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Postfire deciduous canopies drive patterns in snowshoe hare herbivory of regenerating black spruce

Justin Olnes, Knut Kielland, Hélène Genet, and Roger Ruess

Abstract: The future of boreal forests in Alaska, United States, will likely consist of more deciduous-dominant stands because larger and more severe fires facilitate the establishment of deciduous species such as trembling aspen (*Populus tremuloides* Michx.) and Alaska birch (*Betula neoalaskana* Sarg.). Whether stands transition to a deciduous-dominant system or mixed-wood forest or return to being dominated by black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) depends on the capacity of regenerating black spruce to grow and produce seed before the next fire. We hypothesized that winter herbivory by snowshoe hares (*Lepus americanus* Erxleben, 1777) can suppress black spruce under deciduous canopies. We addressed this question by measuring changes in spruce height and herbivory across 54 plots in Interior Alaska that burned 8–88 years ago and related these data to plot-level data collected by the Bonanza Creek Long-Term Ecological Research program. Spruce were more likely browsed at deciduous-dominant sites with dense canopies, and this browsing likely reduced their height growth. Although we found more subtle effects of browsing on height at the individual level, browsing was an important variable in a confirmatory path analysis at the plot level. These observations affirm our broader hypothesis of the selectivity of hare browsing, in that snowshoe hares prefer to browse spruce that are taller and faster growing, effectively "leveling" regenerating seedlings and saplings so that browsed and unbrowsed individuals within a site are the same height.

Key words: boreal forest, postfire regeneration, Alaska, *Lepus americanus*, *Picea mariana*.

Résumé : Les futures forêts boréales en Alaska comporteront probablement plus de peuplements dominés par des feuillus parce que les feux plus vastes et plus sévères facilitent l'établissement d'essences feuillues telles que le peuplier faux-tremble (*Populus tremuloides* Michx.) et le bouleau d'Alaska (*Betula neoalaskana* Sarg.). À savoir si la transition des peuplements évoluera vers un système dominé par les feuillus, une forêt mélangée, ou le retour à la dominance de l'épinette noire (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.), dépend de la capacité de la régénération d'épinette noire de croître et de produire des semences avant le prochain feu. Nous avons émis l'hypothèse que le broutement hivernal du lièvre d'Amérique (*Lepus americanus* Erxleben, 1777) peut supprimer l'épinette noire sous des couverts feuillus. Nous avons abordé cette question en mesurant les changements dans la hauteur de l'épinette et le broutement dans 54 parcelles situées à l'intérieur de l'Alaska, qui ont brûlé il y a 8 à 88 ans, et en mettant ces données en relation avec des données à l'échelle de la parcelle collectées dans le cadre du programme de recherche à long terme en écologie de Bonanza Creek. Les épinettes avaient plus de chances d'être broutées dans les stations dominées par des feuillus avec un dense couvert forestier et ce broutement a probablement réduit leur croissance en hauteur. Bien que nous ayons observé des effets plus subtils du broutement sur la hauteur à l'échelle de l'individu, le broutement était une variable importante dans une analyse causale de confirmation à l'échelle de la parcelle. Ces observations confirment notre hypothèse plus étendue de sélectivité du broutement du lièvre selon laquelle ce dernier brouterait les épinettes plus hautes qui croissent plus vite, ce qui nivellerait effectivement la régénération de semis et de gaules de telle sorte que les individus broutés et ceux qui ne l'ont pas été dans une station ont la même hauteur. [Traduit par la Rédaction]

Mots-dés : forêt boréale, régénération après feu, Alaska, *Lepus americanus*, *Picea mariana*.

Introduction

The future boreal forest of Alaska, United States, is predicted to differ from the current boreal forest, as a greater proportion of the landscape will likely be dominated by deciduous or mixed-wood forests (Shenoy et al. 2011). Similar changes are expected across the world's boreal region, which will significantly affect both regional economies and global ecosystem services provided by the boreal forest (Gauthier et al. 2015). For example, changes in forest composition will influence the rate of biomass accumulation (Chen and Luo 2015), the location of carbon accumulation during postfire succession (Alexander and Mack 2016), and the degree to which increased biomass production will offset the release of carbon from permafrost as the boreal region warms (Abbot et al. 2016). This potential shift to a new ecological state has significant implications for climate–ecosystem feedbacks (Mann et al. 2012), creating a need to understand factors that facilitate or inhibit the transition towards deciduous dominance in regions like Alaska's boreal forest.

In Alaska, a primary driver of this shift in forest composition is changes to the fire regime (Kelly et al. 2013). Fire scientists have documented a significant increase in the annual extent of area burned (Kasischke et al. 2010) and in the severity of fires (Turetsky

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J. Olnes. Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, AK 99775, USA.
K. Kielland and R. Ruess. Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, AK 99775, USA; Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775, USA.
H. Genet. Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775, USA.
Corresponding author: Justin Olnes (email: jrolnes@alaska.edu).

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et al. 2011). Larger and more severe fires facilitate postfire establishment of trembling aspen (*Populus tremuloides* Michx.) and Alaska birch (*Betula neoalaskana* Sarg.) in moderately drained to well-drained areas that were once dominated by the conifer black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.). The presence of trembling aspen and Alaska birch reflects a shift away from the self-replacement of black spruce that is thought to most commonly occur (Johnstone et al. 2010). Rather, a deciduous canopy may persist for half a century or more before black spruce, if also present following fire, could emerge as the canopy dominant by way of relay succession (Kurkowski et al. 2008).

Several studies suggest that the fire-return interval in boreal Alaska is often too short to allow for relay succession (<100 years; Kurkowski et al. 2008; Johnstone et al. 2010; Shenoy et al. 2011). However, historical fire-return intervals are based on wildfires occurring in spruce-dominated landscapes, and fire records are not long enough or old enough to assess the reburn potential of these novel, postfire deciduous stands that are less flammable than conifer-dominated stands (Bernier et al. 2016). For example, the Bonanza Creek Long-Term Ecological Research (BNZ LTER) program maintains a Regional Site Network (RSN) of 94 plots within fire scars of varying age and burn severity (described in more detail in the following section). Nearly all young and intermediate-aged sites classified as deciduous forest contain regenerating black spruce that grow slowly beneath the deciduous canopy. Whether boreal landscapes transition more permanently to a deciduous-dominated state or mixed-wood forest or return to a system dominated by black spruce will depend on the capacity of black spruce to survive and produce seed while outlasting Alaska birch and trembling aspen before the next fire. In the absence of fire, stands of Alaska birch and trembling aspen may begin to senesce after ~100 years; however, black spruce can persist for hundreds of years (Kurkowski et al. 2008). Thus, factors affecting the growth and mortality rates of black spruce under deciduous canopies can influence the likelihood of relay succession and whether black spruce can produce seed for regeneration prior to reburning (Chapin et al. 2004).

Herbivory by snowshoe hares (*Lepus americanus* Erxleben, 1777; hereafter referred to simply as "hares") is one mechanism that could suppress regenerating black spruce in the understory of deciduous trees. Following moderate to severe fire, recruiting deciduous trees create dense cover that is preferred by hares. Although black spruce, trembling aspen, and Alaska birch may simultaneously recruit immediately following fire (Johnstone and Chapin 2006), differences in growth rates may result in deciduous trees creating suitable canopy cover for hares while black spruce lingers in the understory, within browsing range. If this period of postfire succession aligns with a peak in the 10-year hare-population cycle (Krebs et al. 2013), then it is possible that abundant hares may significantly browse recruiting black spruce under these dense deciduous stands.

Although black spruce is considered among the least palatable of boreal tree species (Bryant and Kuropat 1980), it is known to be an important component of the hare's winter diet (Wolff 1978). Studies from Canada's boreal forest have shown that herbivory can reduce the growth and survival of black spruce seedlings in collapse-scar bogs (Camill et al. 2010) and at the elevational tree line (Munier et al. 2010). In Alaska, hares are known to similarly affect the establishment of white spruce (*Picea glauca* (Moench) Voss) during floodplain succession (Olnes and Kielland 2017) and at the tree line (Olnes et al. 2018), particularly during periods of high population abundance. These studies revealed complex interactions among the height growth and survival of white spruce, hare herbivory, canopy cover, and snow depth that suggest that hares browse taller seedlings that protrude above the winter snowpack (Olnes et al. 2017, 2018). By browsing, and thus suppressing, white spruce seedlings that are initially taller, hares increase the time required for cohorts of white spruce to escape browsing and reach the canopy (Olnes et al. 2018). Although we have observed evidence of hares browsing regenerating black spruce following fire at several RSN sites, their capacity to influence the height growth of black spruce, and thus postfire vegetation dynamics, is not well understood.

Here we address the question of whether herbivory by hares on black spruce negatively affects black spruce regeneration during postfire succession in the boreal forest of Interior Alaska. We hypothesize that herbivory by hares suppresses regenerating black spruce, specifically under deciduous canopies. By suppressing seedlings in the understory, browsing by hares may reduce or delay the emergence of black spruce into the canopy, altering the structure and composition of postfire forests.

Methods

The RSN

The BNZ LTER program maintains research plots (n = 94) throughout Interior Alaska that make up the RSN and vary in site drainage conditions, topography, disturbance history (time since fire and burn severity), and conifer and deciduous tree densities. A description of the RSN can be found at the BNZ LTER website (http://www.lter.uaf.edu/research/study-sites-regional). We sampled 54 RSN plots across all 14 fire scars within the network, capturing the range of variability in time since disturbance, landform, and vegetation composition representative of the entire RSN (Table S1[1]). Dominant tree species at each plot were either black spruce, trembling aspen, or Alaska birch. Although many plots include significant numbers of white spruce, this species was excluded from our analysis because our focus is the effect of deciduous tree species on interactions between black spruce and hare. Twenty plots were within young burns (<20 years since fire), 24 plots were at intermediate-aged burns (45–75 years since fire), and 10 plots represented mature forest stands (>80 years since fire). Plots in young and intermediate-aged stands were dominated by black spruce, mixed-wood trees, or deciduous trees, whereas all mature plots were dominated by black spruce. All plots had been dominated by black spruce prior to burning.

By sampling plots within the RSN, we were able to use BNZ LTER forest inventory data to inform our analysis of hare herbivory and postfire succession. For each plot, we obtained data on seedling (<1.4 m tall), sapling (<2.5 cm diameter at breast height (DBH; breast height = 1.37 m)), and tree (>2.5 cm DBH) densities for Alaska birch, trembling aspen, and black spruce (individuals per hectare) and calculated tree basal area (BA) by species (square metres per hectare). All data are available online via the BNZ LTER database (http://www.lter.uaf.edu/data/data-catalog) and are summarized in Table S1.[1] From the inventory data, we calculated the proportion of trees that were deciduous and the proportion of total stand BA made up of deciduous trees.

Field sampling

We collected additional site variables for each plot in the summer of 2017. Each RSN plot is 50 m × 60 m and is subdivided into thirty 10 m × 10 m subplots, delineated by plot markers every 10 m. We sampled within the perimeter subplots to limit our effect on the core subplots, where long-term monitoring of tree growth and mortality takes place. At each plot, we began sampling at the northwest corner and sampled along the center (5 m from the edge) of each perimeter subplot. We sampled every black spruce seedling or sapling nearest to a transect running through the center

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[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2019-0150.

of the perimeter subplots at 5 m intervals (~36 individuals per plot). Within each corner subplot, as well as at the center point (30 m) of transects running along the 60 m sides of the plot, we measured canopy cover from a height of 1.4 m above the ground using a spherical densiometer and facing towards the center of the plot (n = 4–6 subsampling points per plot). At each location where we measured canopy cover, we also counted the number of hare pellets within a 1 m^2 quadrat. Canopy-cover readings and hare-pellet densities were averaged to obtain a single value for each plot. Additionally, we counted the total number of standing dead black spruce with visible hare-browse scars within a random selection of subplots (n = 3–5 subplots per plot).

We made a series of measurements to inform our understanding of hare herbivory and its effect on the height growth of black spruce. For each individual black spruce sampled, we measured the height (in centimetres) and basal diameter (in millimetres) and counted the total number of apical browse scars. Hares most commonly browse the apical leader of spruce, and their bite marks are easily distinguished as a sharp browse scar at a 45° angle. Additionally, we estimated the year of browsing for the three most recent browse scars on each black spruce by counting annual growth segments from the current annual growth to the browse scar and then subtracting this value from the year of sampling (2017) (Olnes et al. 2017). We also measured the height of the tallest browse scar on each spruce.

Analysis

All analyses were conducted using R statistical software (version 3.5.1; R Core Team 2018). Significance was determined by an alpha value of 0.05 for all statistical tests ($\alpha = 0.05$).

Individual effects of browsing

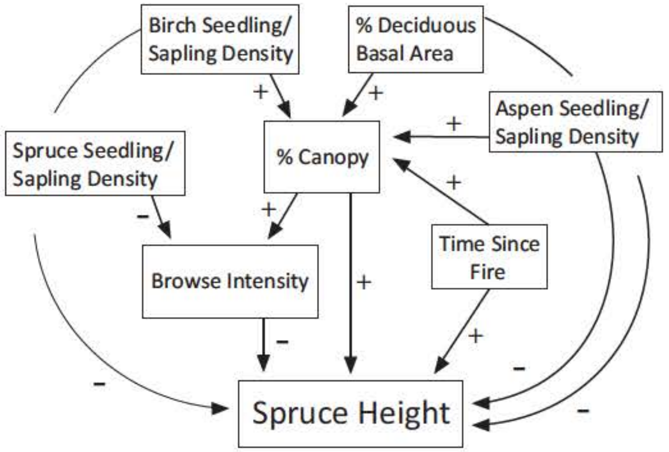
To estimate the probability of an individual spruce being browsed, we used generalized linear mixed-effects models that included plot-level estimates of the percentage of deciduous stand BA, individual spruce height (0–200 cm), and their interaction term as our fixed effects (library: lme4, function: glmer; Bates et al. 2015). We compared five separate models that included our full model and models with sequentially removed terms to a final intercept-only model using Akaike's information criterion (AIC; function: aic). We included the percentage of deciduous stand BA as a fixed effect because we hypothesized that browsing would be positively associated with denser, deciduous-dominant stands and their associated closed canopies (Olnes and Kielland 2016). We further assumed that spruce height would positively relate to the probability of being browsed because of interactions between winter browsing and snow depth (Olnes et al. 2018), as well as the fact that taller spruce have likely been exposed to browsing hares for a longer amount of time than shorter spruce. We used a binomial distribution with a logit link function, and sampling plot and plot within fire scar were random effects to avoid pseudoreplication. To test for overdispersion, we used the R function dispersion_glmer (library: blmeco; Korner-Nievergelt et al. 2015) to calculate a dispersion factor, for which values close to 1.0 suggest that overdispersion is not an issue (Bolker et al. 2009). We estimated the importance of fixed effects by calculating z scores to determine whether coefficient values were significantly different from zero. We calculated both the marginal coefficient of determination (R_m^2) and the conditional coefficient of determination (R_c^2), which explain the amount of variation due to the fixed effects and the fixed effects plus the random effects, respectively (library: MuMIn, function: r.squaredGLMM; Nakagawa and Schielzeth 2013).

We investigated the effect of hare herbivory on height of individual black spruce using two sets of linear mixed-effects models (library: lme4, function: lmer; Bates et al. 2015). To specifically capture the effect of hare browsing, we only included seedlings and saplings with apical growth points below 200 cm, within the browsing range of hares (mean tallest browse scar ± standard error (SE) = 74.72 ± 1.65 cm). This cutoff also improved our ability to meet the assumptions of linear regression (equal variance and normality of residuals) while preserving 89% of the data set for the height analyses (n = 1256). Our explanatory variables for spruce height were the time since fire, browsing intensity, their interaction term, and the proportion of deciduous tree BA in the plot. We used time since fire as a proxy for spruce age because of large uncertainty around the estimates of black spruce age in the field (data not shown) and assumed the relationship with spruce height would be positive. Our browsing-intensity variable was categorical and was defined by the number of apical browse events. Spruce were either not browsed, moderately browsed (1 or 2 apical browse events), or severely browsed (≥3 apical browse events (mean ± SE = 3.5 ± 0.07 events)). We included proportion of deciduous tree BA to compare spruce height across a spectrum of stand types (purely coniferous to purely deciduous). Again, we sequentially removed terms from our full model to generate a set of six models that were compared using AIC. We then created a set of identical models, except we used the ratio of spruce height to basal diameter as the response variable instead of absolute height. Spruce basal diameter served as an alternative proxy for spruce age, and by assessing the relationship between height and basal diameter, we also gained insight into how browsing may influence individual spruce structure (tall and thin versus short and wide). Our models included the random effects of fire scar and plot within fire scar. Assumptions of linear models were confirmed graphically, and the significance of fixed effects were determined by F tests for mixed-effect models (library: lmerTest, function: anova; Kuznetsova et al. 2017). To assess where significant differences in our response variables occurred between browsing categories, we performed pairwise comparisons for mixed-effects models (library: emmeans, function: emmeans; Lenth 2016).

Postfire stand-level effects on interactions between black spruce and hare

The R statistical package piecewiseSEM allows users to explore hypothesized complex ecological interactions by using linear or generalized linear mixed-effects models to define pathways in a confirmatory path analysis, also known as piecewise structural equation modeling (SEM) (Lefcheck 2016). We used confirmatory path analysis to further test our hypothesis that deciduous-dominant canopies promote browsing and lead to reduced height in black spruce. This analysis was performed at the plot level, and because hare browsing appeared minimal in mature plots (fire scars ≥ 80 years old), we built our model paths using only young and intermediate-aged plots (n = 42). Our data set was suitable for confirmatory path analysis using piecewiseSEM because (*i*) this methodology allowed us to account for the hierarchical nature of the data and use fire scar as a random effect for each path, (*ii*) our data set met the rule of thumb that the ratio of data to variables be at least 5 to 1, and (*iii*) our individual paths met the assumptions of linear mixed-effect models (equal variance and normality of residuals) (Lefcheck 2016). For this analysis (Fig. 1), browse intensity was a continuous variable defined as the mean number of apical browse events per individual spruce within a plot. We hypothesized that browsing intensity is directly related to the density of spruce seedlings and saplings (–, negative correlation) and hare abundance that is spatially driven by habitat suitability (e.g., canopy cover) (Olnes and Kielland 2016). Therefore, we predicted that canopy cover would positively influence browsing intensity on black spruce (+, positive correlation) and that canopy cover would be influenced by time since fire (+), the proportion of stand BA that is deciduous (+), and the density of deciduous (trembling aspen and Alaska birch) seedlings and saplings (+). We then predicted that spruce height would be positively influenced by canopy cover (+), based on studies of the susceptibility of white spruce and black spruce to drought stress (Angell and Kielland 2009; Walker et al. 2015). We also hypothesized that spruce height is

Fig. 1. Hypothesized paths that place herbivory of black spruce by snowshoe hares into postfire ecological context. +, positive correlation; –, negative correlation. Spruce refers to black spruce, birch refers to Alaska birch, and aspen refers to trembling aspen.



positively related to time since fire (+) and negatively affected by both browsing intensity (–) and competition with deciduous trees (–). With piecewiseSEM, model suitability was tested using Fisher's C, which tests whether the model pathways appropriately describe relationships in the data. P values > 0.05 suggest a suitable set of models and imply that no critical paths are missing (Lefcheck 2016). Because confirmatory path analysis using piecewiseSEM is built from linear mixed-effects models, we also compared the validity of including browsing intensity in our model by performing a likelihood ratio test on input models with or without the pathway of browse intensity to spruce height. All variables within the models were standardized and centered on a mean of 0 and a standard deviation of 1 to allow for direct comparison of effect size among variables.

To further test our broader hypothesis of selectivity of hare browsing, in which hares preferentially browse spruce that are taller and faster growing and protrude above the winter snowpack (Olnes et al. 2018), we compared how variation in spruce height changes with increasing browsing at the plot level. We used linear regression (R base function: lm) to build a model in which the standard deviation in spruce height was our response variable and the mean number of apical browse events and stand age class (young or intermediate) were the fixed effects. A likelihood ratio test confirmed that including the random effect of fire scar was not necessary, and we did not include mature sites for this analysis, as browsing was minimal at mature sites.

Results

We sampled 1411 individual black spruce at 54 sites. Past apical browse events were evident on 40% of all sampled spruce (33% moderately browsed (1 or 2 events) and 7% severely browsed (≥3 events)). Most browsing occurred during periods of high abundance of hare (2008–2009 and 2015–2018), particularly within sites of intermediate age (Fig. 2*a*). For young sites, browsing had only occurred within the recent rise in hare abundance across the region, as determined by ongoing mark–recapture studies (K. Kielland, unpublished data). Browsing was minimal across the mature sites.

Individual effects of browsing

The probability of an individual spruce being browsed is a function of stand-level vegetation characteristics and spruce height. The full logistic mixed-effects model that included percent deciduous BA, individual spruce height, and their interaction term produced the lowest AIC score among our candidate models (1203 versus 1208 in the next model). The probability of being browsed increased with increasing deciduous dominance (Fig. 2*b*; $z = 2.82$, $p = 0.004$), and individual spruce height positively interacted to further increase the probability of being browsed (Fig. 2*b*; $z = 2.72$, $p = 0.006$). Nearly all individual black spruce recruiting under purely deciduous canopies were likely to be browsed at least once before escaping the hares' browse range, which is around 200 cm. Percent deciduous BA and spruce height explained 27% of the variation in the probability of being browsed, whereas the random effect of plot explained an additional 35% of the variation ($R_c^2 = 0.62$).

For our subsample of spruce under 200 cm, the best model for individual spruce height included only our browsing variable (Table 1). Among browsing categories, only moderately browsed spruce differed from spruce that had not been browsed, and these individuals tended to be taller than unbrowsed individuals (Fig. 2*c*; mean difference ± SE = 6.7 ± 2.5 cm, $t = -2.6$, $p = 0.02$). Despite statistical significance, browsing explained <1% of the variation in individual tree height, whereas the random effects of plot and plot within fire scar explained 50% of the variation in spruce height ($R_c^2 = 0.50$), suggesting that unaccounted site variables have a greater influence on individual spruce height than that of browsing by hares.

The ratios of spruce height to basal diameter were best explained by our full model (Table 1). These ratios significantly varied across all browsing categories in a negative relationship (Fig. 2*c*; $F = 15.75$, degrees of freedom (df) = 1, 1243.3, $p < 0.001$), and there was a significant interaction with time since fire in which moderately browsed spruce tended to have larger ratios of height to basal diameter with greater stand age ($\beta = 0.017$, $t = 3.04$, df = 0.001, $p = 0.002$). Time since fire did not affect the ratios of height to basal diameter for unbrowsed or severely browsed spruce. Moderately browsed spruce were 0.73 ± 0.15 $\text{cm}\cdot\text{mm}^{-1}$ shorter than spruce that had not been browsed ($t = 4.8$, df = 1241.7, $p < 0.001$). Severely browsed spruce were 1.87 ± 0.29 $\text{cm}\cdot\text{mm}^{-1}$ shorter than unbrowsed spruce ($t = 6.5$, df = 1259.2, $p < 0.001$) and 1.14 ± 0.27 $\text{cm}\cdot\text{mm}^{-1}$ shorter than moderately browsed spruce ($t = 4.1$, df = 1237.7, $p < 0.001$). The proportion of deciduous tree BA was also significant ($F = 8.32$, df = 1, 47.40, $p = 0.005$) and positively influenced the ratios of spruce height to basal diameter ($\beta = 1.01$, $t = 2.88$, df = 0.47, $p = 0.005$). Together, these variables explained 8% of the variation in the ratios of spruce height to basal diameter ($R_m^2 = 0.08$), and plot and plot within fire scar explained an additional 17% of the variation ($R_c^2 = 0.25$).

Postfire stand-level effects on interactions between black spruce and hare

Our confirmatory path analysis placed interactions between black spruce and hare into a broader (postfire) ecological context and was a suitable description of the data according to Fisher's C test (Fig. 3; $C = 6.2$, df = 12, $p = 0.90$). Our likelihood ratio test of the input models further affirmed browsing as an important variable ($\chi^2 = 5.6$, df = 1, $p = 0.02$). For our pathway analysis, time since fire was positively related to spruce height ($\beta = 0.69$, $p = 0.04$). Browsing intensity was negatively related to spruce height ($\beta = -0.31$, $p = 0.03$), but this effect was counteracted by the direct positive effect of canopy cover on spruce height ($\beta = 0.51$, $p = 0.02$). These three variables explained 55% of the variation in spruce height at the plot level ($R_m^2 = 0.55$). Canopy cover had an indirect negative effect on spruce height by positively relating to browsing intensity ($\beta = 0.69$, $p < 0.001$), explaining half of the variation in hare browsing ($R_m^2 = 0.49$). Percent canopy cover was largely explained ($R_m^2 = 0.71$) by the percentage of BA that was deciduous ($\beta = 0.49$, $p < 0.001$), time since fire ($\beta = 0.83$, $p < 0.001$), and seedling density of Alaska birch ($\beta = 0.23$, $p = 0.01$).

The standard deviation in spruce height within plots decreased with increasing browse levels for both young and intermediate-

Fig. 2. Individual effects of browsing. (*a*) The proportion of sampled spruce browsed each year averaged across plots (mean ± standard error) for each age group of fire scars (young (<20 years since fire), intermediate (45–75 years since fire), and mature (>80 years since fire)). The pattern in browse events demonstrates that most browse events occurred during the peak in hare population of 2008–2009 and during the two recent winters (2015–2016 and 2016–2017). Periods of peak hare abundance are denoted by black triangles along the *x* axis. (*b*) The probability of an individual spruce seedling or sapling being browsed increases with increasing deciduous dominance (percentage of stand basal area (BA) that is deciduous) and with increasing spruce height. Curves represent how the probability varies for different spruce heights ranging from 10 to 195 cm. R^2_m, marginal coefficient of determination; R^2_c, conditional coefficient of determination. (*c*) The relationships between hare browsing and black spruce height (mean and 95% confidence interval, grey dots) and hare browsing and ratio of height to basal diameter ratio (height/diameter, black dots). Different letters note significant differences between browsing categories for each response.

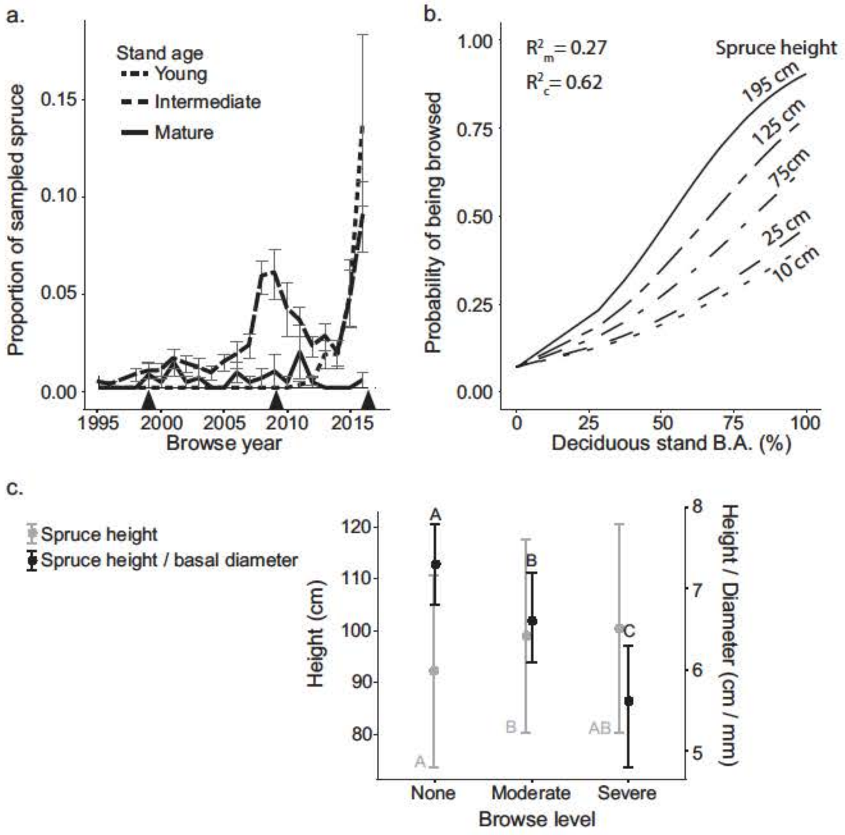


Table 1. Mixed-effect models for height and ratio of height to diameter in black spruce.

Model	AIC for height	AIC for the ratio of height to diameter
TimeSinceFire × browse + %BA deciduous	12 526	**5 439**
TimeSinceFire × browse	12 524	5 444
TimeSinceFire + browse	12 521	5 449
TimeSinceFire	12 525	5 492
Browse	**12 519**	5 450
Intercept only	12 523	5 493

Note: Top models are indicated in boldface type, and all covariates within top models were statistically significant. AIC, Akaike's information criterion; TimeSinceFire, time since fire (years); browse, categorical browse variable (none, moderate (1 or 2 apical browse events), or severe (≥3 browse events)); %BA deciduous, percentage of basal area that is deciduous.

aged plots (Fig. 4; $F = 15.96$, df = 2, 43, $p < 0.001$, $R^2 = 0.42$). For every increase of 1 in the mean number of apical browse events, the standard deviation in height decreased by 12.72 cm.

Discussion

Hares are browsing regenerating black spruce at a high rate (40% of seedlings and saplings browsed when averaged across all stands), likely resulting in some reduced height growth. The positive influences of deciduous dominance on canopy cover and canopy cover on hare browsing (Fig. 3) imply that hare herbivory does suppress recruiting black spruce, specifically under deciduous canopies. However, the magnitude of the browse effect on the height of an individual black spruce was much smaller than we anticipated, based on the low marginal R^2 values for our height models. The seemingly negligible effect of browsing at the individual level highlights the capacity of black spruce seedlings and saplings to succeed under deciduous canopies despite pressure from browsing hares. Because browsing is strongly associated with deciduous canopy cover, negative browse effects may be masked by other positive effects associated with cover such as improved microclimate for seedling height growth. This net positive effect suggests a level of resiliency to changing stand dynamics (i.e., canopy cover and hare browsing).

Although black spruce appears largely resilient to hare browsing, the browse effect we did observe was similar to what we previously described for regenerating white spruce in Alaska (Olnes et al. 2018). The response of spruce to browsing is consistent with the hypothesis that fast growth resulting in a taller plant that reaches above the snow surface results in increased risk of being browsed (Olnes et al. 2018). We interpret this phenomenon as a plant-vigor effect (Price 1991). Browsed black spruce differ marginally in height from unbrowsed individuals; however, they have significantly greater basal diameters. This results in reduced ratios of height to

Fig. 3. Pathways placing hare browsing into its broader ecological context. Numbers represent relative effect size of each parameter on the corresponding variable. All values shown are statistically significant ($p < 0.05$); statistically nonsignificant pathways have been omitted for visual clarity (see Fig. 1). Birch refers to Alaska birch. R^2_m, marginal coefficient of determination.

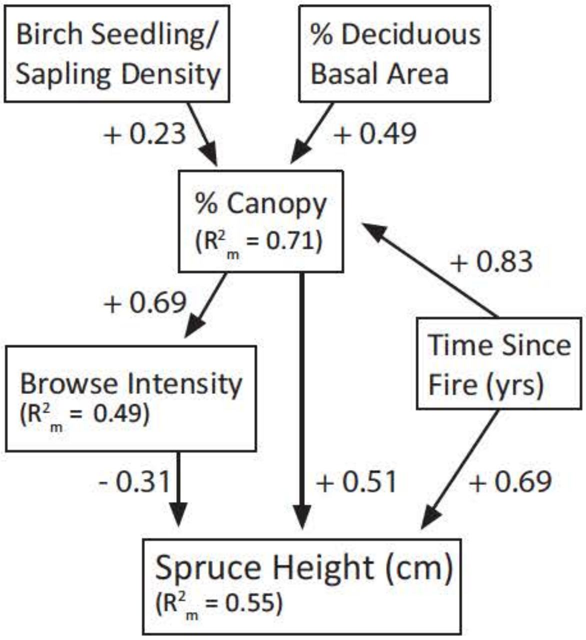
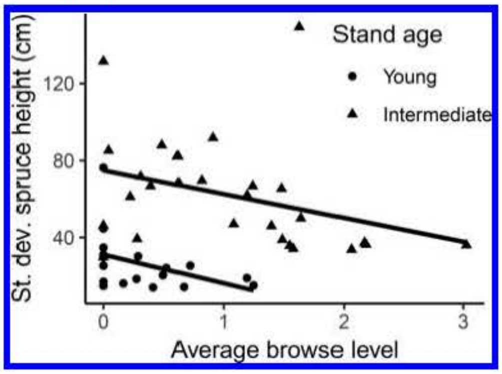


Fig. 4. Variation in spruce height (presented as the standard deviation (St. dev.) around mean spruce height at the plot level) declines with increasing browse intensity (mean number of apical browse events per spruce).



diameter with increasing browsing (Fig. 2c) and suggests that hare browsing suppresses either older or more vigorous spruce that would otherwise be taller. Spruce that are not browsed tend to be shorter because they are still shielded from hares under the snowpack, they are too young (less time exposed to hares), or hares may be selecting against individuals that are slower growing (Olnes et al. 2018). If so, browsing by hares suppresses the individuals that grow fastest following fire, causing black spruce that are slower growing to determine the rate of emergence into the canopy. Although we observed these patterns as significant, browsing intensity as a variable explained very little of the variation in black spruce height and the ratio of height to diameter (<10%), making it important to note that browsing is one of numerous influences on the growth of individual black spruce.

The magnitude of the browse effect observed at any time is influenced by the timing of the hare cycle because browsing frequency and intensity track fluctuations in hare abundance (Fig. 2a; Olnes et al. 2017). Recruiting black spruce that are in browse range during a period of low hare abundance have a lower probability of being browsed. On the other hand, if the window for early recruitment following fire aligns with a peak in hare population, then hares browse black spruce at a high rate (Sinclair 2003). The time since last fire and stage of postfire succession interact with the hare cycle because habitat suitability changes over time and only some successional stages provide suitable cover and sufficient forage for hares (Feierabend and Kielland 2014). There is a narrow window of time following fire during which there is sufficient cover to attract hares and black spruce are within browsing range, and the capacity of hares to limit regeneration of black spruce depends on how this narrow window of time aligns with the peak in hare population.

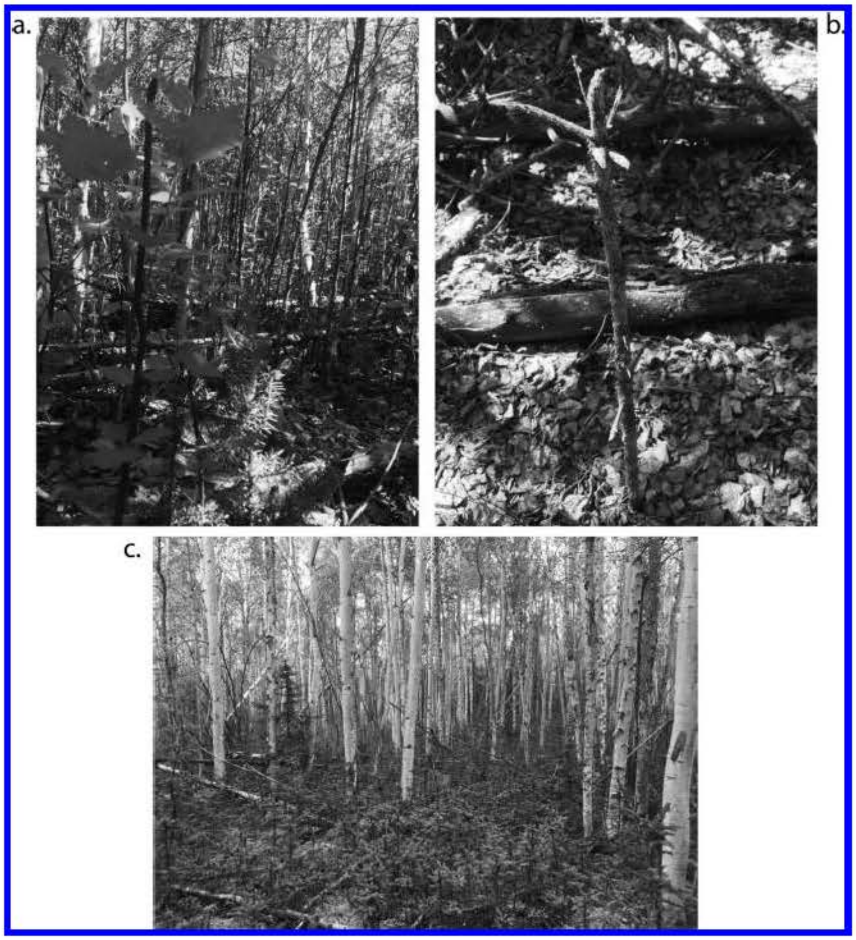
For example, browsing is just beginning to occur within the young sites corresponding to the recent, slow increase in hare densities (Fig. 2a). Many of these sites present an opportunity to observe the true potential for hares to affect postfire succession because they represent good hare habitat and experience increasing hare abundance coinciding with regenerating black spruce within the browse range of hares. It is likely that browsing will significantly affect densities of black spruce over time at some of these younger sites where high densities of deciduous seedlings and saplings favor greater hare abundance (Fig. 5a). We predict that these sites will show more dramatic effects of hare browsing with time, as regenerating black spruce will likely encounter multiple peaks in hare population (Sinclair 2003).

Similarly, many intermediate-aged sites ($n = 10$) had significant numbers of standing dead black spruce seedlings with prevalent hare-browse scars (Fig. 5b; 100 to 10 000 dead spruce·ha^{-1}), suggesting that herbivory was a contributing factor to mortality in the past for black spruce that experienced multiple peaks in hare density (Fig. 2a). Although standing dead spruce made up a significant percentage of total standing black spruce (living and dead) for three of these sites (30%–90% of standing spruce), the remaining sites consisted of >90% standing living black spruce. It is unlikely that hares can significantly increase mortality at locations where black spruce is recruiting at very high densities because of herbivore satiation (Fig. 5c; Crawley and Long 1995). Interestingly, these dense stands of black spruce can later become refugia for hares because of the suitable cover that they provide (Wolff 1980; Feierabend and Kielland 2015).

Browsing was minimal in most mature stands of black spruce, most likely because of insufficient cover and low availability of suitable forage deterring hares from using these habitats. For example, our data for hare-pellet density (per square metre) suggest that hares prefer denser canopies over those typically found at more open, mature black spruce sites. Mean canopy cover (±SE) for mature stands of black spruce was 44% ± 8%, whereas plots with higher pellet densities (>10 pellets·m^{-2}) tended to have estimates of canopy cover greater than 75% (Table S1[1]). Hares are known to use dense stands of black spruce as refugia (Wolff 1980), but such stands seem to be represented by only a small number of spruce-dominant, intermediate-aged and mature sites. The only mature site with pellet densities > 10 pellets·m^{-2} also had the greatest density of black spruce seedlings and saplings (77 590 spruce·ha^{-1}).

Our path analysis clarified these interactions among tree species composition, canopy cover, hare browsing, and black spruce height and partly supported our assumptions regarding herbivory during postfire succession (Fig. 3). As we hypothesized, time since fire and the presence of deciduous seedlings, saplings, and trees explain most of the variation in canopy cover. Subsequently, canopy cover had the strongest effect on black spruce height, both directly and indirectly via hare browsing. Black spruce may benefit from canopy cover, which may reduce desiccation risk (Angell and Kielland 2009) or cause black spruce to allocate more resources to primary growth as a result of a low-light regime in the understory (Landhäusser and Lieffers 2001). The latter possibility

Fig. 5. (*a*) In young sites with high levels of deciduous recruitment resulting in suitable cover, hares can suppress spruce that are recruiting at lower densities. These locations may reveal a greater capacity for hares to alter postfire succession in the future, as current spruce regeneration coincides with an increase in hare abundance. (*b*) At many intermediate-aged sites, standing dead spruce with hare-browse scars suggest that herbivory has played a role in spruce mortality. (*c*) However, many fire scars consist of black spruce recruiting at high densities under a fairly open overstory where hares are unlikely to cause significant spruce mortality.



was supported by our models of individual black spruce that showed deciduous BA positively influencing the ratios of height to basal diameter in black spruce, implying that canopy cover promotes height growth over radial growth. Further, locations with dense deciduous canopies may reflect greater site productivity (D'Arrigo et al. 2000), and thus the positive correlation in spruce height and deciduous canopy cover may actually be the result of more optimal conditions for tree growth at those sites. The presence of deciduous tree species following fire has both positive (increased canopy cover) and negative (increased hare browsing) consequences for regenerating black spruce, with the net outcome appearing positive.

At the plot level, our path analysis suggested that black spruce are shorter in plots with more browsing, whereas little effect was observed with our mixed-effects models for spruce height at the individual level. These seemingly contradictory results actually agree with our hypothesis of selectivity of hare browsing, in that hares are browsing the taller spruce within plots. Within plots, all spruce seedlings and saplings are similar in size because browsed seedlings are browsed down to the height of shorter spruce that are likely buried by snow during the winter when hares are most likely to eat black spruce (i.e., the hares are "pruning the spruce hedges"). Thus, an individual-level height analysis accounting for variation across plots might not detect the browse effect because all the plants are leveled to the same height by hares within plots. If so, the variance around plot-level means for spruce height should decrease with increased browsing, which we observed for both young and intermediate-aged sites (Fig. 4). At the plot level, however, plots without browsing, and thus no suppressed tall spruce, would have higher plot-level mean heights than plots where taller spruce are suppressed by hares, and the browse effect would not be masked by the selectivity of hare browsing. Therefore, the true browse effect on spruce height may be better evaluated by tracking individuals over time rather than comparing browsed with unbrowsed individuals at a single point in time. The use of hare exclosures to compare populations of spruce exposed to browsing with those excluded from browsing may also better reveal the browse effect on the height of black spruce (Olnes and Kielland 2016).

Surrounding vegetation is the primary driver influencing whether regenerating black spruce seedlings are likely to be browsed by hares. The presence of deciduous trees following fire increases the susceptibility of black spruce seedlings to browsing because hares are more abundant under their dense canopies. This negative association has the potential to influence postfire succession, as increased browsing can reduce the height of black spruce seedlings and likely increases mortality. Although we found statistical support for our hypotheses, the biological significance of our results is not clear, as little of the variation in individual spruce height was explained by browsing. This is most likely because the selectivity of hare browsing for the tallest spruce seedlings masks the browse effect. For young sites, our sampling period coincided with an initial increase in browsing that will likely continue for several more years while spruce recruits within the browsing range of hares. We anticipate that these sites will show that the true capacity for hares to influence forest succession may only be revealed through long-term monitoring efforts. Because fire-related changes are occurring across North America's boreal forest (Kelly et al. 2013; Hanes et al. 2019), and hares are abundant throughout this broad region (Krebs et al. 2013), long-term monitoring efforts to better understand how factors such as herbivory influence postfire succession are warranted.

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