly to herbivore exclusion with increased height four years after the exclosures were established. Moose browse was the dominant form of herbivory at all six sites with the majority (95%) of browsing occurring on deciduous saplings. Trembling aspen and Alaskan paper birch are both expected to be more palatable to moose than black spruce (Bryant and Kuropat 1980); however, only birch saplings benefited from being inside exclosures. Thus, palatability to herbivores was not the best predictor of responses to the exclosure treatment. Instead, the relative position of each tree species within the canopy (Simončič et al. 2018) best predicted growth responses to herbivore exclusion. Birch and aspen were found in similar densities; however, birch was the tallest species and within the optimal height range of moose browsing contrary to aspen that were short and likely protected below snow. Thus, the order of positive, neutral and negative responses corresponds to species canopy dominance and browsing opportunity in our study area: birch, aspen, and black spruce, respectively.

In forests where moose is the predominant herbivore, the rate of succession has been both hastened or reversed by moose browsing (Davidson 1993, Persson et al. 2005, McLaren et al. 2009). Our study supports observational work (Conway and Johnstone 2017) that severe moose browsing can slow the rate of deciduous height growth in Alaskan post-fire forests, however the successional trajectories remained unaltered. The results presented here suggest opposing aboveground growth patterns of Alaskan paper birch versus black spruce that were mediated by preferential herbivory on the dominant species. However, whole plant growth for black spruce could have been maintained within the exclosures through allocation of resources to belowground components. For example, at a fine-scale, belowground and aboveground fine-root community structure can respond differently to varying grazing intensities (Onatibia et al. 2017). Inside exclosures, birch released from herbivory may be acquiring more resources which decreases resource availability for understory conifers. For example, taller broadleaf trees in 11 year old boreal stands have negative effects on neighboring conifers (Simard and Sachs 2004). Furthermore, we detected lower rates of black spruce height and basal diameter growth, but no differences in crown width inside and outside exclosures. White spruce has been reported to decrease in height, but not lateral growth (i.e., crown width) under increasing levels of shade (Sims et al. 1990). We suspect that growth of trembling aspen saplings was unaffected by the exclosure treatment as these light-intolerant saplings were already light suppressed before our experiment began. Thus even if saplings experienced a release in the control plots due to decreased birch growth, trembling aspen saplings could have slow (>5 years) growth recovery after being released from suppression (Wright et al. 2000). Minimal height growth, when compared to birch and spruce (Fig. 4), further supports our hypothesis of aspen sapling growth experiencing suppression.

In order to predict when birch will reach three meters in height, i.e. the safe height from moose browsing (Lord 2008, Seaton et al. 2011), we used the average 2017 height (227 and 213 cm for exclosure and control, respectively) and applied an average proportional annual growth rate of 10% for exclosures and 7 % for control plots. Birch saplings inside exclosures are projected to reach three meters in height in three years, or a total of seven years after being protected from herbivores. Birch saplings subjected to natural herbivory at the level we observed would only take an additional three years to reach a safe height from moose. Presumably, once birch in control plots reach three meters, individuals would have comparable growth rates to individuals inside exclosures (Conway and Johnstone 2017). Thus, this level of herbivory does not seem significant enough to affect canopy dominance when sites reach maturity in 75 years. ; this is until black spruce is considered. Although birch is likely to dominate the canopy of post-fire sites, moose herbivory even at the level we observed could enable black spruce to reach a co-dominant status more quickly. in a mixed broadleaf-conifer canopy. However, snowshoe hare browsing targeting black spruce may influence the potential for growth and co-dominance of black spruce (Olnes and Kielland 2016). We expect to have a better understanding of the role of snowshoe hares in this system in the next 5-10 years as black spruce in both the control and exclosure plots were ~50 cm tall in 2017 and are now more vulnerable to browsing by hares as they are likely emerging above the winter snowpack (Olnes et al. 2018).

Long-term studies of forest growth and succession are crucial as short-term and long-term results can be contradictory (Chapin et al. 2016). The duration of our study did not allow for observations of larger ecosystem processes that can be altered with the presence of large herbivores due to direct and indirect effects (Persson et al. 2000). Selective browsing often results in a shift in the canopy composition towards increased dominance of less palatable species (McInnes et al. 1992, Kielland and Bryant 1998). We found lower survivorship rates in aspen and birch compared to spruce; however, survivorship was still high for all three species. With a longer duration (10-20 years) of mammalian exclusion, indirect impacts of herbivores on ecosystem processes through trampling, defecation and urination could become more apparent (McKendrick et al. 1980, Persson et al. 2000, Rooney and Waller 2003). For example, moose can depress soil N availability through trampling (Pastor et al. 1998), whereas the contribution of nutrients from feces and urine to plants and microbes could cause significant fertilization effects at small scales (Hobbs 1996). We did observe evidence of moose trampling in control plots as many birch saplings had broken branches. Moose and hare herbivory could also lead to an increase in the density of alder, an unpalatable, N2-fixing shrub present at low density at our sites (personal observation), as was found on Alaskan floodplains (Kielland et al. 2006). Moose presence could slow the rate of birch growth more than estimated; however, the density of birch saplings is high enough that birch will still likely dominate the canopy in 10-20 years.

Alaskan paper birch, trembling aspen, and black spruce, the three tree species that have the potential to dominate the forest canopy, responded to exclosures in a manner consistent with their relative biomass and browse availability in these upland post-fire boreal forests. Birch was the most dominant species based on density and height before exclosures were erected, and experienced the highest occurrence of past browsing, indicating it was either the preferred diet species for moose or it was simply the most available forage in the area. Birch responded quickly to being safe from herbivores, and increased height at an annual rate of 3% more than individuals in control plots. Aboveground spruce growth was lower inside exclosures, potentially due to competition with birch acquiring more resources. Overall, these results suggest that the natural rate of moose browsing in control plots in these sites is unlikely to switch the projected canopy dominance of Alaskan paper birch in post-fire areas. However, herbivore activity may increase the rate at which black spruce saplings can reach a co-dominant status with broadleaf species in a mixed-wood forest, although this will be dependent on whether they are browsed by snowshoe hares before they reach hare escapement height (Olnes and Kielland 2016).

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