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Article title: **Asynchronous recruitment dynamics of snowshoe hares and white spruce in a boreal forest**

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Abstract

Herbivores have the capacity to modify plant community composition and ecosystem structure and function via browsing. For example, moose and snowshoe hare facilitate succession in Alaska's boreal forest by preferentially browsing early successional species over late successional conifers. Snowshoe hares also eat conifers, including white spruce, and this browsing may affect the pattern of spruce establishment over time. We measured over 800 spruce at 18 locations along the Tanana River floodplain in interior Alaska, USA and demonstrated that the proportion of spruce browsed annually positively correlates with annual hare abundance. Nearly all seedlings sampled had been browsed. Further, we modeled the pattern of spruce establishment over the last 40 years and found that hare abundance, growing season temperature, early season snow depth, and flooding explain the majority of this pattern. This model demonstrated that less spruce established during periods of high hare abundance than during periods of low hare abundance. The extensive browsing of white spruce that occurs during periods of high hare abundance may further compound the negative effects of climate warming on spruce recruitment in these floodplain forests.

Key Words: Alaska; Boreal forest; Herbivory; Succession; Snowshoe hare; White spruce

Abbreviations:

BNZ-LTER: The Bonanza Creek Long Term Ecological Research site

BIC: Bayesian Information Criterion

GDD: Growing Degree Days

1. Introduction

Herbivores have the capacity to modify plant community composition and ecosystem structure and function via browsing (Bryant and Chapin 1986; McNaughton et al. 1988; Brandner et al. 1990; Davidson 1993). For example, in the boreal forests of North America, moose (*Alces alces*) and snowshoe hare (*Lepus americanus*) facilitate succession by preferentially browsing early successional species. Exclosure studies have demonstrated that browsing decreases the time required for thin-leaf alder (*Alnus incana* subsp. *tenuifolia*) to replace willows (*Salix* sp.) in interior Alaska (Kielland and Bryant 1998) and for conifers, mainly white spruce (*Picea glauca* (Moench) Voss), to replace more palatable tree species at Isle Royal National Park, Michigan (McInnes et al. 1992). These transitions, facilitated by browsing, further alter forest dynamics by affecting soil biogeochemical properties (Pastor et al. 1992; Kielland et al. 1997). The browsing behavior of hares differ from that of moose, however, in that hares also browse the seedlings of late successional conifers, including many species valued as timber resources and for use in reforestation (Bergeron and Tardiff 1988; Milakovksy et al. 2011). Despite an extensive record noting the capacity of hares to browse and even eliminate conifers (see Cook and Robeson 1945; Peterson et al. 2005; Olnes and Kielland 2016), few studies have sought to understand this effect in a natural setting and how this browsing may influence forest dynamics over longer time scales.

White spruce is a dominant boreal tree species in North America, and in Alaska, an indicator of a rapidly changing landscape as its distribution is shifting in response to climate warming (Jorgenson et al. 2014; Juday et al. 2015). The floodplains of Alaska's Yukon and Tanana Rivers represent the most productive landscape for white spruce and are the most

important timber regions for interior Alaska (Wurtz et al. 2006; Juday et al. 2015). Presently, however, reduced annual growth has been documented and this phenomenon is projected to continue in the future, along with reduced viable seed production (Lloyd et al. 2013; Roland et al. 2014; Juday et al. 2015). Over time, reduced white spruce establishment will likely contribute to the projected shift in interior Alaska from a conifer dominant ecosystem to mixed-wood boreal forest, altering successional processes and community composition (Hollingsworth et al. 2010), as well as forest productivity (Barber et al. 2000). Consequently, areas sufficiently productive for sustainable forestry are shifting westward into regions previously below the climate envelope of white spruce (Juday et al. 2015). Properly managing these shifting forests requires better understanding of the rate and extent of change that may occur, and what factors may influence future regeneration patterns.

Patterns of white spruce establishment are likely affected by snowshoe hare herbivory. Both hares and white spruce are present throughout boreal North America, however, differences in plant community composition (McInnes et al. 1992; Hollingsworth et al. 2010), hare population patterns (Krebs et al. 2014) and plant defensive chemistry (Bryant et al. 1994), imply this interaction varies throughout their range. Previous studies in the Yukon (Smith et al. 1988) and Saskatchewan (Milakovsky et al. 2011), Canada, have noted minimal effects of browsing on spruce, while elsewhere, such as in New York, USA, studies detail more significant impacts (Cooke and Robeson 1945). Observations from interior Alaska have noted that browsing of white spruce seedlings by snowshoe hares can be extensive (Walker et al. 1986; Angell and Kielland 2009; Olnes and Kielland 2016), despite spruce being well defended chemically (Sinclair et al. 1988). Most of this browsing likely occurs during the winter, when hares rely on the twigs of willows, birch (*Betula sp.*), and spruce (Wolff 1978; Bryant 2003). During the

83 summer months, hares are able to shift their diet toward more herbaceous and leafy forage
84 (Bryant 2003; Seccombe-Hett and Turkington 2008). Spruce are also more likely browsed during
85 periods of high hare abundance when more preferable food sources, such as willows and birch
86 are depleted (Fox and Bryant 1984; Smith et al. 1988). Given the unique periodicity of the hare
87 population cycle at high latitudes, where populations fluctuate on a roughly decadal basis
88 (Kielland et al. 2010; Krebs et al. 2013), spruce is subject to a temporal variation in browsing
89 pressure. Because white spruce exhibit synchronized cone production (masting), severe browsing
90 by hares has the potential to eliminate entire cohorts of seedlings if a large cone crop aligns with
91 the peak of the hare cycle. This outcome could delay spruce dominance by years to decades,
92 given the periodic nature of viable seed production in spruce (Roland et al. 2013). Thus,
93 browsing by hares may compound the effect of climate change on the shifting distribution of
94 productive lowland white spruce.

95 Several environmental variables may influence the effect of hare browsing on spruce
96 establishment. Previous studies have demonstrated the susceptibility of spruce seedlings
97 recruiting along the Tanana River to heat stress and desiccation (Angell and Kielland 2009), as
98 well as to damage from flood events (Yarie et al. 1998). However, flood events that occur prior
99 to seedling establishment may benefit seedlings by providing open mineral beds for recruitment
100 (Walker et al. 1986). Thus, growing season temperature and fluvial dynamics may interact in
101 ways that either favor or deter seedling establishment. For example, years with a high flood stage
102 would indicate an elevated water table that spruce can more easily access with their shallow root
103 systems, reducing the risk of desiccation (Yarie 2008). Because hares primarily browse spruce
104 during the winter months, early season snow depth may also affect the vulnerability of seedlings
105 to browsing (Telfer 1974).

We sampled white spruce seedlings along the Tanana River, near Fairbanks, Alaska, to understand spruce-hare interactions in a landscape that may see reduced white spruce establishment in the future. We hypothesized that browse frequency would positively correlate with hare abundance across years, and that browsed spruce seedlings would have significantly reduced height growth. Thus, our first objective was to quantify the level of browsing by hares on white spruce seedlings over a reasonable time scale - the last four decades. Our second objective was to reconstruct the pattern of yearly spruce establishment since 1970 and examine this distribution in relation to historical and simulated data of white spruce seed production and the snowshoe hare cycle. We hypothesized that the relative number of trees established in a given year positively varies in proportion to viable seed production of the two years prior, and negatively correlates with snowshoe hare density for the years following establishment. We further hypothesized that fewer white spruce would establish during hotter and drier summers, and that an early snowpack would benefit seedlings by insulating them from colder temperatures and browsing hares. If so, then the unique periodicity of the hare cycle may act as a demographic filter where spruce most successfully recruit during periods of low hare abundance.

2. Methods

2.1 Study area

The Bonanza Creek Long Term Ecological Research site (BNZ-LTER, 64°43'N, 148°12'W) is located along the Tanana River in and around the Bonanza Creek Experimental Forest, approximately 30 km southwest of Fairbanks, Alaska, USA. The floodplain is

approximately 120 m a.s.l. and exhibits a mosaic of successional stands dominated by willows, thin-leaf alder, balsam poplar (*Populus balsamifera*) and white spruce. Eighteen square, 625 m² sampling plots were selected along a 50 km stretch of the Tanana River that encompassed the BNZ-LTER (Fig. 1). Because our focus was on sampling younger spruce, we primarily selected early-to-mid-successional sites with a mixed canopy of thin-leaf alder and balsam poplar, as these stands represent the successional stage at which spruce becomes abundant in the understory (Walker et al. 1986). Plot selection was based on field observations and then points selected via satellite imagery prior to sampling in the field, which included six previously established LTER research plots.

2.2 Sampling design

All field sampling took place during the months of June - August of 2014. We started at the southeast corner of each plot and measured between 50 and 100 individual white spruce. We measured all white spruce individuals encountered; however, because we focused on sampling early and mid-successional forest stands, most spruce measured were either seedlings (< 1.37 m tall) or saplings (> 1.37 m tall, < 12 cm diameter at breast height (d.b.h.)). We measured the height and basal diameter, and recorded browsing history for all white spruce individuals by noting the presence of browse scars along the apical meristem. Estimating browsing history for larger saplings and trees (> 1.37 m, > 12 cm d.b.h.) was not always possible as browse scars may no longer be visible. We determined the age of most individual spruce trees from whorl counting (counting the number of apical annual growth segments). For older spruce with growth whorls that were too obscured to accurately age in this manner, we collected basal core samples using

standard techniques (Grissino-Mayer 2003). From these age estimates, we reconstructed the age structure of young spruce since 1970 by averaging the proportion of sampled spruce established each year across sampling plots.

We additionally back-counted current annual growth segments to estimate the year when the apical meristem was browsed for each browse event (year of browsing) on a subset of 52 individuals measured at four separate locations within the floodplain, consisting of alder-poplar, poplar, and poplar-spruce dominant canopies. For an additional 114 trees we also estimated the age via whorl-counting and by collecting a core or disc from the base to compare age estimates using both methodologies.

2.3 Historical and simulated datasets

We collected additional datasets that spanned 1970 until 2011 in order to model the pattern of yearly spruce establishment during this period. Hare abundance (hares ha⁻¹) at BNZ-LTER has been estimated via mark-recapture surveys that have taken place from 1998 to present (Kielland et al. 2010, Feierabend and Kielland 2015, Fig. 2a), and known hare peaks occurred around 1971, 1981, 1990, 1999, and 2009 (Rexstad and Kielland 2006, Kielland et al. 2010, Feierabend and Kielland 2015). For years prior to 1998, we modeled annual hare abundance using a modified sine curve to reflect these known periods of high and low abundance (Fig. 2a). Hare abundance for the year t was calculated as: $hare\ abundance_t \sim 4 + 6.5 * \sin((t + 1) / 1.5)$. We compiled additional data on viable seed production from BNZ-LTER (viable seeds m⁻², http://www.lter.uaf.edu/data_detail.cfm?datafile_pkey=14, Fig. 2b), and climate data from the Western Regional Climate Center (<http://www.wrcc.dri.edu/summary/Climsmak.html>);

specifically, the total sum of growing degree days (GDD, base 5°C) from May to September (Fig. 2c) and the average snow depth between September and December (cm) for each year (Fig. 2d). We also obtained the maximum flood stage achieved by the Tanana River (m) for each year (USGS, <http://water.weather.gov/>, Fig. 2e).

2.4 Analysis

We performed all statistical analyses in R statistical software version 3.2.3 (R Core Team 2015). To compare changes in browsing frequency with changes in snowshoe hare abundance, we calculated the percentage of sampled spruce browsed for each year from our estimates of the year of browsing. We pooled data from all sampling locations to generate a pattern at the regional scale. We then calculated the Pearson's correlation coefficient between these data and the record of annual hare abundance (function: cor).

We used linear mixed models to test the effects of browsing on spruce height growth for spruce seedlings (function: lmer). We focused on seedlings to ensure that all spruce included were within the browsing range of hares (< 200 cm, Telfer 1974), and because apical browse events were clearly identifiable among seedlings. Our fixed effects were spruce age, browse history, and their interaction, while sampling plot was a random effect. We log-transformed the response variable of height to improve model fit and meet model assumptions. We evaluated the significance of each fixed effect using F tests (function: lmerTest), and assessed the overall fit by calculating R-squared values for mixed models (function: r.squaredGLMM, Nakagawa and Schielzeth 2013). We calculated both the marginal (R_m^2) and conditional (R_c^2) R-squared values, which give the amount of variation explained by the fixed effects alone and by the fixed effects plus the random effect of plot, respectively. We then compared the marginal R-squared values

for models with and without browsing as a fixed effect to determine how much the browsing parameter improved model fit.

We first calculated the proportion of sampled spruce that germinated each year at the plot level. We then tested for significant relationships between historical and modeled data of seed production, annual hare abundance and patterns in yearly spruce establishment using multiple linear regression. To accomplish this, we averaged the proportion of spruce established in each year (t) across plots and used this as our response variable. Our fixed effects were the number of viable seeds produced in the two years prior to spruce establishment, $t - 1$ and $t - 2$, and the relative abundance of hares for the year of establishment and three years following, t to $t + 3$. We also included the total sum of GDD from May to September and the average snow depth between September and December for the years t to $t + 3$, and the maximum flood stage achieved by the Tanana River for the years $t - 1$ to $t + 1$ as additional model covariates. All fixed effects variables were standardized to have a mean of zero and a standard deviation of 1 in order to improve model fitting.

Given zeroes in our dataset, we first added 0.01 to each datum of our response variable in order to perform a log-transformation. This transformation allowed us to fit a full model using all covariates that met the assumptions of homoscedasticity and normality of the residuals for multiple regression. After fitting the full model, we then used an automated sampling routine to determine the top five models with the highest R^2 values (library: leaps, function: regsubsets). To reduce the risk of selecting an over fitted model, we used two criteria to select the best model from the top five models chosen by R^2 values. First, we calculated the Bayesian Information Criterion (BIC) for each model, where the best model is that with the lowest BIC value. We used BIC values rather than the Akaike's Information Criterion (AIC) because BIC tends to select

more parsimonious models (Quinn and Keough 2002). We considered models with a difference in BIC (Δ BIC) greater than 2 to be less informative than the top model. Secondly, to further assess model fit and predictive ability, we performed a ten-fold cross validation on each model and calculated the overall mean square error (MSE) from each iteration (library: DAAG, function: CVlm). Models with lower average MSE values had better predictive power. For our final models, we checked for any temporal autocorrelation by plotting an autocorrelation function of the residuals (function: acf).

3. Results

3.1 Summary

Substantial browsing of white spruce occurred throughout our study area. We measured a total of 871 individual white spruce that varied widely in height (11 cm - > 1000 cm) and age (9 – 72 years old). 54%, 40% and 6% of sampled spruce were either seedlings, saplings, or trees, respectively. For all spruce, 80% had their apical meristem browsed at least once by hares. Browsing frequency and hare abundance were correlated at BNZ-LTER ($r = 0.60$, Fig. 3) and most browse events occurred during periods of high hare abundance, whereas almost no browsing occurred during periods of low abundance (< 5% browsed, Fig. 3).

3.2 The effect of herbivory on spruce seedling height growth

Browsing had a minimal, positive effect on the relationship between spruce seedling height and age. Specifically, browsing increased the intercept of the regression line but had no effect on the slope (Table 1). Browsing explained 3% (1% total) of the remaining variation in height of white spruce seedlings after accounting for age (Table 1). Including the random effect of plot increased the total amount of variation in height explained to 75% (Table 1). Browsed spruce were significantly older (median age difference: 5 years, ANOVA, $F_{1,466} = 20.01$, $p < 0.001$, Fig. 4a) and taller (median height difference: 25 cm, $F_{1,466} = 19.71$, $p < 0.001$, Fig. 4b) than spruce that had not been browsed.

3.3 The pattern of yearly spruce establishment

Our estimates of spruce age using whorl counts closely approximated spruce age determined by counting annual growth rings ($Age_{ring} \sim 2.63 + 0.93Age_{whorl}$, $F_{1,112} = 292$, $p < 0.001$, $R^2 = 0.72$). This near 1:1 relationship affirmed whorl counting as a suitable method for estimating spruce age and reconstructing the pattern of yearly establishment across our sampling area. We found that spruce recruited continuously throughout 1970 – 2011, although the number of established spruce varied greatly from year to year. The periods of greatest successful spruce establishment were 1987-1989, 1993, 1994, and 1998 (Fig. 5).

The top five models of spruce establishment, chosen by our automated model selection routine, ranged in R^2 values from 0.41 to 0.64 (Table 2). Of these, only one model had ΔBIC less than 2 from that of our top model. For each model the average MSE following ten-fold cross validation ranged from 0.25 – 0.31 given a range of -4.61 to -2.50 for the response variable of the log-transformed proportion of sampled spruce established. The top two models with the lowest

BIC scores also had the lowest average MSE values. Of these two models, we selected the most parsimonious model (Tables 2 and 3).

Our model explained 61% of the total variation in spruce establishment from 1970 – 2011 ($F_{7,34} = 7.43$, $p < 0.001$, Tables 2 and 3, Fig. 5). In general, our model of spruce establishment revealed a negative effect of both hare abundance (years t and $t + 2$) and GDD (years $t + 2$ and $t + 3$). We found a positive relationship between spruce establishment and both snow depth (years $t + 1$ and $t + 2$) and flood stage (year $t - 1$). Interestingly, none of our models showed any significant relationships between viable seed production and the pattern of yearly spruce establishment.

4. Discussion

4.1 Summary

We have demonstrated that snowshoe hares extensively browse white spruce at BNZ-LTER and that this browsing likely reduces spruce establishment throughout this portion of the Tanana River floodplain. Over the last four decades, nearly all spruce sampled have had their apical growth segments removed at least once by hares, particularly during periods of high hare abundance. Browsing is likely a source of direct mortality for spruce, which is reflected by the negative relationship between hare abundance and spruce establishment over time.

The response of spruce to herbivory is complex because spruce has many strategies to deter browsers, including low palatability and high concentrations of toxins, such as camphor (Sinclair et al. 1988). Moreover, its reproductive strategy of masting can overwhelm both

granivores and herbivores with an abundance of seeds and then seedlings (Janzen 1971), creating dense patches of spruce cohorts that largely escape browsing. Hares are formidable browsers during periods of high abundance, however, and are capable of eliminating nearly all available woody vegetation, including spruce (Cooke and Robeson 1945; Peterson et al. 2005). This unique and dynamic plant-herbivore interaction leads to high temporal and spatial variability in spruce recruitment, where spruce may remain untouched by hares in some locations, but in others browsing can result in 100% seedling mortality (Olson and Kielland 2016).

4.2 The effect of herbivory on spruce seedling height growth

We argue that the apparent positive effect of hare browsing on spruce height growth is a byproduct of age differences between each browse category. Spruce trees that were not browsed tended to be the youngest individuals, whereas spruce that were browsed tended to be the oldest (Fig. 4a). It is likely that the increase in intercept with browsing is a reflection of age differences, rather than a browse effect. The median age for spruce seedlings that had not been browsed was 7 years, and given that 75% of this group were under nine years old in 2014 (3rd quartile = 9 years, Fig. 4a), most individuals were under five years old at the time of the last hare peak (2009, Fig. 3). Using our regression relationship for spruce seedling height and age (Table 1), we estimate that five-year-old seedlings should be approximately 18 cm tall (mean height of all five-year-old seedlings sampled ($n = 10$): 17.6 ± 1.54 cm). This is nearly equal to the average early snow depth from 1970 to 2011 of 15.04 ± 1.12 cm (Fig. 2d). Therefore, most seedlings that have not been browsed were still short enough to be buried by early season snow during the last hare peak. Exclosure studies may demonstrate more accurately the true effect of browsing by hares on

spruce height growth by allowing for more even sample sizes of browsed and unbrowsed spruce. For example, previous exclosure studies we conducted on the floodplain demonstrated a significant negative effect of hare browsing on spruce height growth (Olness and Kielland 2016). Our results likely differed from those of the exclosure studies because very few seedlings avoid being browsed in a natural setting. Further, we defined our browsing effect as a binary categorical variable (browsed or not browsed). We may have found a more significant negative effect of browsing if we had defined our browse effect as a continuous variable (number of apical browse events or percent current annual growth (CAG) browsed).

4.3 The pattern of yearly spruce establishment

Spruce trees browsed in the first few years of establishment are most vulnerable to mortality because a single browse event may suffice to remove all meristematic tissue. In the autumn, newly recruited spruce may appeal to hares as the only green browse available. Our model reflected this vulnerability as hare abundance for the year of establishment and two years following establishment were significant negative terms (Table 2). Other lag years for hare abundance may not have been significant because of multicollinearity, where hare abundance for a specific year was sufficient to represent abundance for multiple surrounding years. An early snow pack can benefit seedling survival, likely by burying seedlings and reducing the amount of time they are vulnerable to hares during the onset of winter each year.

Although it is known that flood events can damage or kill spruce seedlings along the floodplain (Angell and Kielland 2009), our model results suggest that recruiting spruce mainly benefit from flooding as this produces mineral beds optimal for seedling establishment. This

effect may in part explain the lack of correlation between viable seed production and spruce establishment. Many seeds are deposited along the floodplain during a masting event, but the number that actually germinates may also depend on the extent of suitable recruitment sites (Walker et al. 1986). Therefore, the timing of flood events that lead to more suitable microhabitats for spruce establishment may mask the relationship between seed production and spruce establishment along the floodplain. Growing season temperatures can further obscure this relationship as entire seedling cohorts that are unable to reach the water table may succumb to desiccation during hot and dry summers (Yarie 2008; Angell and Kielland 2009). It is likely that spruce establishment in upland environments would more strongly reflect the pattern in viable seed production over time (G.P. Juday, *unpublished data*).

4.4 Implications for management

Forest and plantation managers should promote spruce regeneration during the low in the hare cycle. Our model for the pattern of spruce establishment along the Tanana River floodplain suggests that seedlings establishing immediately following a hare peak can have twice the survival rate of seedlings establishing during peak years (Table 3). In areas with abundant snowfall, seedlings established during periods of low hare abundance will likely be short enough to be insulated by the snowpack during the subsequent hare peak. Although the timing of establishment appears to affect survival rates, managers in areas that see significant hare peaks should expect that all seedlings will eventually be browsed, including those that established during periods of low hare abundance. Many seedlings were able to withstand browsing during the most recent peak of 2009, however, we observed very few individuals with browse scars

corresponding to the prior peak year of 1999, despite a similar abundance of hares and seedlings at the time of both peaks. This may reflect a ‘missing record’ of seedlings that survived the 1999 hare peak, but succumbed to browsing during the 2009 peak.

Spruce seedlings in the boreal forest will likely encounter two hare peaks before they are released from hare herbivory (~200 cm in height, Telfer 1974; Drew 1988). Forest managers in the boreal region should be cognizant of the stage of the hare cycle and consider more intensive herbivore management practices during peak years (Drew 1988). Methods for deterring hares from establishing spruce include the use of repelling odors (Sullivan and Crump 1984; Sullivan et al. 1992) and protective plastic covers (Zimmerling and Zimmerling 1998), or reducing the amount of vegetative cover available to hares around seedlings (Parker 1984). Manipulating cover presents a trade-off for managers, however, as reduced cover may negatively affect seedling growth (Angell and Kielland 2009; Milakovsky et al. 2011; Olnes and Kielland 2016).

4.5 Homage to Aldo Leopold

The potential for asynchrony between herbivores and seedling recruitment did not escape the attention of the observant Aldo Leopold. In his famous book, *A Sand County Almanac*, he details the life history of an oak (*Quercus sp.*) he has recently harvested from his property in Wisconsin (Leopold 1949). Within this passage he writes:

“Indeed, it is all too clear that every surviving oak is the product either of rabbit negligence or rabbit scarcity. Some day some patient botanist will draw a frequency curve of oak birth years, and show that the curve humps every ten years, each hump originating from a low in the ten-year rabbit cycle”

As Leopold postulated for oaks in Wisconsin, we have demonstrated for white spruce in Alaska. Other studies have also noted this asynchronous plant-herbivore interaction (Brandner et al. 1990), however, our study is the first to demonstrate an inverse relationship between conifer recruitment and the hare population cycle over time. It is likely that browsing by hares influences the pattern of establishment for other boreal species in a similar manner (Fox and Bryant 1984, Smith et al. 1988).

5. Conclusion

Northern ecosystems have received recent attention regarding climate change because of polar amplification (Coumou et al. 2015). In response to climate change, the distribution of white spruce is shifting dramatically, with increased growth and seed viability leading to expansion in some locations, but decreased growth and seed viability resulting in contraction at others (Roland et al. 2013, 2014; Juday et al. 2015). This contributes to changing Alaskan landscapes characterized by increasingly deciduous forests where conifers once dominated, and coniferous forests expanding into former tundra landscapes (Mann et al. 2012; Lloyd et al. 2013; Jorgenson et al. 2014).

Across this region, we posit that snowshoe hares are a demographic filter to white spruce establishment, acting in a pulsed manner in addition to the current (warming) climate press. On the Tanana River floodplain, browsing appears to be as important a predictor of spruce success, if not greater, than growing season temperatures or early season snowfall during the first few years of establishment. Spruce that recruit during a high in the hare cycle are less likely to successfully establish than spruce recruiting during periods of low hare abundance. The large

geographic extent over which spruce-hare interactions occur emphasizes the potential significance of browsing by snowshoe hares in modifying the shifting distribution of this important conifer in the boreal forest.

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549

550 **Tables**

551 **Table 1.** Results of linear mixed model for white spruce seedling height, with spruce age, browse
552 history and their interaction terms as fixed effects. Spruce height was log-transformed. Plot was a
553 random effect with varying intercept. $\beta_{0,0}$ = the intercept when spruce is not browsed, $\beta_{0,1}$ =
554 added intercept for browsing, β_1 = slope for fixed effect of spruce age, β_2 = slope for spruce age
555 and browsing interaction term. Significant model parameters are indicated with *.

Model	$\beta_{0,0}$	$\beta_{0,1}$	β_1	β_2	R^2_m Age	$R^2_{m,}$ Age x Browse	$R^2_c,$ Age x Browse
Age	2.40±0.15*	0.10±0.01*	0.30±0.14*	-0.01±0.01	0.70	0.71	0.75

556 Notes. Marginal R^2 (R^2_m) is the amount of variation explained by the fixed effects alone. Conditional R^2 (R^2_c) is that amount of
557 variation explained by both fixed and random effects.

558

559 **Table 2.** Top five models chosen by an automated routine to select for highest R^2 value. Also presented is
560 the results for the full model. BIC is the Bayesian Information Criterion, and $\overline{MSE}$ is the averaged
561 mean square error after performing a ten-fold cross validation for each model. Model in bold
562 indicates the final model selected. Model parameters are defined in Table 3.

Model	Parameters	BIC	R^2	$\overline{MSE}$
1	$Hare_t + Hare_{t+2} + Hare_{t+3} + GDD_{t+2} + GDD_{t+3} + Snow_t + Snow_{t+1} + Snow_{t+2} + Flood_{t-1} + Flood_t$	74.92	0.64	0.25
2	$Hare_t + Hare_{t+2} + Hare_{t+3} + GDD_{t+2} + GDD_{t+3} + Snow_t + Snow_{t+1} + Snow_{t+2} + Flood_{t-1}$	75.61	0.61	0.26
3	$Hare_t + GDD_{t+2} + GDD_{t+3} + Snow_{t+1} + Snow_{t+2} + Flood_{t-1}$	77.05	0.56	0.26
4	$Hare_t + GDD_{t+3} + Snow_{t+1} + Snow_{t+2} + Flood_{t-1}$	79.99	0.48	0.30
5	$Hare_t + GDD_{t+3} + Snow_{t+1} + Flood_{t-1}$	81.43	0.41	0.31
Full	$Seed_{t-2} + Seed_{t-1} + Hare_t + Hare_{t+1} + Hare_{t+2} + Hare_{t+3} + GDD_t + GDD_{t+1} + GDD_{t+2} + GDD_{t+3} + Snow_t + Snow_{t+1} + Snow_{t+2} + Snow_{t+3} + Flood_{t-1} + Flood_t + Flood_{t+1}$	93.97	0.75	0.40

Table 3. Parameters used in full model to explain the pattern in yearly spruce establishment. Parameters in bold were included in final model. The response variable, the proportion of sampled spruce established each year, was log-transformed. All model parameters were standardized to have a mean of 0 and a standard deviation of 1. ‘NS’ means parameter was not significant in final model.

Parameter	Description	β value	p
Intercept	-	-3.59	<0.001
Hare_t	Relative hare abundance in year <i>t</i>	-0.34	<0.001
Hare _{t+1}	Relative hare abundance in year <i>t</i> + 1	NS	
Hare_{t+2}	Relative hare abundance in year <i>t</i> + 2	-0.15	0.04
Hare _{t+3}	Relative hare abundance in year <i>t</i> + 3	NS	
Seed _{t-1}	Viable seeds m ⁻² produced in year <i>t</i> - 1	NS	
Seed _{t-2}	Viable seeds m ⁻² produced in year <i>t</i> - 2	NS	
GDD _t [†]	Sum GDD May – September for year <i>t</i>	NS	
GDD _{t+1}	Sum GDD May – September for year <i>t</i> + 1	NS	
GDD_{t+2}	Sum GDD May – September for year <i>t</i> + 2	-0.20	0.009
GDD_{t+3}	Sum GDD May – September for year <i>t</i> + 3	-0.30	<0.001
Snow _t	Average snow depth (cm) September – December for year <i>t</i>	NS	
Snow_{t+1}	Average snow depth (cm) September – December for year <i>t</i> + 1	0.30	<0.001
Snow_{t+2}	Average snow depth (cm) September – December for year <i>t</i> + 2	0.24	0.002
Snow _{t+3}	Average snow depth (cm) September – December for year <i>t</i> + 3	NS	
Flood_{t-1}	Maximum flood stage achieved for year <i>t</i> - 1	0.21	0.006
Flood _t	Maximum flood stage achieved for year <i>t</i>	NS	
Flood _{t+1}	Maximum flood stage achieved for year <i>t</i> + 1	NS	

[†]GDD is the growing degree days (base 5° C)

Figures and figure captions

Fig. 1 (2-column width)

Fig. 1. Locations of 18 study plots along the Tanana River floodplain (white dots) in the vicinity of the Bonanza Creek Experimental Forest (outlined in white).

579 Fig. 2 (2-column width)

580 **Fig. 2.** Model parameters used to explain the pattern in yearly establishment of white spruce from 1970 –
581 2011. (a) is the annual snowshoe hare abundance at BNZ – LTER. (b) is the average number of viable
582 spruce seeds m^{-2} produced at BNZ-LTER. (c) is the sum Growing Degree Days (base 5°C) from May –
583 September. (d) is the average monthly snow depth from September – December (cm). (e) is the maximum
584 flood stage achieved by the Tanana River for each year (m).
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587 **Fig. 3 (single column width)**

588 **Fig. 3.** The proportion (%) of white spruce browsed annually (shaded bars) in relation to the
589 snowshoe hare population cycle (line) at the Bonanza Creek LTER sites located along the
590 Tanana River, interior Alaska. n = 52.
591
592

Fig. 4. Box and whisker plots of age (a) and height (b) distributions among spruce seedlings that were not browsed (n = 27) and browsed seedlings (n = 441). Thick lines represent the median value and the rectangles represent the interquartile range. Whiskers are equal to the minimum and maximum values of the sample, and dots reflect outliers in the data. Significant difference indicated by *.

601 Fig 5. (1.5-column width)

602
603 **Fig. 5.** Pattern in yearly spruce establishment along the Tanana River, interior Alaska. Actual
604 BNZ-LTER data represent the mean proportion of sampled spruce established each year across
605 plots (n = 18). Error bars represent standard error around the mean. Model coefficients are
606 presented in Table 3.
607