



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.

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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; Butler and Kielland, 2008). 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 Tardif, 1988; Milakovskiy 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

Abbreviations: BNZ-LTER, The Bonanza Creek Long Term Ecological Research site; BIC, Bayesian Information Criterion; GDD, Growing Degree Days.

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

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

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