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Moose alter the rate but not the trajectory of forest canopy succession after low and high severity fire in Alaska

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ABSTRACT

Mammalian herbivory on palatable trees affects tree growth, forest composition, and forest succession. Antecedent effects of herbivores can be identified through remnants of dead stems and altered tree morphology as well as changes in tree ring patterns and growth. Increases in fire severity, particularly surface fuel combustion, in the boreal forest of western North America can cause a shift in the successional trajectory from coniferous to deciduous dominated forests, which may alter plant–animal interactions. We measured height and tree ring growth of the two dominant canopy tree species, trembling aspen (*Populus tremuloides* Michx.) and black spruce (*Picea mariana* (Mill.) BSP), in sites that experienced stand-replacing fire with deep versus shallow surface fuel combustion 20 years ago. We also classified individual trees into a category of browsing damage based on external features and morphology. We hypothesized the effects of browsing to be contingent on fire severity. Using linear mixed effect models, we investigated the main and interactive effects of fire severity and browsing intensity on aspen growth. We also developed tree ring chronologies to test for growth releases in aspen and black spruce.

Effects of moose browsing on aspen growth depended on fire severity (surface fuel combustion), with negative effects in high severity sites and no effects in low severity sites. Spruce growth showed no direct or indirect browsing effects, indicating moose have not altered the potential for spruce to reach the forest canopy. Aspen in severely burned sites showed abrupt growth releases in tree rings corresponding to changes in herbivore pressure and density. Height-growth projections indicated that moose slowed the rate of aspen growth and canopy dominance in severely burned areas by ten years, through repeated stunting of apical growth in aspen, without affecting the initial trajectory to an aspen-dominated canopy. Lightly burned areas, with their larger proportion of spruce biomass, slower aspen growth, and reduced browsing pressure during the first 20 years after fire, will likely provide accessible aspen forage until >50 years post-fire as sites return to spruce dominance. Heterogeneously burned forests could thus sustain high rates of available moose forage for a much longer period than previously reported. Our study highlights the importance of including fire severity when considering the impacts of large herbivores on tree growth and forest structure.

1. Introduction

Herbivores act as ecosystem engineers (Jones et al., 1994), with cumulative effects on the physical, chemical, and biological components of an ecosystem that can alter its structure and function (Kielland et al., 2006). Large mammals can impact forest structure and successional dynamics across temporal (years to decades) and spatial (tens of meters to kilometers) scales (Peterson et al., 1998). These impacts occur due to both direct and indirect effects of mammalian herbivores on the recruitment, survival, and growth of woody species. Direct effects often include browsing and consumption of biomass, with associated reductions in plant size (Chouinard and Filion, 2001), trampling (Schrama et al., 2013), and a decrease in plant reproduction by consuming flowers (Augustine and Frelich, 1998). These direct effects can alter animal–plant and plant–plant interactions, such as through changes to quality and quantity of food (Danell et al., 1994), and habitat modifications that affect vegetation structure and nutrient cycling (Rooney and Waller, 2003). Understanding the cumulative impacts of herbivores is a critical but complex element in predicting dynamic patterns of ecosystems in managed and unmanaged systems (Bailey and Whitham, 2002).

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Forest ecosystems across the globe are changing, and natural forest ecosystems appear particularly vulnerable to warming temperatures and altered natural disturbances (Allen et al., 2010). The vegetation composition of the boreal forest in Alaska has remained relatively stable for the past 6000 years; however, boreal forest vegetation is likely to change due to projected warming and associated changes in disturbance regimes (Chapin et al., 2010). Altered seedbeds from high severity fires have caused a shift from pre-fire mature black spruce (*Picea mariana* (Mill.) BSP) stands to early assemblages of deciduous broadleaf trees, such as Alaskan paper birch (*Betula neoalaskana* Sarg.) and trembling aspen (*Populus tremuloides* Michx.) (Johnstone et al., 2010). With these ecological shifts, deciduous trees may become increasingly dominant on the landscape (Mann et al., 2012). However, mammalian herbivores have the potential to alter successional pathways in forest ecosystems (Thompson et al., 1992) and may alter initial trajectories of deciduous dominance after high severity fires. Post-fire environmental conditions can influence tree growth and dominance (Bailey and Whitham, 2002) as well as species-specific strategies for response to potential herbivory (e.g., tolerance, escape, or resistance (Lindroth and St. Clair, 2013)). Aspen can use multiple strategies when responding to post-fire herbivory (Bailey and Whitham, 2002; Wan et al., 2014), and it is unclear whether these different strategies (particularly escaping herbivore pressure by growing quickly) will be affected by fire severity levels that affect aspen productivity in Alaska (Shenoy et al., 2011).

Historical impacts of mammalian herbivores can be detected through changes in tree architecture and/or tree ring growth. For example, browsed Sitka spruce (*Picea sitchensis* (Bong.)) on the Haida Gwaii islands off the coast of British Columbia, Canada, display two types of growth within an individual: stunted, wider growth when 'trapped' below the browsing height limit of local herbivores, and normal structure and shape once 'escaped' (Vila et al., 2003). Tree rings have been used to assess historical browsing through aging fraying scars from black-tailed deer (*Odocoileus hemionus sitkensis* Merriam) (Vila et al., 2004) and measuring ring width patterns before and after herbivore introduction (Speed et al., 2011). Furthermore, growth releases often occur in trees that escape the negative effects of chronic disturbance (e.g., browsing by an animal, canopy gaps, insect outbreaks) (Bretfeld et al., 2015; Karlsson et al., 2004; Vila et al., 2003) or experience competitive release when neighbors are subject to stronger disturbance impacts. These approaches allow for characterization of browsing effects in a historical context and can enhance our understanding of plant–animal interactions.

Stand-replacing disturbances, such as fire, create even-aged tree cohorts that are optimal for studying the importance of ecological filters (disturbance, climate, competition, and herbivory) on stand development (Hansen et al., 2016; Turner, 2010). In interior Alaska, a stand-replacing fire (the Hajdukovich Creek burn) in 1994 created a landscape mosaic of low and high severity burn areas that varied in the level of surface fuel combustion (Michalek et al., 2000). Heterogeneity of surface fuel combustion within the burned area altered post-fire seedbeds and induced differential patterns of tree recruitment across the landscape (Johnstone and Kasischke, 2005). Initial effects on tree recruitment caused a divergence in successional trajectories of the forest canopy that have persisted into the second decade of post-fire growth (Shenoy et al., 2011). Aspen recruitment dominated severely burned sites in the 1994 burn (Johnstone and Kasischke, 2005), and the warmer soils at these sites fostered rapid aspen growth compared to low severity sites where aspen and black spruce co-dominated the regeneration (Shenoy et al., 2011). High severity sites continued to produce the highest amount of forage biomass 19 years post-fire, however the proportional removal of forage by moose (*Alces alces*) peaked 13 years post-fire and then declined (Brown et al., 2015; Lord, 2008). It remains unclear how the effects of initial disturbance and woody stem competition on post-fire establishment and community assembly (Johnstone and Kasischke, 2005; Shenoy et al., 2011) may be modified by mammalian herbivores that are themselves responsive to severity effects on forage availability.

The purpose of our study was to understand how herbivory by large mammals affects post-fire tree growth, and whether herbivory may influence differing pathways of succession triggered by fire severity. Specifically, we tested two hypotheses relating to herbivore effects: (1) herbivore impacts will be greatest in sites with the highest forage availability (severely burned areas), and (2) herbivore impacts on dominant forage species will lead indirectly to increased growth of less palatable species. Severely burned sites, compared to lightly burned, have promoted increased productivity of aspen (Shenoy et al., 2011) which should increase the success of escaping browse damage (e.g., Wan et al., 2014). However, in our study area aspen have been subject to increased moose browsing pressure in only severely burned sites (Brown et al., 2015; Lord, 2008). Thus, in severely burned sites, we predicted browsing damage would overcome the aspen escape strategy by slowing the rate of aspen growth, allowing non-palatable species, such as black spruce, to increase growth and potentially altering the rate or trajectory of canopy succession. We used external tree damage quantified in the field, growth rates below and above the browse limit, and growth patterns from tree rings to determine effects of browsing. From these results, we compared height-growth projections for aspen and black spruce growing in low and high severity sites, accounting for the effect of moose browsing on height growth. Our predictions of forest structure under different fire severity and browsing intensity scenarios provide information on duration of forage availability for moose and their influence on patterns of forest development.

2. Material and methods

2.1. Study area

We conducted our research in the 1994 Hajdukovich Creek burn, located in a flat, glacial outwash plain north of the Alaska Range mountains and approximately 35 km southeast of Delta Junction in interior Alaska (USA). The Hajdukovich Creek fire burned 8900 ha of black spruce forest between mid-June and late September 1994 (Michalek et al., 2000). Typical for interior Alaska, pre-fire vegetation was predominately black spruce with a few mixed stands of aspen and black spruce (Johnstone and Kasischke, 2005). Most of the spruce canopy was consumed by the fire, leading to 100% stand mortality. However, another metric of fire severity, the combustion of surface organic material (dead moss and undecomposed organic material), varied substantially across the burn due to variations in weather and soil thaw (Kasischke and Johnstone, 2005). Remote sensing classified 61% of the burn as low severity (little combustion of surface organic material), 6% as medium severity, and 33% as high severity (extensive combustion of up to 30 cm organic layer depth) (Kasischke and Johnstone, 2005; Michalek et al., 2000). Variations in fire severity affected seedbed quality and led to extensive recruitment and rapid growth of aspen in severely burned areas formerly dominated by black spruce (Johnstone and Kasischke, 2005; Shenoy et al., 2011). Aspen recruitment was principally from seed (Johnstone and Kasischke, 2005) as opposed to the clonal (asexual) reproduction that is common when aspen stands self-regenerate after fire (Barnes, 1966).

The Hajdukovich Creek burn is located in one of six subunits of Game Management Unit 20 (GMU 20D), which supported some of the highest moose densities in the state in the early 2000's due to wildfires and predator control (1.78 moose/km^2 in 2006 (DuBois, 2010); moose density in Alaska ranges from 0.01 to 1.93 moose/km^2). However, aerial surveys in GMU 20D estimated that moose populations subsequently decreased during 2007–2009 (DuBois, 2010).

2.2. Sampling design and field work

In the summer of 2014, we sampled 12 previously established sites (Fig. 1, Table S1) in the Hajdukovich Creek burn that experienced low (n = 6) and high (n = 6) fire severity, resulting in different forest composition (Johnstone and Kasischke, 2005). Study site selection took advantage of previous research documenting fire severity, environmental conditions, and post-fire plant recruitment (Johnstone and Kasischke, 2005; Shenoy et al., 2011), as well as recent herbivore activity and habitat use (Brown et al., 2015). We selected all low severity sites that were most recently sampled (Brown et al., 2015), and randomly selected an equal number of high severity sites, excluding those with pre-fire aspen stems to ensure all aspen regeneration was from seed. All sites experienced a stand-replacing burn, were on flat terrain, and the primary factor driving initial (8–15 years post-fire) tree growth and composition was fire severity (Johnstone and Kasischke, 2005; Shenoy et al., 2011). Detailed site data is available online in the Bonanza Creek Long-Term Ecological Research (LTER) data archive (Johnstone and Kasischke, 2003).

At each site, we established a 30 m baseline transect through a homogeneous area with visually similar tree density and height. We then placed three 24 m transects perpendicular to the baseline transect at 0, 15, and 30 m (Fig. S1). On each of these perpendicular transects, we established sampling points at the 0 m mark, and at 6 m intervals thereafter (i.e., 5 sampling points along each transect). At each sampling point, we identified the two closest individuals of black spruce or aspen (n = 30 individuals of each species, per site). For aspen, if the closest individual was short (<25 cm), we pulled the individual out of the ground to check for evidence of suckering (produced by recent asexual growth). Because one of our goals was to estimate how browsing has affected individuals that regenerated shortly after the fire, we included suckers (n = 13) in density measurements but measured and collected the next closest individual that established from seed.

We measured tree height and distance from the sampling point, and collected an intact basal disk from each individual. We examined each individual for bite marks, cut stems, and broken branches, and classified each individual into a browse category based on the presence, density, and growth of specific morphological features called twig clusters (Fig. 2) (Keigley et al., 2003). Individuals were either classified as having zero evidence of browsing, light (one twig cluster, or up to five minor twig clusters that only contain one broken stem), or heavy (multiple twig clusters distributed along the stem below the browse limit). Only one aspen in all high severity sites experienced no past browsing, so we combined the ‘zero’ and ‘light’ browsing categories. We recorded the height of browse damage, and the type of herbivore when possible (browsing by snowshoe hares, *Lepus americanus*, was distinguished from moose browsing by stems cut cleanly at a 45° angle). The browse limit used for moose in Alaska is generally 3 m (Lord, 2008; Seaton et al., 2011), therefore we also collected tree disks at the 3 m mark from all individuals (that were >3 m tall) to determine the age at which trees escaped browsing damage.

2.3. Laboratory work

Aspen and black spruce stem disks were dried and sanded with increasingly fine sandpaper, up to a grit of 600, to accentuate visible rings. We scanned all disks and measured annual rings (resolution 0.001 mm) on two radii per disk using WinDENDRO software version 2012 (Regent Instruments 2012). The year 2014 was not included in analyses, as the growing season was not fin-

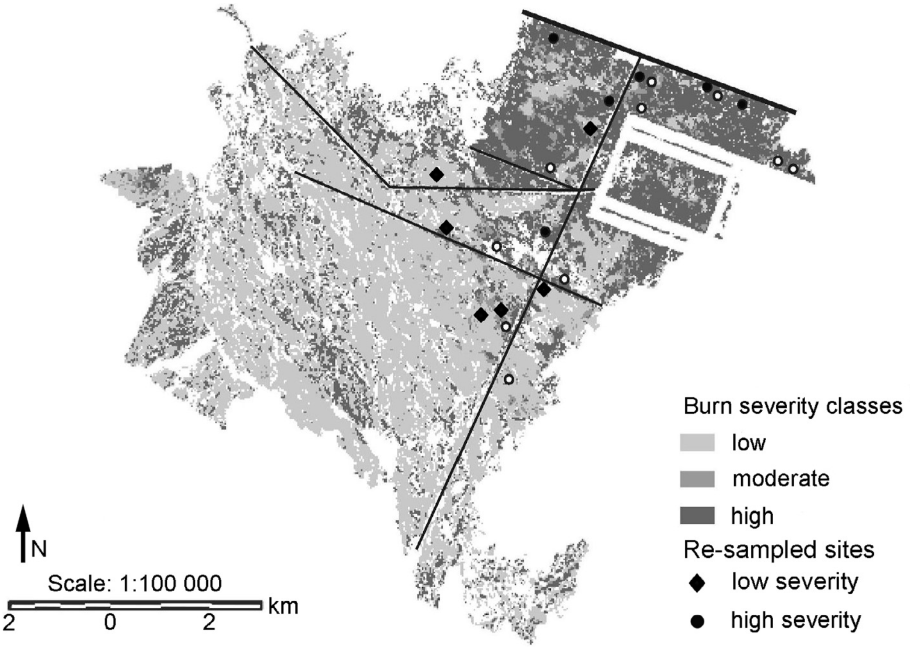

Fig. 1. A map of the burn severity classes (light, moderate, high) after the 1994 Hajdukovich Creek burn (modified from Johnstone and Kasischke, 2005). Black symbols are sites re-sampled in 2014 in either low (diamonds) or high (circles) severity areas. Black and white circles are additional sites sampled in 2001/2002, not included in this study. Thin black lines represent dirt trails, while the thicker black line at the northern edge of the burn is the Alaska Highway. The white grid is a disturbed area that was non-forested prior to the fire.

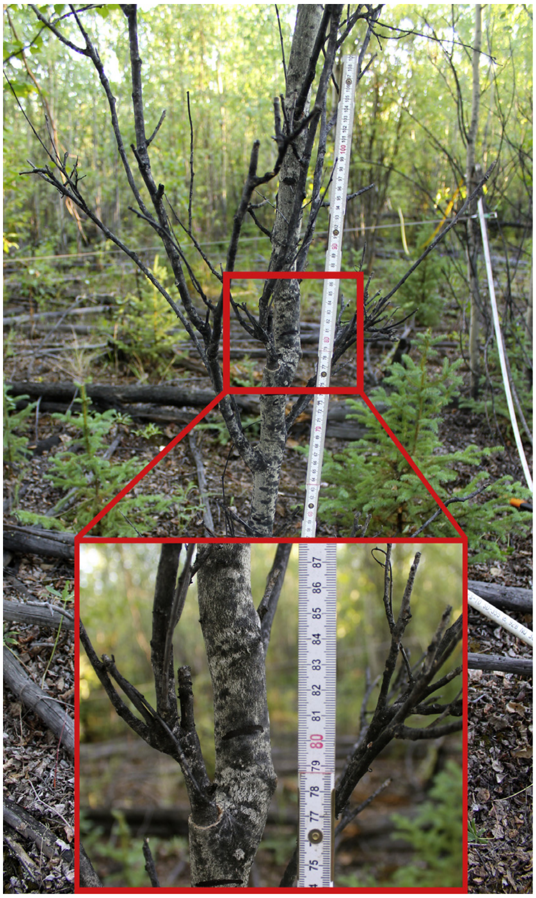

Fig. 2. A heavily browsed aspen located in a high fire severity site in the Hajdukovich Creek burn. The inset is a close-up of the place where the original apical meristem was removed, generating a twig cluster, and causing apical dominance to switch to a new branch at a stem height of 77 cm.

ished; time series are from 1995 to 2013. All samples were visually cross-dated within sites using WinDENDRO.

Ring-width series were analyzed in R version 3.1.2 (R Development Core Team, 2014) and the package 'dplR' version 1.6.3 (Bunn, 2008). We took the average of two measured radii per disk to obtain a raw ring width. Each raw ring width series was detrended and standardized (to produce dimensionless units known as ring width index) (Fritz and Swetnam, 1989) using the modified negative exponential curve (Fritz, 1976). The modified negative exponential curve attempts to fit a classic nonlinear model of biological growth; however, if a nonlinear model cannot fit then a linear model is used (Bunn, 2008). Trees with growth trends that did not fit an exponential or linear model were excluded from the final chronology (see below for final sample sizes). We also calculated basal area increment (BAI) for each raw ring width series. BAI represents overall tree growth better than ring width (Husch et al., 2003) because it calculates the ring width area for each year, whereas ring width does not account for tree radius. For aspen, chronologies were built using detrended and standardized ring width and BAI measurements, and grouped for trees that experienced different browse intensities within low ($n = 39$ and 88) and high fire severity ($n = 34$ and 74, for light and heavy browse, respectively). Spruce chronologies were also assembled for low ($n = 178$) and high ($n = 178$) fire severity. Autocorrelation in the final chronologies was removed using the prewhitened function. All chronologies met general chronology statistics (i.e., expressed population signal >0.85) (Wigley et al., 1984).

2.4. Data analysis

All analyses were performed in R version 3.1.2 (R Development Core Team, 2014) and reported means include ±1 standard error. Sample units were individuals nested within site. All dependent variables were log-transformed to meet assumptions of normality and homoscedasticity. Spatial autocorrelation among sites was first assessed by calculating Moran's I using the 'ape' package (Paradis et al., 2004). We found no evidence of spatial autocorrelation (Table S2) but accounted for the nesting of individuals within sites by including site as a random effect in linear mixed effect models (LME) (Zuur et al., 2009).

We used LME models, with the package 'nlme' (Pinheiro et al., 2016), to determine the effect of: fire severity and tree species on tree growth; fire severity and past browsing on aspen growth; and past browsing and 3 m threshold (below or above) on annual aspen height growth. Each model included an interaction between fixed effects and all within-level comparisons were examined by changing the reference levels for fixed effects. We considered browsing and fire severity as crossed effects, although they technically could be considered a split-plot design. We used this approach because fire behavior is a spatially contagious process and thus difficult to get spatially independent, random samples. Furthermore, previous work (Johnstone and Kasischke, 2005) indicates that pre-fire conditions in low and high severity sites were comparable thus justifying our decision to treat severity as a crossed design and include site as a random effect. The best random structure for each model was selected based on the lowest Akaike information criterion value and an F-test comparison (see Table S3 for model syntax).

To detect growth releases in tree ring chronologies, we used a radial-growth averaging criteria (Nowacki and Abrams, 1997), which is based on the running mean: $\%GC = [(M2 - M1)/M1] \times 100$ where $\%GC$ is the percentage of growth change, $M1$ is the average ring width growth over a preceding time period (e.g., 10 years) including the target year, and $M2$ (excluding the target year) is the average ring width growth over the subsequent time period (e.g., 10 years). Although a 10-year interval is common, shorter time periods have been used to investigate recent growth responses to insect outbreaks (Bretfeld et al., 2015). For our analyses, we used

Table 1

Trembling aspen and black spruce height (cm) (average ± standard error), basal area increment (BAI) (mm^2/year), and density (individuals/m^2) for low ($n = 6$) and high ($n = 6$) severity sites.

	Height (cm)	BAI (mm^2/year)	Density (individuals/m^2)
Aspen			
Low severity	126.47 ± 11.98	8.22 ± 0.74	1.11 ± 0.62
High severity	346.26 ± 37.86	50.47 ± 10.24	3.83 ± 0.65
Spruce			
Low severity	133.44 ± 6.94	18.81 ± 3.43	5.49 ± 1.57
High severity	61.39 ± 6.78	3.79 ± 0.78	1.48 ± 0.32

Table 2

Summary of browsing intensity (number of individuals) on trembling aspen and its effects on height (cm) (average ± standard error) and basal area increment (BAI) (mm^2/year) in low and high fire severity sites.

	Light browse	Heavy browse
Low severity		
Individuals browsed (#)	59	121
Height (cm)	103.13 ± 20.36	139.11 ± 10.71
BAI (mm^2/year)	6.88 ± 1.32	8.93 ± 0.66
High severity		
Individuals browsed (#)	66	114
Height (cm)	492.16 ± 106.76	250.73 ± 17.27
BAI (mm^2/year)	119.52 ± 51.65	20.37 ± 1.20

Table 3
Parameter estimates from linear mixed effect models of the effects of browsing (light and heavy) and fire severity (low and high) on aspen height (log transformed) and aspen average basal area increment (BAI) (log transformed) with a random intercept and slope for browsing effects within sites to account for site-specific responses of individual trees.

Within-level	Fixed effect	Estimate	Standard error	t-statistic	p-value
Height					
Light browse	Severity[a]	1.392	0.355	3.916	0.003
Heavy browse		0.536	0.106	5.064	<0.001
Low severity	Browse[a]	0.350	0.222	1.576	0.116
High severity		−0.505	0.228	−2.217	0.027
	Severity * Browse	−0.855	0.318	−2.687	0.008
Average BAI					
Light browse	Severity[a]	1.922	0.569	3.379	0.007
Heavy browse		0.600	0.155	3.873	0.003
Low severity	Browse[a]	0.384	0.348	1.104	0.270
High severity		−0.937	0.358	−2.617	0.009
	Severity * Browse	−1.322	0.499	−2.647	0.009

[a] Reference levels were set to low severity and light browsing, thus fixed effects are comparing: high severity to low severity, within each level of browsing, and heavy browsing to light browsing, within each level of fire severity. The interaction term (Severity * Browse) has reference levels set to low severity and light browsing.

the 'TRADER' (Tree Ring Analysis of Disturbance Events in R) package (Altman et al., 2014). Our criteria to detect growth releases included a moderate threshold of growth change between 25 and 50%, a 3 year time period averaged for pre- and post-potential release, and a 2 year time period that must exceed the growth change (Altman et al., 2014). We tested for growth releases in all standardized detrended chronologies for both aspen and black spruce. Thus, hypothesis two was tested through examination of black spruce growth patterns associated with time periods of aspen suppression and growth. Chronologies were also compared graphically and statistically, with the Gleichläufigkeit (G) coefficient (Schweingruber, 1988), to measure the similarity in tree ring growth for different time periods between browse intensities.

We projected future patterns of height-growth in aspen and black spruce depending on fire severity and browse intensity using the following assumptions. We calculated the annual height growth by taking the height of each individual and dividing by basal age, and then projected the average time it would take to reach 3 m. This approach is conservative because it assumes growth rates of lightly and heavily browsed trees will continue at their current average rate, which could change if browsed again. We used the difference in growth rate between heavily and lightly browsed aspen in high severity sites (49.6% lower in heavily browsed) to project aspen height under high intensities of moose browsing, as a negative effect on aspen growth is expected to occur (see discussion), in low severity sites after 20 years post-fire. We used 3 m as the cut-off for our projections as aspen are then safe from moose browsing, and height growth becomes nonlinear as growth increases (Chen et al., 1998).

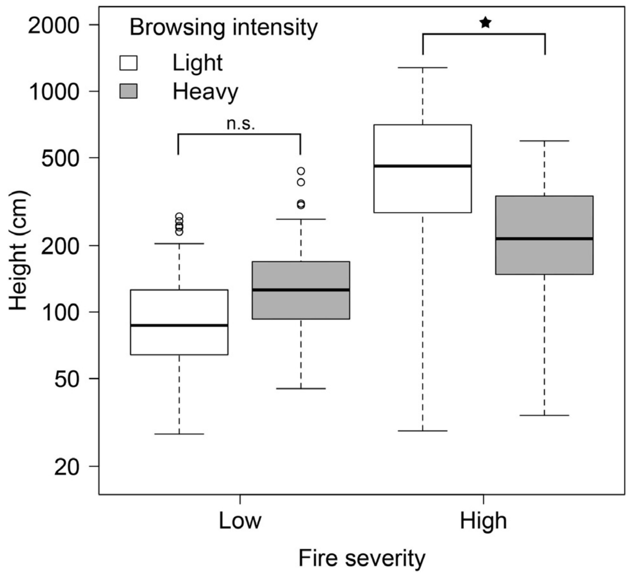

Fig. 3. Height (cm) of trembling aspen in high (n = 6) and low (n = 6) severity sites that experienced light (white boxes) and heavy (grey boxes) browsing. Boxes encompass 25–75% quantiles of the data, while whiskers encompass 5–95%. The median is indicated by the black horizontal line, and outliers are shown as dots. Note the y axis is plotted on the natural log scale. Significant differences from a linear mixed effect model comparing the effect of browsing within fire severity levels are indicated by: $^{*}P < 0.05$; n.s. $P > 0.05$.

3. Results

3.1. Study site characteristics

Tree composition and growth varied among sites with different levels of fire severity. High severity sites supported higher densi-

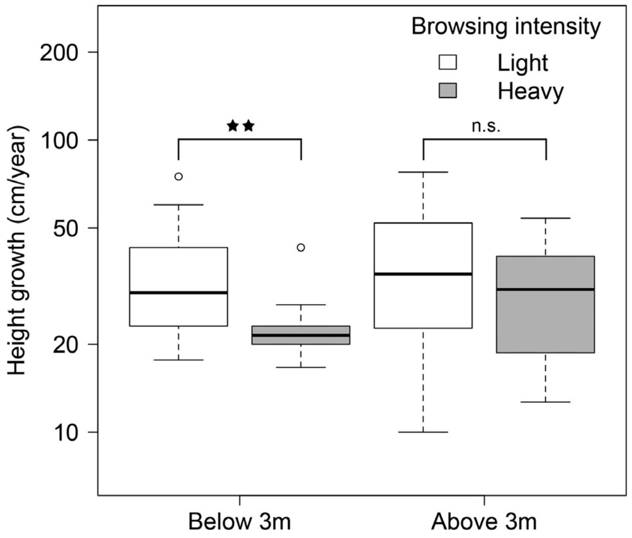

Fig. 4. Aspen height growth (cm/year) below and above three meters for individuals that were lightly (white boxes) and heavily (grey boxes) browsed; n = 46 and 29 for light and heavy browsing, respectively. Note the y axis is plotted on the natural log scale. Significant differences from a linear mixed effect model comparing the effect of browsing within the 3 m height threshold levels are indicated by: $^{**}P < 0.01$; n.s. $P > 0.05$.

ties of aspen than black spruce, whereas the opposite was true for low severity sites (Table 1). For tree height, we found a significant interaction between fire severity and tree species (Table S4). Aspen were twice as tall in high fire severity sites compared to low severity sites, while the opposite was found for black spruce (Tables 1 and S4). Aspen and black spruce were similar in height in low severity sites, whereas aspen was over five times taller than spruce in high severity sites. Average BAI of aspen and black spruce showed similar patterns as height.

3.2. Effects of browsing

Aspen and black spruce were browsed in low and high fire severity sites by moose and snowshoe hares. Aspen was heavily browsed in both fire severities (63% and 67% for high and low severity, respectively; Table 2). 94% of browsing on aspen was from moose, while the remaining individuals were browsed by snowshoe hare, or both moose and snowshoe hare. Moose browsing occurred at an average height on an aspen stem of 80.0 ± 13.9 cm and a maximum height of 261 cm. We found evidence of snowshoe hare browsing on spruce (n = 46; 360 total) with more occurrences in high severity than low severity sites. Due to the high intensity of past browsing on aspen, we focused our analyses on the effect of moose browsing on aspen growth.

Past browsing had different effects on aspen growth depending on fire severity (Table 2). With respect to aspen height and average BAI, we found a significant interaction between past browsing and fire severity (Table 3). In high severity fires, aspen that were heav-

Table 4
Parameter estimates from linear mixed effect models of the effects of past browsing (light and heavy) and three meter threshold (below and above) on annual height growth rate (log-transformed) with a random intercept for individual nested within site and random slopes for browse effects within sites.

Within-level	Fixed effect	Estimate	Standard error	t-statistic	p-value
Light browse	3 m threshold[a]	−0.029	0.076	−0.377	0.707
Heavy browse		−0.212	0.096	−2.215	0.030
Below 3 m	Browse[a]	−0.406	0.146	−2.765	0.007
Above 3 m		−0.220	0.146	−1.509	0.136
	3 m threshold * browse	−0.183	0.122	−1.500	0.138

[a] Reference levels were set to above 3 m and light browse, thus fixed effects are comparing: annual height growth below 3 m to above 3 m, within levels of browse, and heavy browse to light browse, within levels of below or above 3 m. The interaction term (3 m threshold * Browse) has reference levels set to above 3 m and light browse.

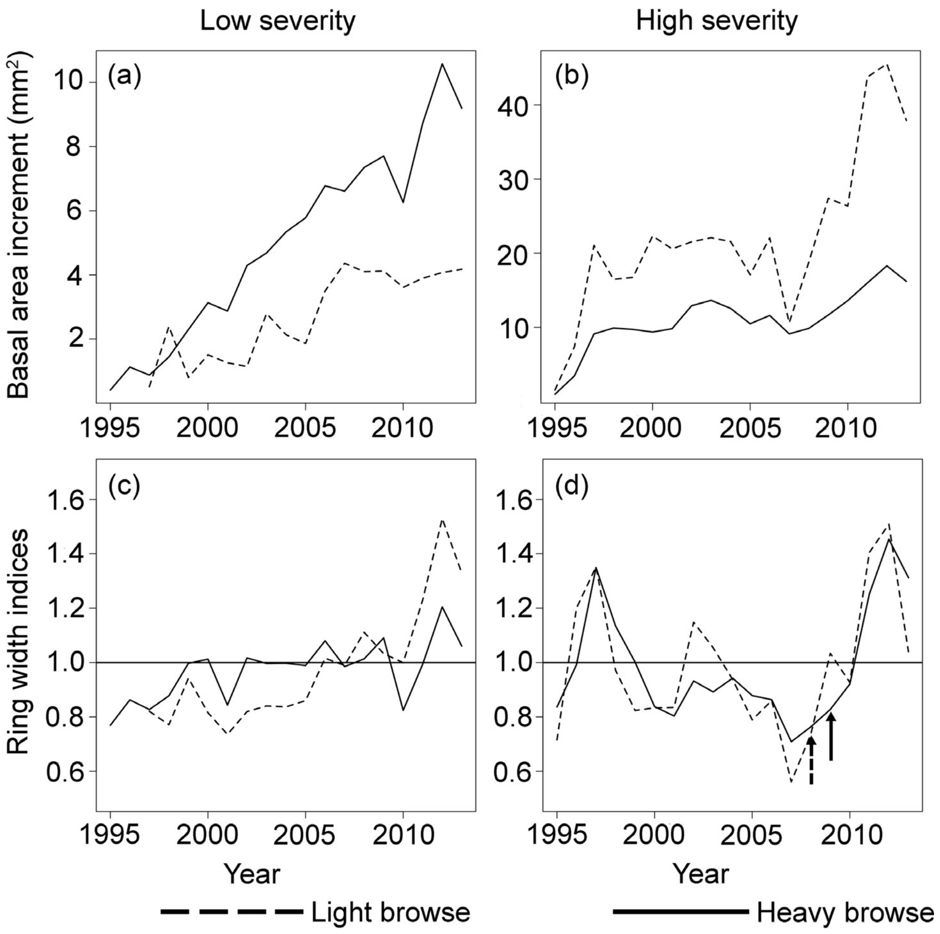

Fig. 5. Aspen basal area increment (mm^2/year) and standardized ring width chronologies from 1995 to 2013. Chronologies for light (dashed line) and heavy (solid line) browsing intensities in both low (a, c) and high (b, d) fire severity sites are included. Ring width indices are standardized with a mean of 1.0, with the black horizontal line indicating when growth was below or above average. Growth releases, detected through growth-averaging, are indicated on the ring width index plots with arrows for either low (dashed arrow) or high browsed (solid arrow) chronologies. Note the difference in y-axis values for basal area increment.

ily browsed were shorter and had a lower average BAI than those that experienced light browsing (Fig. 3). In contrast, heavy browsing had no effect on aspen growth in low severity sites (Table 3).

Of the 360 aspen trees we measured, 75 were over 3 m tall. All but one of the >3 m individuals were from high fire severity sites. The majority of these trees (61%) were lightly browsed. Lightly browsed trees reached 3 m in height before those that were heavily browsed (averaging 10.0 ± 1.3 and 13.2 ± 0.7 years for light and heavy browse, respectively). The shortest time to reach 3 m in height was 5 years post-fire. Height growth rate below and above three meters differed between browsing intensities (Fig. 4). Heavy browsing had a negative effect on annual height growth when individuals were below 3 m; there was no difference between browsing intensities once trees surpassed 3 m in height (Table 4).

3.3. Tree ring chronologies

Basal area index chronologies showed that aspen in low severity sites that established earlier were heavily browsed (Fig. 5a). Visually, similar growth patterns were present for lightly and heavily browsed aspen in low fire severity sites (Fig. 5c). Statistically, browsed aspen chronologies were moderately similar (G = 58%). For low fire severity aspen chronologies, we did not detect any growth releases for either browse intensity. In high severity sites, lightly browsed aspen were consistently larger than heavily browsed trees (Fig. 5b). Growth for both browse intensities was relatively slow from 1997 to 2007, however increased thereafter, particularly for lightly browsed trees. Lightly and heavily browsed aspen visually followed similar standardized ring width patterns, except between 2001 and 2005 (Fig. 5d). Short divergent trends in chronologies can be indicative of different responses to browsing pressure and intensity (Chouinard and Filion, 2001). Lightly browsed aspen experienced a small spike and decline in growth (2001–2005), whereas growth of heavily browsed aspen remained constant and relatively low. Overall, the two browsed chronologies in high fire severity were moderately similar (G = 0.59%). When we separated out the divergent time period (time period 2001–2005, G = 50%), we found that growth was more similar during the time periods exclusive of the divergent period (1995–2000 & 2006–2013, G = 69%). In the high fire severity chronologies, a moderate growth release occurred in 2008 for aspen that were lightly browsed, and in 2009 for aspen that were heavily browsed (Fig. 5d).

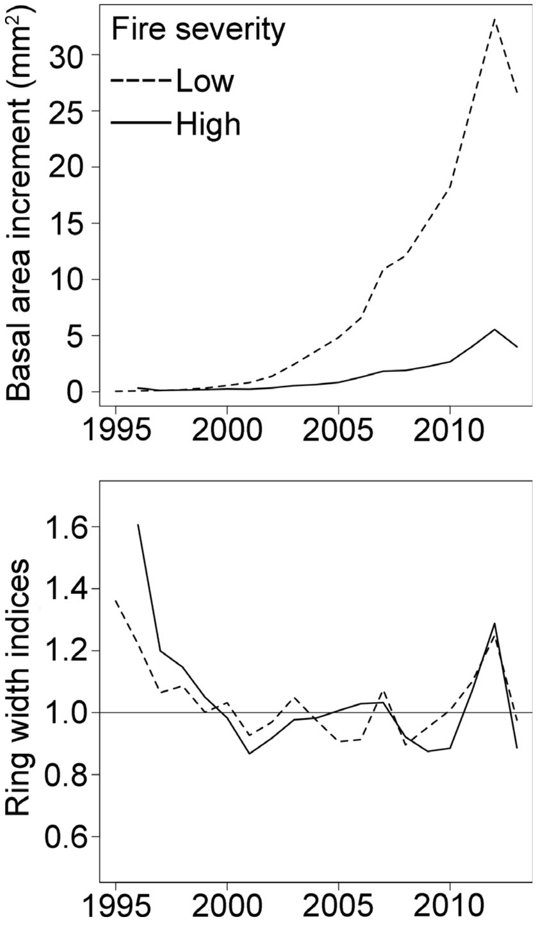

Fig. 6. Black spruce basal area increment (mm^2/year) and standardized ring width chronologies from 1995 to 2013. Chronologies for low (dashed line) and high (solid line) fire severities are included. Ring width indices are standardized with a mean of 1.0, with the black horizontal line indicating when growth was below or above average.

Growth of BAI in spruce was similar between low and high fire severities until 2000, when spruce in low severity sites grew at a faster rate (Fig. 6). Standardized ring width growth was similar between fire severities for spruce. We detected no growth releases for spruce in either the low or high fire severity chronology.

4. Discussion

Our results strongly suggest that moose are affecting the *rate* but not the *trajectory* of canopy dominance in these mixed aspen and black spruce forests. Initial effects of fire severity on post-fire tree regeneration and growth, which suggest an aspen-dominated trajectory in high severity sites (Johnstone and Kasischke, 2005; Shenoy et al., 2011), provided large amounts of available moose forage (Brown et al., 2015; Lord, 2008). Twenty years post-fire, moose had substantially reduced the rate of aspen growth in sites that burned severely during the Hajdukovich Creek fire. However, aspen at these sites have shown high tolerance to moose damage, with heavily browsed individuals approaching three meters in height. We found no growth releases in black spruce at these sites, indicating that even high levels of moose browse have been insufficient to cause these sites to revert to the dominance of black spruce that was present prior to the fire. Moose browsing in low severity sites had no effect on aspen growth rate. Browsing in low severity sites has likely been relatively light, compared to high severity sites, and has yet to cause any negative effects to aspen growth. Reconstructed patterns of aspen and spruce growth indicate that herbivory by moose has slowed the development of aspen canopy dominance in severely burned sites, but has not affected the initial trajectories of succession at high and low severity sites. Nevertheless, variations in the severity of the Hajdukovich burn has persisted as heterogeneity in tree growth and moose herbivory and had consequences for the period of time that forage is available to moose within the burn.

In high fire severity areas, moose browsing negatively affected aspen height and basal growth rates as evinced by the occurrence of twig clusters, a slower height growth rate for heavily browsed aspen under 3 m, and tree ring chronologies that diverged between heavily and lightly browsed. This finding is supported across temperate and boreal forests where ungulates have been observed to suppress growth of browsed trees (Rooney and Waller, 2003). Similarly, in Arizona, foraging by elk (*Cervus canadensis*) reduced aspen regeneration in high severity sites due to greater rates of browse damage compared to intermediate severity sites (Bailey and Whitham, 2002). In contrary, in Utah, Wan et al. (2014) found lower browse damage on aspen in moderate and high severity sites due to successfully escaping herbivore pressure by growing at a

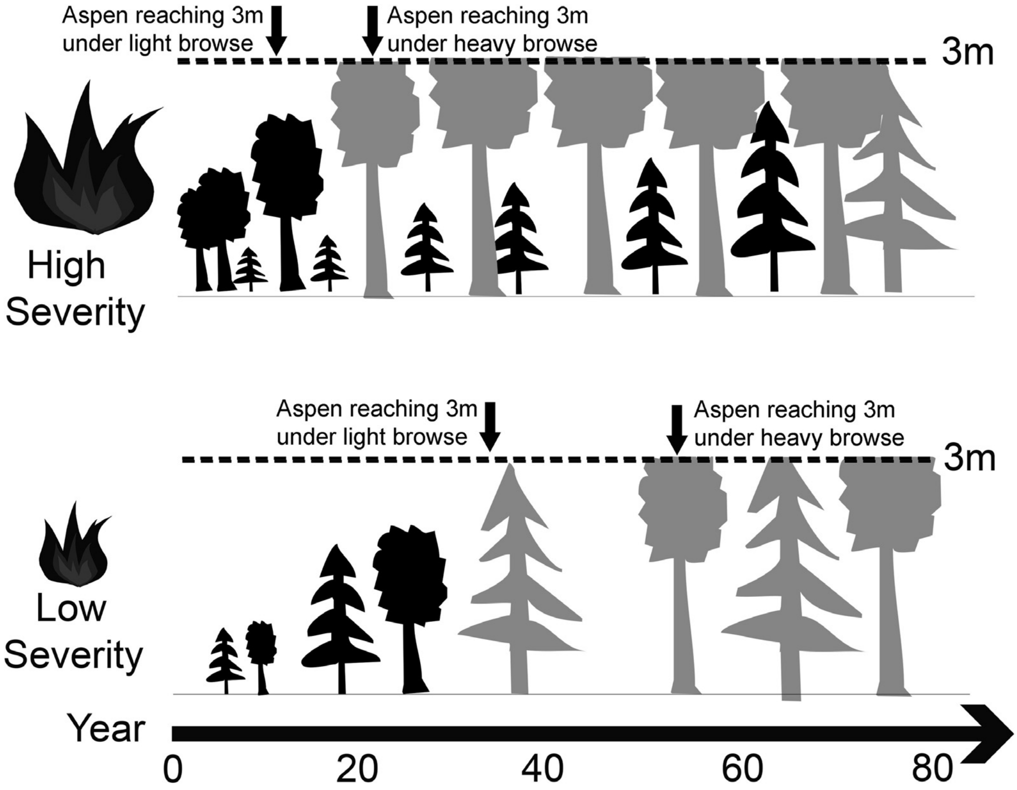

Fig. 7. Projected height-growth of aspen and black spruce after high and low severity fires. Trees below three meters are black whereas grey trees have surpassed the three meter mark. Greyed out trees are based on a heavy browse intensity, and thus represent the maximum time aspen are available as forage for moose. Arrows indicate the time period in which aspen will escape browsing pressure, based on either light or heavy browse.

faster rate. Heavily browsed aspen in our severely burned sites averaged half the height of lightly browsed individuals, and on average had yet to reach a height safe from moose browsing (>3 m) twenty years after fire (Table 2). Nevertheless, even under high browse pressure, aspen in high severity sites were still four times taller than spruce and continue to dominate these sites. Of the suppressed individuals that reached three meters in height, growth rates increased and were comparable to lightly browsed individuals (Fig. 4). The high tolerance of aspen to browsing is likely supported through mechanisms such as the utilization of reserves stored in roots or stems, increased photosynthetic activity, or the activation of dormant meristems (Tiffin, 2000).

Our results show that decreased browsing pressure can produce large increases in radial growth rates in both lightly and heavily browsed aspen in high fire severity sites. It is unlikely that growth releases were due to climatic conditions, as low and high severity sites are in close proximity to each other (Fig. 1), but no growth releases were detected at low severity sites. The observed decrease in the local moose population from 2007 to 2009 (DuBois, 2010) coincides with the growth releases. Furthermore, the proportional removal of forage by moose declined by 50% from 2007 to 2013 in high fire severity sites (Brown et al., 2015), indicating a decrease in the presence of moose at the time of the growth releases. Our results show that radial growth releases can be detected in aspen that are likely associated with a reduction in mammalian browse pressure, which is promising for future studies aiming to quantify historical effects of plant–mammal interactions.

In low severity sites, browsing had no apparent effect on aspen growth. We propose two explanations for this result: compensation and overall low browse intensity. It is plausible that moose may preferentially browse on larger individuals, increasing the chance of heavily browsed aspen being able to compensate for or adjust to the loss of tissue sufficiently to maintain similar growth rates to lightly browsed individuals (Hjálten et al., 1993). Furthermore, up until 19 years post-fire, low severity sites produced less available forage than high severity (Brown et al., 2015; Lord, 2008), which likely translates to an overall lower browsing intensity in these sites. However, twenty years post-fire in low severity sites, aspen were still vulnerable to moose browsing (i.e., below 3 m in height; Table 2), which indicates that there will be impacts from moose over decades in heterogeneously burned areas.

Differences in rates of aspen growth and timing of browsing between fire severities could affect black spruce growth and presence. In severely burned areas, lightly browsed aspen dominated the lower canopy (3 m) as early as 11 years post-fire (Figs. 7 and S2). Although moose have slowed the rate of aspen growth by 10 years in high severity areas, this did not translate into a detectable increase in black spruce growth (Fig. 6). If we assume slow black spruce growth under the dominant aspen canopy, likely due to light limitations, black spruce seedlings will be vulnerable to snowshoe hare browsing, which may further reduce their growth and/or presence in the understory (Wolff, 1978). Twenty years post-fire, aspen and black spruce are similar in height in low severity areas, which suggests a co-dominant mature forest. Moose browsing could be important in these mixed areas by targeting aspen and shifting the competitive balance towards spruce, causing growth suppression for the shade intolerant aspen (Wright et al., 2000).

Similar to moose impacts on primary succession in the floodplains in Alaska (Kielland and Bryant, 1998), we found that moose significantly affected the early stages of secondary succession by affecting the rate of aspen growth (Table 3). In contrast, in eastern North American boreal and temperate forests, large ungulates have altered forest successional trajectories (McInnes et al., 1992; Rossell et al., 2005; Thompson et al., 1992). For example, on Anticosti Island, Québec, an alternative successional trajectory of broadleaf-dominance, as opposed to *Picea* spp., was found only when white-tailed deer (*Odocoileus virginianus*) were excluded immediately after logging (Hidding et al., 2013). The high resilience and tolerance of aspen to browsing (Lindroth and St. Clair, 2013), and lower densities of large herbivores (e.g., our study with 1.78 moose/km^2 compared to the study by Rossell et al. (2005) in Virginia, USA with 67 deer/km^2) in our study area contribute to the differences between our results and those in eastern North American forests.

In interior Alaska, the highest density of moose is associated with areas that are 11–30 years post-fire, without consideration of fire severity (Maier et al., 2005; Weixelman et al., 1998). However, height-growth projections from our data illustrate that moose affect the time period of forage availability and forest structure differently in low and high fire severity patches (Fig. 7). Within the Hajdukovich Creek burn, forage was available soon after fire (fast growth in high fire severity sites) and could remain until 54 years post-fire in low severity sites. In our study, 19 years after fire, forage removal has diminished in high severity areas (Brown et al., 2015) and moose are now spending their winters in low severity areas (Kielland and Brown, 2015). Thus, the long time period of forage availability in low severity sites is attributed to an expected increase in intensity and effects of browsing twenty years after fire. However, these effects will also be contingent on the nutritional quality of forage which could decrease as time since disturbance increases, in turn affecting moose fitness and browsing (Wam et al., 2016). Low and high fire severity patches will provide forage over different periods and lengths of time, thus predictions of optimal post-fire moose habitat should include variations in fire severity.

5. Conclusion

In high fire severity sites, moose browsing had direct negative effects on aspen growth, but had no associated indirect effects on spruce growth. Although moose browsing slowed aspen growth in severely burned areas, aspen still dominated the canopy, demonstrating high tolerance to browsing. Extrapolation of herbivory effects from high to low fire severity suggests that moose effects on aspen growth in low severity burns may hasten the recovery of black spruce canopy dominance, but such effects were not yet apparent 20 years after fire. Heterogeneous patterns of fire severity can play an important role in maintaining variations in post-fire succession and sustaining high rates of available moose forage for a much longer period than previously reported.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.02.018.

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