Species-specific responses to herbivore exclusion: implications for post-fire succession in Alaskan boreal forests

Alexandra J Conway1, Katherine Hayes2, Mélanie Jean3, Roger W Ruess4, Jill F Johnstone4

1 Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan, Canada, S7N 5E2

2 Cary Institute of Ecosystem Studies, Millbrook, New York, USA, 12545

3 Department of Biology, Université de Moncton, Moncton, New Brunswick, Canada, E1A 3E9

4 Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, Alaska, USA, 99775-7000

Corresponding Author

Alexandra J Conway

Email: [alix.conway@usask.ca](mailto:alix.conway@usask.ca)

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# Abstract (200 words)

Fire disturbance initiates secondary succession in northern boreal forests and variations in fire severity that affect community assembly can determine subsequent patterns of forest succession. However, the potential for biotic interactions to alter these patterns is less clear. Here, we investigated how mammalian herbivory may influence emerging patterns of boreal tree dominance initiated by variations in fire severity.Paired exclosure and control plots tested effects of native moose (*Alces alces)* and hare (*Lepus americanus*) on postfire tree growth at five sites in interior Alaska across a gradient of fire severity. Browsing and growth were monitored on tagged individuals of black spruce (*Picea mariana)*, trembling aspen (*Populus tremuloides)*, and Alaskan paper birch (*Betula neoalaskana*) over a four-year period. Linear mixed effect models indicated distinct species-specific responses to herbivore exclusion. Birch and aspen grew taller inside exclosures, while spruce exhibited increased height and diameter growth outside exclosures. Relative height structure of tree species emerged as the best predictor of growth responses to herbivore exclusion.Despite species-specific responses, modest impacts of herbivore exclusion on tree growth suggest that mammals are unlikely to 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

Predicting how forest ecosystems will respond to global change factors is of broad importance, as changes in forest composition significantly influence many of the services ecosystems provide that support human well-being (refs). In Alaska and other parts of the North American boreal forest, climate warming and associated changes to the fire regime associated are predicted to alter broad patterns of forest dominance (Mann et al. 2012, Foster et al. 2019). Multiple field studies have documented recent shifts in post-fire recovery of burned upland forests towards greater proportions of deciduous broadleaf species over the historically dominant conifer, black spruce (*Picea mariana* (Mill.) B.S.P.). As increasing fire activity combusts greater amounts of above and belowground organic material (Walker et al. 2020, Buma et al. 2022), exposure of mineral soil and disruption of aerial seedbanks favors recruitment of broadleaf tree species such as trembling aspen (*Populus tremuloides* Michx.) and Alaskan paper birch (*Betula neoalaskana* Sarg.) (Johnstone et al. 2010, Walker et al. 2019) (Johnstone et al. 2016, Hayes and Buma 2021). However, we lack the long-term data to confirm that contemporary patterns in early succession will translate into long-term dominance. In particular, 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 an important element in predicting the long-term consequences of changes in fire and climate for Alaskan boreal forests.

Herbivores are known in some situations to 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 mammalian 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 differ from 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 vegetation composition and growth rates within a burned area, variations in fire severity can increase the distribution and longevity of available moose habitat (Kielland and Brown 2015, Conway and Johnstone 2017). In interior Alaska, recently burned (11-30 years postfire) stands are associated with high moose densities (Maier et al. 2005), while dense black spruce forests are associated with high densities and survival of snowshoe hares (Feierabend and Kielland 2015). Adequate understory cover provides shelter from predators, a key element of habitat quality of snowshoe hares (Carreker 1985). Differences in forest structure and community due to local contexts of fire severity, pre-fire cover, and topography in Alaskan upland forests influence habitat use by moose and hare and thus, their potential impacts on early succession.

There remains substantial uncertainty about the potential for mammalian herbivory to shape patterns of future canopy composition via differential effects on the growth and survival of alternative tree species in early succession. We used a combination of field experiments and simulation modeling to assess how moose and hare affect post-fire growth and survival of black spruce, paper birch, and aspen upland forests that varied in composition and density in association with differences in fire severity (Johnstone et al. 2010). Experimental exclosures provided protection from moose and hare and growth responses of three dominant tree species were monitored in paired exclosure and control plots across four years. Field data on tree growth were input into a model of forest dynamics to simulate the overall trajectory of growth during early succession and estimate longer term impacts of herbivores on tree dominance. 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 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 mammalian herbivores may drive successional patterns and change in Alaskan upland boreal forests.

# 2.0 Methods

## 2.1 Study area

The study area for this research lies within the Caribou-Poker Creek Research Watershed (CPCRW), located within Interior Alaska approximately 50 km northeast of Fairbanks, Alaska. 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) and are the dominant forest type within CPCRW (ref). 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 approximately decadal snowshoe hare cycle 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).

Field sites were established in stands dominated by black spruce until 2004, when they were burned by a large wildfire. Monitoring of vegetation succession across a broad network of sites burned in 2004 in Interior Alaska has documented an increase in deciduous tree recruitment at sites that were severely burned ￼(Johnstone et al. 2010, Hollingsworth et al. 2013; Johnstone et al. 2020￼.

## 2.2 Field experiment

We established five pairs of plots in 2013, nine years after fire, that were co-located with the long-term monitoring sites and selected to capture a range of deciduous canopy dominance (Figure 1). 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. To avoid any effect of the fencing, a one-meter 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 summer 2013 in each exclosure and control plot. Density was averaged between the two transects for each plot. Measurements were made within two randomly spaced, parallel belt transects (10 m x 1 m) spanning the length of the plot. We measured height, basal diameter, diameter at breast height (DBH), when present, and the presence/absence of any historical herbivore damage by moose or hare (2005-2013) 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. In early June (in 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 low tree seedling density and abundant graminoid tussocks (site BF84, top) and an upslope area with high density of birch seedlings (site BF86, bottom). Both sites were dominated by a black spruce canopy when they burned in 2004.

## 2.3 Statistical analyses

Analyses were performed using R version 4.3.2 (R Core Team 2024). 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. Growth response variables were tested for normality and homogeneity of variance prior to analyses and logarithmic transformations were used in analyses, when underlying assumptions were not met (example of which ones). Growth response models included fixed effects of initial height (measured in 2013 when exclosures were erected) and treatment (i.e., exclosure), with site as the random term and individuals as sample units nested within site and treatment. We ran models for final height, basal diameter, crown width, and crown depth; all final measurements were made four years after exclosures were erected (2017). While mixed effect models are generally considered robust to violations of distributional assumptions (Schielzeth et al. 2020), residual plots were visually examined to ensure symmetrical distribution and no clustering or clear patterns were present.

Marginal and conditional R2 values were calculated for each model using the ‘performance’ package in R (Lüdecke et al. 2021). Standard error (SE) measurements included in the text (sections 3.1 and 3.3) are at the site level (n = 5).

## 2.4 Simulation modeling

We used simulations with the model iLand to estimate 50-year growth trajectories of black spruce, paper birch, and trembling aspen in Interior Alaska, with and without mammal herbivory. iLand is an individual-based forest process model that simulates the growth and mortality of trees in 1-ha stands within spatially explicit landscapes, with growth dynamics constrained by light interception, climate, and soil nutrients (Seidl et al. 2012a, 2012b). The model has been previously tested in landscape simulations of forests in the western United States (Hansen et al. 2018, Turner et al. 2022) and Alaska (Hansen et al. 2021, 2023). \*\*Add in description of herbivory module, and set up for simulations presented here\*\*

# 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 (Table A1). 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. Compared to black spruce, density of broadleaf species was higher and more variable across sites. However, black spruce had the highest density (~6 individuals·m-2) 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, short (~50 cm), with very low evidence of browsing due to their height.

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 |
| BF79 | 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 historical (i.e., pre-exclosure) browsing, with approximately double the number of birch saplings browsed compared to aspen (Figure 3). Exclosures were effective barriers to mammalian herbivory as the establishment of fencing eliminated signs of new browsing inside exclosures for all species. In control plots, browsing rarely occurred on spruce: only two individuals showed pre-treatment browsing damage and only a single individual was browsed in 2015 and 2017 (data not shown). 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 3. 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. 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 previous winter 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 survivors in our final dataset.

## 3.3 Effects of herbivore exclosures on tree growth

Four years after establishing exclosures, we observed species-specific effects on growth of saplings, encompassing changes in height, basal diameter, and crown size. Notably, birch and aspen displayed a positive response to exclosures, and spruce exhibited a negative response (Table 2). Final height of aspen and birch was greater inside exclosures after four years of protection from herbivory (Figure 4). The opposite was true for black spruce, with significantly smaller individuals inside exclosures (Figure 4). Birch saplings were taller than aspen across the sites, and although birch showed the greatest height response to exclosures, the mean proportional change in birch and aspen were similar (give values).

Stem height was more sensitive to exclosure effects than other metrics of plant size, although treatment effects on basal diameter and crown width were significant for at least one species. Crown depth was unresponsive to the treatment. Not surprising, initial growth measurements had a strong influence on final measurements for all metrics of plant size (Table 2). Overall, R2 values were high, with models explaining 46.5 to 78.7% of the model variance. Initial height and the treatment of exclosures explained 64.7%, 76.4% and 74.8% of the final height of aspen, birch, and spruce, respectively. Random effects explained 0.3 to 19.9% of the model (Table 2).

Table 2. Linear mixed effect model results for aspen, birch, and spruce growth models.

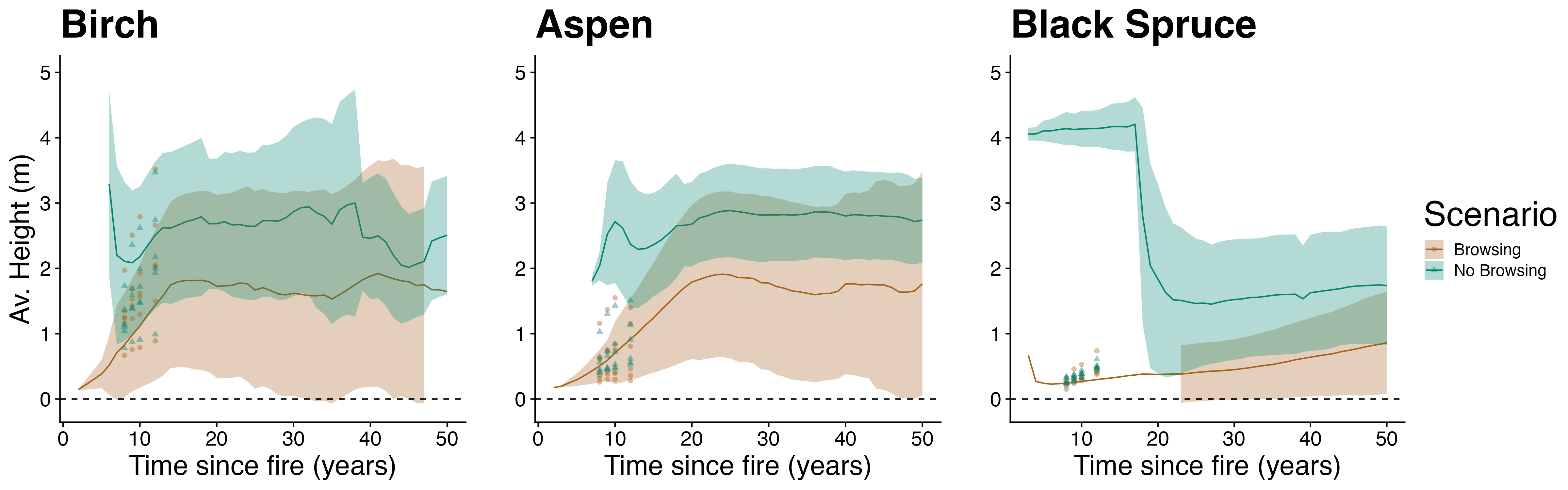
|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Response | Fixed Effect | Value | Standard Error | t-value | *p*-value | Conditional R2 | Marginal R2 |
| Aspen | | | | | | | |
| Height\* | Initial height | 0.014 | <0.001 | 14.174 | **<0.001** | 0.647 | 0.585 |
| Treatment | 0.207 | 0.070 | 2.970 | **0.003** |
| Basal diameter\* | Initial basal | 0.159 | 0.010 | 16.500 | **<0.001** | 0.663 | 0.636 |
| Treatment | -0.050 | 0.055 | -0.909 | 0.365 |
| Crown depth\* | Initial crown depth | 0.016 | 0.002 | 9.389 | **<0.001** | 0.465 | 0.374 |
| Treatment | 0.128 | 0.120 | 1.069 | 0.287 |
| Crown width\* | Initial crown width | 0.026 | 0.002 | 11.080 | **<0.001** | 0.567 | 0.403 |
| Treatment | 0.190 | 0.090 | 2.114 | **0.040** |
| Birch | | | | | | | |
| Height | Initial height | 1.440 | 0.086 | 16.798 | **<0.001** | 0.764 | 0.565 |
| Treatment | 28.919 | 7.862 | 3.679 | **<0.001** |
| Basal diameter | Initial basal | 1.737 | 0.085 | 20.432 | **<0.001** | 0.750 | 0.660 |
| Treatment | 0.212 | 1.005 | 0.211 | 0.833 |
| Crown depth | Initial crown depth | 1.184 | 0.065 | 18.186 | **<0.001** | 0.765 | 0.680 |
| Treatment | 8.186 | 7.211 | 1.135 | 0.258 |
| Crown width | Initial crown width | 0.959 | 0.055 | 17.470 | **<0.001** | 0.710 | 0.650 |
| Treatment | 2.857 | 3.318 | 0.861 | 0.390 |
| Spruce | | | | | | | |
| Height | Initial height | 1.578 | 0.074 | 21.298 | **<0.001** | 0.748 | 0.658 |
| Treatment | -6.114 | 1.891 | -3.234 | **0.001** |
| Basal diameter | Initial basal | 1.314 | 0.083 | 15.795 | **<0.001** | 0.570 | 0.567 |
| Treatment | -0.886 | 0.290 | -3.057 | **0.003** |
| Crown depth | Initial crown depth | 1.503 | 0.063 | 23.724 | **<0.001** | 0.776 | 0.720 |
| Treatment | 0.300 | 1.753 | 0.171 | 0.865 |
| Crown width | Initial crown width | 1.151 | 0.046 | 24.821 | **<0.001** | 0.787 | 0.745 |
| Treatment | -0.745 | 0.862 | -0.864 | 0.389 |

\*Indicates response variable was log-transformed.

A graph of a number of species

Description automatically generated

Figure 4. Treatment effects on total height growth (cm) of aspen, birch, and spruce after 4-years (2013-2017). Exclosure treatments had a significant effect on sapling height for each species (see Table 2).

Figure X. A) Relationship between height and time since fire. B) \*\*second panel, will add\*\* Relationship between DBH and time since fire.

# 4.0 Discussion

The three tree species included in this study responded individualistically to protection from mammalian herbivory. Alaskan paper birch showed the greatest height increase in response to herbivore exclusion followed by trembling aspen, while black spruce exhibited a small negative response. We hypothesize that relative palatability to herbivores, as well position of each tree species within the canopy, explain the pattern of species responses to the exclosure treatment. Moose browsing was the predominant form of winter herbivory across all five sites, with the majority (95%) of browsing focused on deciduous saplings. Both trembling aspen and Alaskan paper birch are more palatable to moose than black spruce (Bryant and Kuropat 1980) and these were the species exhibiting increased growth within exclosures. Birch and aspen were present in similar densities; however, birch was within optimal height range for moose browsing and responded more rapidly to exclusion. While aspen similarly increased in height within exclosures, the majority of individuals were short and likely protected below snow so the growth release due to herbivore exclosures was not as rapid compared to birch.

Additionally, growth responses were ordered according to the relative position of each tree species within the canopy (Simončič et al. 2018). Positive responses of birch and aspen growth to herbivore protection likely increased canopy competition for the smaller-statured black spruce, causing a decrease in spruce growth within exclosures. 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 young boreal stands have shown to result in 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).

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. Likewise, herbivore effects of the magnitude observed in this study are likely to have modest effects on the pace of secondary succession. Using the growth rates observed in this study, we estimate that birch will reach the estimated escape height of 3 m for moose browsing (3 meters, Lord 2008, Seaton et al. 2011) with three additional years of herbivore protection in exclosures. 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 versus 7 % for control plots. From this we estimate birch saplings subject to observed natural herbivory would take an additional three years to reach escapement 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 nitrogen (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, 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 likely the most readily available forage. Once protected from herbivores, birch responded quickly (within 4 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. 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). Overall, these results suggest that the natural rate of moose browsing is unlikely to switch the projected canopy dominance of birch in post-fire upland boreal forest sites in Interior Alaska.

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