Excluding herbivores in upland forests of Interior Alaska did not alter post-fire succession

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# Abstract (265/ 300)

*Questions*:

Shifts in disturbances at high latitudes may stimulate significant changes in plant communities, such as shifts in forest succession pattern driven by a changing fire regime. This study explores how biotic interactions, such as herbivory, mediate the effects of disturbance on early succession. Specifically, we investigated the potential for mammalian herbivory to influence emerging patterns of boreal tree dominance initiated by variations in fire severity.

*Location*:

The study was conducted in upland (?) boreal forest stands near Fairbanks, Alaska, USA.

*Methods*:

We established paired exclosure and control plots to exclude moose (*Alces 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.

*Results*:

After four years, we observed distinct species-specific responses to mammalian herbivore exclusion. Birch grew taller inside exclosures, while spruce exhibited increased height and diameter growth outside exclosures. Aspen showed no response to the exclosure treatment. Survival rates remained high for all three species regardless of herbivory. Relative height structure of tree species emerged as the best predictor of growth responses to herbivore exclusion, rather than palatability to herbivores.

*Conclusions*:

Despite species-specific responses, the overall impact of herbivore exclusion on relative tree growth suggests that mammals are unlikely to drastically alter patterns of canopy succession after fire in the upland boreal forests of Interior Alaska.

**Key words**: Boreal forest, moose browsing, tree growth, snowshoe hare, forest structure, forest community, disturbance, herbivory experiment

# 1.0 Introduction

Fire is a dominant landscape-scale disturbance in boreal forests: across recent decades, fire has increased in severity , size, and frequency in boreal Alaska and Canada (Walker et al. 2020, Buma et al. 20). Increasing fire severity or frequency combusts above and belowground organic material in greater amounts (Keeley 2009), exposing mineral soil as a conducive seedbed for recruitment of small-seeded, broadleaf tree species (Johnstone et al. 2010, Walker et al. 2019). By modifying seedbed and aerial seedbanks, frequent or severe fire can lead to shifts in dominance from black spruce (*Picea mariana* (Mill.) B.S.P.) forests towards deciduous broadleaf species such as trembling aspen (*Populus tremuloides* Michx.) and Alaskan paper birch (*Betula neoalaskana* Sarg (Johnstone et al. 2016, Hayes and Buma 2021). Landscape modeling predicts transitions from coniferous to deciduous stands in early post-fire succession and increasing dominance of mature deciduous stands across the Alaskan boreal forest (Mann et al. 2012, Foster et al. 2019). Mammalian herbivores that prefer deciduous species could act as ecosystem engineers to counteract the effects of fire on forest dominance by altering patterns of deciduous tree survival and growth (Côté et al. 2004, Maier et al. 2005, Seaton et al. 2011). Thus, understanding the impacts of mammalian herbivores on early successional forests is crucial for predicting the long-term consequences of changes in fire and climate for Alaskan boreal forests.

Herbivores can be a major driver of forest structure and composition during early and mid-succession following disturbance (Post and Pedersen 2008, Bernes et al. 2018). 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). When browsing pressure is high, herbivores can reorganize stand structure (Tremblay et al. 2007, Gosse et al. 2011) through reducing tree biomass (McLaren 1996), eliminating canopy trees (Chouinard and Filion 2001), or modifying competition (Begley-Mill et al. 2014). Mammalian herbivores are often selective browsers; several factors determine their diet choice, including 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 mamalian herbivores in boreal forests (Thompson et al. 1992, Olnes and Kielland 2016, Conway and Johnstone 2017). Moose and hare have overlapping diets – both mammals prefer broadleaf trees and willows (*Salix* spp.) (Bryant and Kuropat 1980, Seaton et al. 2011). Hares also feed on spruce year-round: almost 40% of their winter diet consists of spruce needles (Wolff 1978, Olnes and Hielland 2017). In Interior Alaskan floodplains, moose and hare have been found to significantly alter species-specific patterns of tree recruitment and growth (Kielland and Bryant 1998, Kielland et al. 2006, Chapin et al. 2016). However, there are important differences in successional dynamics, available forage, disturbance and habitat use in upland forests compared to floodplains. Thus, the influence of mammalian herbivores in upland forests might display key differences than those in floodplains, 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. By altering species recruitment, composition and growth rates within burned area, variations in fire severity can increase the distribution and longevity of available moose habitat (Kielland and Brown 2015, Conway and Johnstone 2017). InIn addition, 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 moose and hare in Alaskan upland forests use and select habitat. Thus, we need to understand how the effects of dominant herbivores on successional patterns in early forest communities vary across fire severity.

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. To examine how moose and hare might alter growth and survival, 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. Based on palatability, we expected deciduous species (aspen and birch) to benefit from the exclusion of herbivores (particularly moose) and undergo greater relative growth inside the 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, Persson et al. 2005). Finally, we hypothesized that black spruce growth after several years 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 deciduous species when safe from mammalian browsing and the indirect effects to conifer-deciduous species competition, which 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 temperatures at the Fairbanks International Airport, in the center of the region, average 59.6°F in summer (June - August) and -6.6°F in winter (October to May) (1949 - 2012). Precipitation is generally low and decreases from west to east (annual average 16.9 in, 1929 to 2016, Western Regional Climate Center 2023). Common tree species in the upland forests of interior Alaska include 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, Hayes and Buma 2021).

We conducted this research approximately 50 km northeast of Fairbanks, Alaska at long-term study sites in the Caribou-Poker Creek Research Watershed (CPCRW). Existing research sites were located in stands that burned in the Boundary Fire in 2004 and have been monitored for vegetation responses to fire since 2005 (Johnstone et al. 2010, Hollingsworth et al. 2013). Previous research has shown early regeneration was strongly driven by fire severity: severely burned areas were dominated by deciduous species while lightly burned areas were dominated by black spruce regeneration (Johnstone et al. 2010). Moose densities have increased in interior Alaska since the 1980s, concurrent with fires creating suitable habitat and reductions in wolf populations (DuBois 2010). Local moose density in our study area (Game Management Unit 20A) were stable across the period of 2011 to 2015 at an average of 0.93 – 0.97 moose per km2 (Alaska Department of Fish and Game 2017). 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

We established five pairs of plots in 2013 near a subset of the long-term sites, selecting based on accessibility and a range of deciduous canopy dominance. All sites were located within ~3 kilometers of each other. At each site, we established two plots approximately ten meters apart that measured 12.2 m x 12.2 m 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 1.8 m tall and constructed of chain-linked fence panels that prevented access by moose and hare throughout the year (Fig. 1).

We measured stem density of potential canopy tree species (trembling aspen, Alaskan paper birch, and black spruce) and shrub willows (*Salix* species) in 2013 in each exclosure and control plot. Density was averaged between the two transects for each plot. Measurements were made within two randomly-placed, parallel belt transects (10 m x 1 m) spanning the length of the plot. 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. Twenty individuals of each tree species were tagged for repeat measurement by systematically marking the closest individuals to each one-meter mark along the transects. At site BF84, where sapling density was very low, we measured stem density along four transects in each plot and selected marked individuals at every two-meter mark. At the start of each summer (early June 2014, 2015 and 2017), we recorded any evidence (number of stems browsed) of herbivory on tagged individuals during the preceding winter. In late summer (August 2014, 2015, and 2017), we measured stem basal diameter, and several dimensions of crown size: average crown width (across the widest part of the crown and perpendicular to that), total stem height, and crown depth of all saplings. Each individual was scored as live or dead; for dead individuals, we noted any evidence of the cause of mortality (e.g., snowshoe hare browsing, broken apical meristem).

Soil temperature in each plot was measured with two Thermochron ibuttons (Maxim Integrated Products, San Jose, CA, USA) installed ~10 cm below the organic layer surface in each plot. Soil temperature records spanned 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. We measured organic layer depth including layers of dead moss, fibric, and humic organic material accumulated above the mineral soil. Soil pH was measured on a sample of mineral soil (upper 10 cm) 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 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.



Figure 1. Photographs of two exclosures in 2014: a moist toe-slope with abundant graminoid tussocks (site BF84, top) and an upslope area with high density of Alaskan paper birch (site BF86, bottom). Both sites were dominated by black spruce canopy when they burned in 2004.

## 2.3 Statistical analyses

To determine the effect of exclosures on growth measurements of each species, we used linear mixed effect models. We built three growth response models, one for each species (aspen, birch, black spruce), each including a fixed effect of treatment (i.e., exclosure), with site as the random term and individuals as sample units nested within site and treatment. We ran models for height, basal diameter, crown width, and crown depth using the nlme’ package in R (Pinheiro et al. 2016). 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 accounted for differences in initial sapling size and was calculated as the difference between two time periods standardized by the initial size measurement. Standard error (SE) measurements included in the text (sections 3.2 and 3.4) are at the site level (n = 5). We performed all analyses using R version 3.5.1 (R Core Team 2018)

# 3.0 Results

## 3.1 Site characteristics

Alaskan paper birch was consistently the tallest species at all five sites, with an average height of 124.1 ± 4.2 cm (mean ± SE); at one site birch approached 200 cm in average height (Appendix Table 1). Trembling aspen was on average 61.2 ± 3 cm tall, while black spruce was the shortest (26.5 ± 1 cm). Over half of all the tagged aspen were below 50 cm and thus likely protected from moose damage by snow in winter. 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 (# individuals/ m2  on average). Average density of all *Salix* species was half that of both broadleaf species (4.5 m-2 ± 1.5) and individuals were mostly single-stemmed and short (~50 cm). Compared to black spruce, density of broadleaf species was higher and more variable across sites.

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) except for lower soil moisture measured in the exclosure in BF76; these apparent differences are confounded by low replication (near-surface rocks limited sampling).

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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 2015). | | | | | |

## 3.2 Browsing and survival of individuals

Birch saplings experienced the highest occurrences of pre-treatment browsing compared to aspen and black spruce. Before the exclosures were established, 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 across all species. In control plots, browsing on spruce was low: only two individuals showed pre-treatment browsing damage and only a single individual was browsed in 2015 and 2017. In all cases, 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. 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 marked individuals was high for all three species (Fig. 3). Limited mortality of aspen did occur in both control (n = 4) and exclosure (n = 6) plots. Of the individuals that died, two aspen and two birch had been browsed in control plots during the winter pre-treatment by snowshoe hare. We also encountered aspen saplings that were recorded as dead in one year, but had resprouted the next year. These individuals were considered as survivors in our final dataset.



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 of 20 seedlings sampled in each treatment across sites (n = 5).

## 3.3 Effect of herbivore exclosures

Four years after establishing exclosures, we observed species-specific effects on proportional growth of saplings, encompassing changes in height, basal diameter, and crown size within exclosures. Notably, aspen growth remained unaffected by the exclosures, while birch displayed a positive response, and spruce exhibited a negative response (see Table 2). By 2017, birch saplings inside exclosures reached an average height of 227.8 ± 41.1 cm, reflecting an increase of 49.6% in height (107.1 ± 29.1 cm). In comparison, birch height increased by an average of 29.0% (84.1 ± 27.4) cm in control plots over the same four-year period (Fig. 4). Conversely, the height of black spruce increased by an average of 40.1% in exclosures compared to 50.0% in control plots, and stem diameters showed a growth of 39.4% in exclosures versus 48.9% in controls. None of the species showed significant changes in crown size in response to the exclosure treatment (Table 2).

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| --- | --- | --- | --- | --- | --- |
| Table 2. Parameter estimates from linear mixed effect modelsΨ assessing the effect of the exclosure treatment on proportionalϕ height, basal diameter, and crown size 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

The three tree species included in this study responded individualistically to protection from mammalian herbivory. Alaskan paper birch responded quickly to herbivore exclusion with increased height four years after the exclosures were established. Moose browsing was the predominant form of herbivory across all six sites, with the majority (95%) of browsing focused on deciduous saplings. Although trembling aspen and Alaskan paper birch were both anticipated to be more palatable to moose than black spruce (Bryant and Kuropat 1980), only birch saplings exhibited benefits within exclosures. Consequently, palatability to herbivores did not emerge as the most accurate predictor of species responses to the exclosure treatment. Instead, growth responses were ordered according to the relative position of each tree species within the canopy (Simončič et al. 2018). Despite birch and aspen being present in similar densities, birch, being the tallest species and within the optimal height range for moose browsing, thrived within exclosures, in contrast to aspen, which remained short and likely protected below snow. Consequently, the sequence of positive, neutral, and negative responses aligns with species canopy dominance and browsing opportunities in our study area: birch, aspen, and black spruce, respectively.

In forests where moose is the dominant herbivore, rates of post-disturbance succession can be either hastened or reversed by moose browsing (Davidson 1993, Persson et al. 2005, McLaren et al. 2009). Our study supports observational work from other upland forests in Alaska (Conway and Johnstone 2017), showing that severe moose browsing can slow the rate of deciduous height growth during post-fire succession, however the successional trajectories remained unaltered. The results presented here suggest opposing aboveground growth patterns of Alaskan paper birch versus black spruce, 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.

Herbivore effects of the magnitude observed in this study are likely to have modest effects on the pace of secondary succession. In order to predict when birch will escape moose browsing (3 meters, Lord 2008, Seaton et al. 2011), we used average height in 2017 (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. In contrast, birch saplings subject to observed natural herbivory would take an additional three years to reach the same height. Presumably, once birch in control plots reach three meters, individuals would have comparable growth rates to individuals inside exclosures (Conway and Johnstone 2017). This level of herbivory appears insufficient to impact species dominance when sites reach full canopy closure, projecting birch as the likely dominant species. While moose herbivory might expedite the eventual co-dominance of black spruce, the influence of snowshoe hare browsing on black spruce growth remains uncertain (Olnes and Kielland 2016). Black spruce in both the control and exclosure plots were ~50 cm tall in 2017 and will become more vulnerable to browsing by hares as they emerge 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 directly or indirectly by herbivores (Persson et al. 2000). Selective browsing can shift canopy composition towards increased dominance of less palatable species (McInnes et al. 1992, Kielland and Bryant 1998). Across longer time scales (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.

The response of Alaskan paper birch, trembling aspen, and black spruce—three tree species with the potential for canopy dominance—in upland post-fire boreal forests was consistent with their relative biomass and browse availability. Birch, initially the most dominant species in terms of density and height, experienced the highest incidence of past browsing, indicating it was either the preferred diet species for moose or the most readily available forage. Once protected from herbivores, birch responded quickly (within # years) 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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