ORIGINAL PAPER

Susceptibility of burned black spruce (*Picea mariana*) forests to non-native plant invasions in interior Alaska

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Abstract As climate rapidly warms at high-latitudes, the boreal forest faces the simultaneous threats of increasing invasive plant abundances and increasing area burned by wildfire. Highly flammable and widespread black spruce (*Picea mariana*) forest represents a boreal habitat that may be increasingly susceptible to non-native plant invasion. This study assess the role of burn severity, site moisture and time elapsed since burning in determining the invisibility of black spruce forests. We conducted field surveys for presence of non-native plants at 99 burned black spruce forest sites burned in 2004 in three regions of interior Alaska that spanned a gradient of burn severities and site moisture levels, and a chronosequence of sites in a single region that had burned in 1987, 1994, and 1999. We also conducted a greenhouse experiment where we grew invasive plants in vegetation and soil cores taken from a subset of these sites. In both our field survey and the greenhouse experiment, regional differences in soils and vegetation between burn complexes outweighed local burn severity or site moisture in determining the invasibility of burned black spruce sites. In the greenhouse experiments using cores from the 2004 burns, we found that the invasive focal species grew better in cores with soil and vegetation properties characteristic of low severity burns. Invasive plant growth in the greenhouse was greater in cores from the chronosequence burns with higher soil water holding capacity or lower native vascular biomass. We concluded that there are differences in susceptibility to non-native plant invasions between different regions of boreal Alaska based on native species regeneration. Re-establishment of native ground cover vegetation, including rapidly colonizing bryophytes, appear to offer burned areas a level of resistance to invasive plant establishment.

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Introduction

While high latitude ecosystems tend to have fewer non-native plant species relative to other places, the introduction and spread of non-native species is accelerating in some arctic and sub-arctic ecosystems (Carlson and Shephard 2007). In Alaska, the number of non-native plant species increased by 46 % between

1941 and 2006 according to statewide herbarium and plant survey records (Carlson and Shephard 2007). Much of this increase in non-native plant introduction and spread may be attributed to increases in anthropogenic disturbances due to increased military activity and resource extraction, and the resulting increases in human population, commerce and road construction, over the this time period (Walker and Walker 1991; U.S. Census Bureau 2000; Carlson and Shephard 2007). Further, researchers in Alaska have begun to observe and document community and ecosystem-level changes to boreal habitats where non-native plants have invaded (Spellman and Wurtz 2011; Roon 2011). A rapidly changing climate may increase the vulnerability of high latitude systems to non-native plant invasions directly by affecting temperature and growing season, and indirectly by affecting the disturbance regimes. Warmer winters (Chapman and Walsh 1993; Serreze et al. 2000) and longer growing seasons (Myneni et al. 1997) may facilitate the survival of a greater diversity of non-native species in Alaska and increase their abundance. Warmer summer temperatures and decreased precipitation in Alaska and northern Canada have dramatically increased wildfire disturbances in the past few decades (Overpeck et al. 1997; Stocks et al. 2000; Gillett et al. 2004; Bachelet et al. 2005), which may provide further advantages to invading non-native plant species. During the 2004 fire season 2.7 million hectares of boreal forest burned, making it the largest fire year in Alaska's recorded fire history (Todd and Jewkes 2006). Fire frequency, severity, and extent are predicted to continue to increase across boreal North America in the future (Flannigan et al. 2001; Kasischke and Turetsky 2006; Balshi et al. 2009). Balshi et al. (2009) predict a doubling of the area burned per decade by 2050 relative to 2000, and 3.5–5.5 times more fires by the end of the century. Black spruce (*Picea mariana*) forest comprises over 40 % of the forested landscape of Alaska's boreal region (Van Cleve et al. 1983) and represents one boreal habitat that is potentially vulnerable to non-native plant invasions. Wildfire, primarily ignited by lightning strikes, is the most frequent disturbance in fire-adapted black spruce forest (Van Cleve et al. 1983).

Wildfire can increase the susceptibility of an area to non-native plant invasions by increasing the availability of resources such as light by reducing competition from native canopy species (Davis et al. 2000; D'Antonio 2000). For an invasion to actually occur, the increased resource availability or decreased competition after a fire must coincide with the availability of propagules of a non-native plant able to compete with the native vegetation (Davis et al. 2000). The increases in fire frequency and spatial extent (Overpeck et al. 1997; Stocks et al. 2000; Bachelet et al. 2005) along with increases in propagule pressure along road corridors in Alaska (Alaska Exotic Plant Information Clearinghouse (AKEPIC) 2013) may further exacerbate the vulnerability of the boreal forest to invasion by non-native plants. The relationship between fire and non-native plant invasions in the northern boreal forest, however, remains little studied (Sanderson et al. 2012).

Currently, Alaska's invasive plants largely occur on road corridors with few instances of spread off the human disturbance footprint (Conn et al. 2008; AKEPIC 2013). The low number of invasions into boreal forest habitats provides an opportunity for Alaska to prevent the spread of these plants, but also makes it more difficult to predict which areas will be most vulnerable to invasive plants in the future. Propagule pressure appears to drive the locations of the few sites where non-native plant species have moved beyond these road corridors into burned forest (Cortés-Burns et al. 2007; Villano and Mulder 2008). However, many burned areas with high propagule pressure from roadsides remain uninvaded (Villano and Mulder 2008). Understanding biotic and abiotic factors within burned areas that contribute to invasive plant seedling success may improve the ability of land managers to target monitoring or control efforts on infested roadways near particularly invasible burned areas.

Differences in burn severity, site moisture, or the amount of time elapsed since fire may influence the suitability of a burned black spruce site for non-native plant colonization. Black spruce forest in interior Alaska can have a thick layer of moss, lichen and organic soil that often overlays the mineral soil and permafrost (Viereck et al. 1992). This layer is referred to as "duff," with partially decomposed organic (Oi/Oe) soil horizons making up the upper duff and the well decomposed organic soil (Oa) horizon comprising the lower duff. This duff layer is commonly up to 50 cm thick and accounts for a large proportion of burnable biomass in late-succession black spruce forest in Alaska (Kasischke et al. 1995). As a result, high severity burns are commonly defined in plant

regeneration studies as areas where little duff remains (defined in this paper as <7 cm of duff remaining after the fire; Johnstone et al. 2008). The total depth of the duff layer remaining after a fire plays a critical role in determining the post-fire plant community composition (Johnstone and Chapin 2006; Johnstone et al. 2010a). Among native boreal species, plants regenerating from seeds tend to have higher establishment rates in high severity burn sites where little duff remains and patches of mineral soil are exposed (Schimel and Granstrom 1996; Johnstone et al. 2010b; Mallik et al. 2010; Bernhardt et al. 2011). In low severity burns, much of the charred, dry upper duff remains, offering a less hospitable surface for germination and establishment (Johnstone and Chapin 2006; Veilleux-Nolin and Payette 2012). Currently non-native plants are regenerating from dispersed seeds rather than clonally or from seedbanks in boreal Alaska (reviewed in Zouhar et al. 2008). We expect invasive plants would face the same recruitment barriers as native plants regenerating by seed in low severity burn sites. In addition, the invisibility of Alaska's burned black spruce forests should decrease with increasing time since fire due to the resurgence of native plants and canopy closure. This trend has been documented in many North American coniferous forests, where non-native species abundance and richness tend to decrease with increasing burn age (Agee and Huff 1987; Turner et al. 1997; Doyle et al. 1998; Klinger et al. 2006; reviewed in Zouhar et al. 2008).

Within a burn site of a particular severity, moisture or age classification, the soil surface exhibits some degree of microvariation due to small-scale differences in soil moisture, vegetation, microtopography, and changes in weather during the fire. For example, within a single site, islands of unburned bryophytes could remain alongside patches of high severity burn with mineral soil or rapidly establishing bryophytes such as *Ceratadon purpureus* or *Marchantia polymorpha* (Johnstone et al. 2008; Bernhardt et al. 2011). If we understand how different invasive plant species respond to small-scale variation within burns, we can better understand which larger-scale areas might be most vulnerable to non-native plant colonization based on the proportions of the soil or vegetation characteristics present.

In the experimental part of this study we focus on three non-native species with very different functional traits and regeneration strategies: a nitrogen-fixing forb, *Melilotus albus* Medik. (Fabaceae); a forb, *Hieracium aurantiacum* L. (Asteraceae); and a graminoid, *Bromus inermis* ssp. *inermis* Leyss. (Poaceae). Each species is highly invasive in many parts of the state and all are from plant families that occur disproportionately among invasive taxa in Alaska (Carlson et al. 2008; AKEPIC 2013). Similarities in responses across several invader species would indicate a particularly vulnerable (or invulnerable) habitat. We pose three primary questions to help identify burned areas most susceptible to non-native plant invasions: (1) Do burn severity, soil moisture, region and burn age of black spruce sites influence the likelihood of non-native plant establishment? (2) What small-scale soil and vegetation characteristics within burns influence vulnerability to invasion? and (3) What cross-taxa trends can be used to help inform invasive plant management decisions in burned boreal forest?

Methods

We used two complementary approaches to address these questions: a field survey of burned areas adjacent to roadways and a greenhouse experiment using soil and vegetation cores taken from some of our field sites. The field survey provided an assessment of current patterns of non-native plant movement into burned areas. The greenhouse approach controlled for propagule pressure (a confounding factor in most field studies on invasibility). We used greenhouse rather than field experiments to prevent accidental introductions of invasives into the largely uninvaded burn sites. Our greenhouse approach could not account for climatic variations or biotic interactions beyond competition from small plants, factors that may further limit or promote invasive growth in the field. At the time of this study, no invasive plants had been recorded moving into undisturbed black spruce stands (AKEPIC 2013); therefore, our research effort focused on burned sites.

Study area

In July 2006, we sampled burned black spruce stands within a 120,000 km^2 area located between the Alaska and Brooks Mountain Ranges (Fig. 1). All sites were established prior to this study as a part of the Bonanza
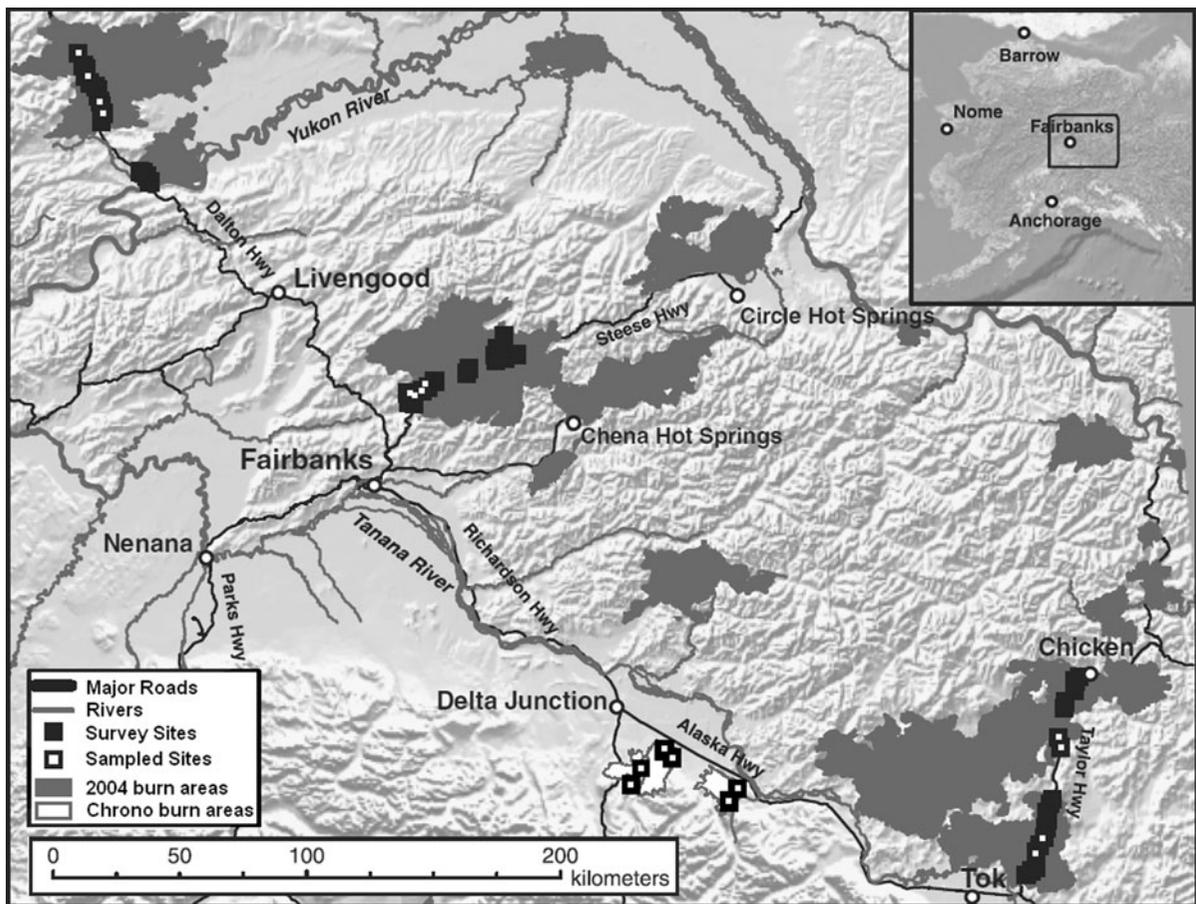
Fig. 1 Map of study sites in interior Alaska (modified from Johnstone et al. 2009). Perimeters of areas burned in 2004 are shown by *gray polygons*. The choronosequence of areas which burned in 1999, 1994, and 1987 ("chrono") are indicated by *white polygons* with *gray borders*. Sites sampled for greenhouse experiments are indicated by *white-filled squares* (N = 18), and sites surveyed for non-native plant species are indicated by *black squares* (N = 99). Roads shown on this map are the only roadways in interior Alaska outside of towns and villages. Because of the small scale of the map, symbols overlap for some of our survey sites

Creek Boreal Long Term Ecological Research Program (BNZ LTER). The sites occurred along roadways within four distinct burn complexes throughout interior Alaska, including the Boundary Fire Complex along the Steese Highway, the Taylor Fire Complex along the Taylor Highway, the Dall City Fire Complex along the Dalton Highway, and the Delta Fire Chronosequence (a set of adjacent areas that burned in 1999, 1994, and 1987) at the junction of the Alaska and Richardson Highways. Although these are considered major roadways in interior Alaska, they differ from major roads in other parts of the U.S. in that they are only one lane wide in each direction, and the Steese, Taylor and Dalton are largely unpaved. The oldest road is the

Richardson Highway (completed in 1910), followed by the Steese Highway (1927), the Alaska Highway (1942), the Taylor Highway (1951), and the Dalton Highway (1974) (Valencia 2007). According to the Alaska Department of Transportation fixed recorder stations nearest to our field sites, the average daily traffic counts the year of our study were greatest on the Steese Highway (1,433 vehicles per day), followed by the Dalton Highway (1,110 vehicles per day), the Richardson Highway (987 vehicles per day), and the Alaska Highway (526 vehicles per day; Birkholz 2013). Traffic is not recorded on the Taylor Highway.

Our sites on the Taylor and Steese Highways occur within the Yukon-Tanana Uplands ecoregion of

Alaska, which is underlain by the metasedimaentary Yukon-Tanana terrane and is typified by rocky soils, and discontinuous permafrost on north-facing slopes and valley bottoms (Nowacki et al. 2001). Our sites along the Dalton Highway are within the Ray Mountains ecoregion, which is underlain by the metamorphic Ruby terrane (Nowacki et al. 2001). The Ray Mountains ecoregion typically has shallow rocky soils and discontinuous permafrost (Nowacki et al. 2001). Both the Yukon-Tanana Uplands and the Ray Mountains ecoregions were largely unglaciated during the Pleistocene ice ages, but the highest peaks in these areas supported small alpine glaciers (Foster et al. 1994; Nowacki et al. 2001). The sites in the Delta Choronsequence occur within the Tanana-Kuskokwim Lowlands ecoregion, which is typified by fluvial and glaciofluvial sediments, overlain by varying depths of eolian silts and organic soils (Nowacki et al. 2001). Surface moisture is abundant in the Tanana-Kuskokwim Lowlands due to the relatively gentle topography, poor soil drainage and patches of permafrost (Nowacki et al. 2001).

Field survey

To assess current patterns of invasion in burned habitats in interior Alaska, we surveyed for presence and abundance of non-native plant species at 99 locations within our study area (Fig. 1). Survey locations were selected based on close proximity to or overlap with BNZ LTER sites to take advantage of large existing datasets on biotic and abiotic variables at each burn site. Ninety-three of these sites had all burned in 2004 and were approximately evenly distributed between the burn complexes along the Steese (33 sites), Taylor (29 sites) and Dalton (31 sites) highways, which we will refer to as regions. The remaining six of these sites were a chronosequence of sites along the Alaska and Richardson Highways which burned in 1999 (7 years old at the time of sampling), 1994 (12 years old), and 1987 (19 years old). We did not include unburned habitat in our survey effort because at the time of the study, invasive plants were not documented in unburned black spruce forest in our sample area (Cortés-Burns et al. 2007; AKEPIC 2013).

We recorded the presence and number of all non-native plant species within a 30 m by 60 m belt transect extending from the edge of the road shoulder into the burn. Percent cover of non-native plants within burned habitat was not used because cover was minimal (≤1 % cover, and only a few individuals in most cases) at all sites where they were present. Using the Alaska Natural Heritage Project invasiveness rankings (Carlson et al. 2008), we categorized the non-native plant species present at each site as "aggressive" (invasive, ranking >50) or as "non-aggressive" (non-invasive, ranking <50). These rankings are based on literature records of species impacts, biological traits, dispersal ability, distribution, and feasibility of control in Alaska and similar habitats elsewhere (see Carlson et al. 2008).

To provide an index of non-native plant propagule pressure from roadsides at a subset of 19 intensively studied sites, we surveyed a 1 m × 100 m belt transect parallel to the road 1 m from the edge of the burned forest in the road right-of-way. Within the belt transect, we visually estimated the cover of all non-native species in ten 1 m × 10 m lengths.

Because we found regional differences in the presence of non-native plants occurring within habitat that burned in 2004, we conducted additional analysis of biotic and abiotic variables that might help explain these differences. We used geographic variables (latitude, longitude, elevation, slope, aspect), surface vegetation cover estimates (percent live moss, dead moss, and burned organics cover), residual organic soil remaining, soil texture categorizations, canopy burn severity, and mineral soil pH from a publicly available BNZ LTER dataset (Johnstone 2013). For detailed information on how each of these variables were collected see Johnstone (2013).

Experimental design

At the intensively studied sites, we conducted two separate experimental manipulations: one which investigated site factors and regional influences that affect invisibility of sites that all burned within a single year (2004) in 12 sites spread across three regions, and another which investigated the influence of the time elapsed since burning on site invisibility in 6 sites within a single region. Sites consisted of 30 m × 30 m plots placed in relatively homogeneous areas with respect to topography and regenerating vegetation. The sites sampled for the experiment were overlapping or adjacent to (<150 m away) the 30 m × 60 m survey transects at those sites.

To understand local and regional factors that affected the susceptibility of areas burned in the year 2004, a low severity-high moisture, low severity-low moisture, high severity-high moisture, and high severity-low moisture site was selected in each of the Steese, Taylor, and Dalton regions, for a total of 12 sites. We used the site classifications determined by Johnstone et al. (2008) in 2005, the summer after the fire. In brief, they assigned burn severity classes by visually estimating the percent mineral soil cover and measuring the remaining organic soil (duff) depth at eleven random points. To determine site moisture level, they evaluated topographic position, soil texture and mean percent moisture in mineral soil (as measured over a 3-week period in July 2006 using a hand-held moisture probe (Hydro-Sense, Campbell Scientific, Edmonton, AB, Canada) at eleven random points). High severity sites had >5 % mineral soil exposed and <7 cm mean remaining duff. Low severity sites had <5 % mineral soil exposed and >7 cm mean remaining duff. High moisture sites tended to have fine soil texture, >30 % mineral soil moisture, and were located in low lying areas. Low moisture sites tended to have coarse soil texture, <30 % mineral soil moisture, and be located on slopes or ridges. Further details on the 2004 site classification protocols are available in Johnstone et al. (2008).

We evaluated the influence of time elapsed since fire on site susceptibility to non-native plant colonization using the Delta Chronosequence sites. In these sites, we crossed the three burn ages with two levels of burn severity to identify six different site types. Site burn severity was assigned in the same manner as for the 2004 burn sites, and severity classifications were established prior to this study by Kasischke and Johnstone (2005). Due to similarities in topography and soil texture, site moisture was not a factor in the chronosequence investigation.

Core collection and measurements

Within each intensively sampled burn site we established three randomly selected 30 m transects in a uniform compass direction with a minimum distance of 2 m between transects. We took three cores (7 cm diameter × 22 cm depth) every 5 m along the transects using a soil corer inserted at the vegetation surface. Cores were inserted into cylindrical pots (Stuewe and Sons D40L pots, Tangent, Oregon) of similar dimensions to bring back to the greenhouse for experimentation. The cores remained intact from the surface vegetation down through the duff layers and mineral soil. Dwarf shrub, herbaceous and bryophyte vegetation remained alive on the surface of the core. We determined the native plant richness of the plants remaining on the surface of the core by counting the number of vascular and non-vascular species. Native non-vascular and vascular biomass were determined for each core by clipping live shoots at the soil surface at the end of the greenhouse experiment.

Inside the core holes, we measured the horizon thicknesses of the different duff layers: live moss, upper duff and lower duff. Every 10 m along each transect an additional core was taken with a soil corer inserted at the soil surface to determine the water holding capacity of the upper duff, lower duff, and mineral soil horizons. To calculate water holding capacity (WHC) of each horizon, we divided field-moist cores into sections based on the field measurements of the horizon thickness. Each horizon section was homogenized in a tray, and then a sub-sample was placed in a pre-weighed and saturated filter paper inside a funnel. We saturated the soil with deionized water and let it drip. When the soil ceased dripping, we weighed it, dried it to a constant weight, and then reweighed it. WHC is expressed in g H_2O per g dry soil.

Invasive plant growth measurements in greenhouse

To assess the invasibility of burn soils independent of propagule pressure, and to examine the influence of edaphic factors and small-scale plant interactions on three different invasive species, we transported the intact soil cores to a greenhouse at the University of Alaska Fairbanks for experimentation. We used two watering treatments in the greenhouse. High moisture availability was maintained in cores from high moisture sites by watering with an overhead boom every 2–3 days and by inserting the bottom 3 cm of the cylindrical pots in trays with water. Cores from low moisture and chronosequence sites were watered on the same schedule with the overhead boom only. High moisture and low moisture treatments cores were staggered evenly along the greenhouse bench to account for potential positional effects.

On each of the three cores from each sampling point, we sowed seeds of one of our focal species *M.*

albus, B. inermis (collected from outside the greenhouse), *H. aurantiacum* (Chiltern Seeds, UK). These focal species were chosen based on the current abundances and potential threat to Alaskan boreal forest ecosystems (e.g. Carlson et al. 2008) rather than their occurrence in our field sites. There were no visible established populations of the three focal invasive species at our sampling locations.

We scarified all *M. albus* seeds by hand using sandpaper to prepare them for germination. We placed five seeds of *M. albus* or *B. inermis*, or seven seeds of *H. aurantiacum* (preliminary experiments indicated lower germination rates for this species) on a core top for all sites to ensure at least one seedling per pot germinated. We scored germination of *M. albus* after 10 days. Due to longer time requirements for germination (as determined in a pilot project), we scored *B. inermis* and *H. aurantiacum* germination after 14 days.

After 30 days, we randomly thinned plants to 1 invasive per pot for the remainder of the experiment. Seedlings were grown at a mean temperature of 22 °C with 20 h of light per day, typical of the growing season in interior Alaska. After 150 days, we determined survival, assessed proportion of reproductive survivors (either flowering or reproducing asexually), and harvested both shoots and roots of 9 plants per species per site. The 9 final plants per species per site used in the final analyses were from the same sampling locations that the cores for additional soil analysis were collected.

Statistical analyses

All statistical analyses were performed using SAS v.9.1 (SAS Institute, Cary, North Carolina). To analyze field survey data, we determined if the presence of non-native plants in burned field sites was influenced by burn severity, site moisture, or region using Chi square analysis. We used multiple logistic regression to investigate geographic and environmental variables that might help predict presence of non-native plants within the burned area. We used ANOVA tukey tests to look for differences in roadside non-native plant cover between site types and regions.

We evaluated the data from greenhouse experiments at two spatial scales: across our sites examining the effects of large-scale fire characteristics (fire severity, moisture, age and region), and within-sites looking at the small scale soil and vegetation variables that might explain differences in invasive plant responses between our sites.

To determine the influence of burn severity, moisture, region, and age on invasive plant growth in the greenhouse, we conducted ANOVA using site-level means (2004 burns experiment N = 12, chronosequence experiment N = 6) of response variables for each of the three focal species. The explanatory variables for 2004 burn sites were burn severity, site moisture, and region; for chronosequence burn sites the explanatory variables were burn age and burn severity. Response variables individually tested for each species included germination (% per pot), survival, final biomass and reproduction (number of tillers, stolons, or flowers). Interaction terms were not significant, so our final models exclude the interaction terms to increase the model degrees of freedom.

To evaluate small-scale mechanisms that might explain differences in invasive plant responses between these sites, we took advantage of the high microvariability in soil and vegetation characteristics within burns. We used core-level data to determine which soil and native vegetation variables best explained the final biomass of the three focal species in both the 2004 burn experiment and the chronosequence experiment. We ran multiple linear regressions for all possible models using the nine soil and vegetation covariates. We then ranked the models using Akaike's Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson 2002). We calculated the average parameter estimates for each covariate in the set of best-supported models (those within 3 AIC_c units of the model with the lowest AICc score) to assess the direction of the response of each invasive plant species to the parameter. We also calculated cumulative AIC_c weights ($0 \leq \sum \omega_i \leq 1$), or importance values, to evaluate strength of evidence for each soil or vegetation variable as a contributing factor to invasive plant final biomass (Burnham and Anderson 2002; Arnold 2010). We considered importance values >0.5 as indication of well-supported parameters.

In the 2004 burn experiment we tested for differences in soil properties and native vegetation on the soil cores between site types using ANOVA on site-level means. Tukey tests were used to distinguish differences between regions and between burn severity and site moisture classes. In the chronosequence

experiment there was only one site for each burn age and burn severity combination, so to analyze differences in soil properties, native vegetation, and surface cover on the soil cores between site types we conducted ANOVA on soil–core level data, followed by Tukey tests to distinguish differences between the sites. Initial graphing of the chronosequence experiment data suggested that there was a difference between sites, but that the relationship between age and invasive plant growth was not linear, therefore, we chose an ANOVA approach over a linear regression approach. In all analyses, final invasive plant biomass data were log-transformed to meet model assumptions.

Results

Field survey

We found eleven non-native plant species established and reproducing along roadsides adjacent to our burn sites: *B. inermis, Chenopodium album* L., *Crepis tectorum* L., *Elymus repens* (L.) Gould, *Lepidium densiflorum* Schrad., *Matricaria discoidea* DC., *M. albus, Plantago major* L., *Polygonum aviculare* L., *Taraxacum officinale* F. H. Wigg. ssp. *officinale,* and *Trifolium hybridum* L. Mean non-native plant cover on the roadsides adjacent to our intensively sampled sites was highest along the Dalton Highway, followed by the Taylor Highway and the Steese Highway (Fig. 2). Roadside cover of non-native plants near the Delta Chronosequence burns was very low (Fig. 2), but this was due to intentional weed control efforts by both the Department of Transportation (L. Johnson, pers. comm.) and the nearby Ft. Greeley Army Base (J. Mason, pers. comm.).

Five of the non-native species present on roadsides were found within burned forest: *C. album, C. tectorum, E. repens, M. albus,* and *T. officinale* ssp. *officinale*. Of these, *C. tectorum*, and *M. albus* are considered aggressive (Carlson et al. 2008). Across all 2004 burn sites surveyed (n = 93), 12 sites had non-native plants occurring within burned areas. Non-native plant presence within burn sites was significantly influenced by the region in which it was located ($X^2_{(3)} = 14.52$, $P = 0.002$). Burns in the Dalton region were more frequently invaded than burns in the Steese and Taylor regions and were the only 2004 burns with aggressive
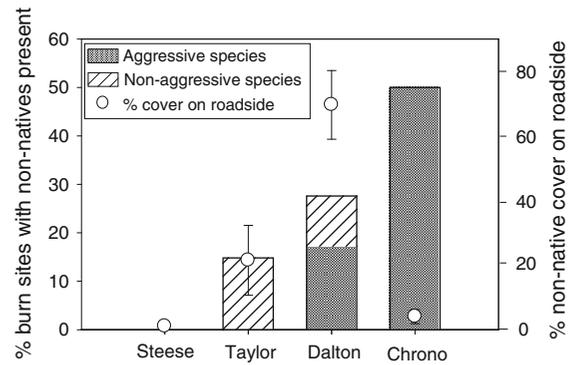
Fig. 2 Percent burn sites with non-native plants present and percent cover of non-native plants on roadsides of different regions in interior Alaska, July 2006. *Bars* indicate percent of burn sites surveyed where non-native plants occurred within the burns on the Steese (n = 33), Taylor (n = 29) and Dalton (n = 31) regions, and in the Delta Chronosequence burns ("Chrono"; n = 6). *Striped bar* segments indicate percent of sites where only non-aggressive non-native species were present, while *solid bar* segments indicate only aggressive non-native species present or aggressive and non-aggressive species co-occurring. *Open dots* indicate mean percent non-native plant cover (±SE) from a subset of sites where we conducted roadside surveys in each region (Steese N = 4, Taylor N = 4, Dalton N = 4, Chrono N = 5)

species (Fig. 2). The Dalton burns also had higher abundances and richness of non-native plants established in burned habitat than in the Taylor or Steese sites (Dalton: 4 species, approx. 150 total individuals; Taylor: 1 species, 4 total individuals; Steese: 0 individuals). Four of the sites with non-native plants growing were high severity burns and eight of the sites were low severity, however there was not a significant association between burn severity and presence of non-native plants. When investigating which geographic and environmental variables that helped predict non-native plant presence within the 2004 burns, the only significant variables ($p < 0.05$) were the slope of the burn site ($b = -0.38$, $p = 0.04$) and the mineral soil pH ($b = 1.78$, $p = 0.01$).

The Delta Chronosequence sites (n = 6) had both aggressive and non-aggressive non-native plants occurring in burned habitat and showed the greatest non-native abundance and richness of all areas surveyed. The highest abundance and richness of non-native plants within a chronosequence site occurred in the 1994 burn (1994 high severity site: 4 species, >500 individuals; 1994 low severity site: 3 species, approx. 150 individuals).

Greenhouse experiment

2004 Burns: burn severity, moisture, and region

Coarse burn severity and moisture levels did not significantly influence the growth or fitness-related responses of any of our focal species (data analyzed using means per site: Table 1, Fig. 3a). The region a burn occurred in tended to outweigh the effect of site-level burn severity or moisture on our focal species growth responses. *M. albus* survival was influenced by region (Table 1), with greatest percent survival in soils from the Dalton region. Shoot biomass of *H. aurantiacum* was significantly influenced by region (Table 1), with lower biomass in soils from the Steese region than in soils from the Dalton or Taylor regions. *B. inermis* grown in Steese region soils had had approximately 77 % fewer tillers than when grown in Dalton and Taylor region soils (Table 1).

Region explained approximately 7 times more variation in *M. albus* survival than did severity or moisture levels combined (region $R^2 = 0.64$, severity + moisture $R^2 = 0.09$). Similarly, region explained 4 times more variation in *H. aurantiacum* shoot biomass (region $R^2 = 0.54$, severity + moisture $R^2 = 0.13$), and 2.2 times more variation in *B. inermis* tiller production (region $R^2 = 0.45$, severity + moisture $R^2 = 0.20$), than did site severity and moisture levels combined.

2004 Burns: small-scale mechanisms

At the small-scale, within-site level, both *M. albus* and *B. inermis* biomass were positively correlated with lower duff thickness, which had the highest variable importance values of all the possible covariates (Table 2). Non-vascular plant biomass had a negative relationship with *H. aurantiacum* and *B. inermis* final biomass, and had the highest and second highest importance values of all the soil and vegetation covariates, respectively (Table 2).

Between regions, we found several differences in the soil and vegetation variables we measured (Table 3). When compared to cores from sites in the Dalton or Taylor regions, cores from the Steese region had significantly greater mineral soil water holding capacity, non-vascular biomass and native plant richness (Table 3). Soil cores from the Dalton region tended to have lower values for upper duff water holding capacity, upper duff bulk density, and

Table 1 ANOVA F values for each explanatory variable (source of variation) in the 2004 burn experiment and chronosequence experiment

Experiment source	df	M. albus					H. aurantiacum						B. inermis					
		Germ	Surv	Shoot mass	Root mass	Total mass	Germ	Surv	Shoot mass	Root mass	Total mass	Stolons	Germ	Surv	Shoot mass	Root mass	Total mass	Tillers
		F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F
2004 Burns																		
Region	2	0.87	8.30**	1.15	1.07	0.98	1.30	3.16	5.79*	2.63	3.86	2.47	0.33	2.41	3.11	3.07	3.05	4.50*
Severity	1	0.15	0.05	0.55	0.83	0.58	0.01	0.45	2.12	1.47	1.69	0.49	0.34	2.80	0.99	2.63	1.77	0.84
Moisture	1	0.00	2.37	0.38	0.78	0.50	0.22	0.00	0.72	0.98	0.86	0.32	0.18	0.00	4.21	2.63	3.35	3.31
error df = 7																		
Chronosequence Burns																		
Age	2	0.11	1.42	2.25	2.57	2.49	0.24	7.00	0.20	0.19	0.19	0.08	1.07	.	0.50	0.43	0.47	2.36
Severity	1	0.08	0.02	3.20	3.45	3.66	0.00	1.00	1.34	1.02	1.25	2.65	1.21	.	3.25	0.41	1.10	4.95
error df = 2																		

Each invasive species was modeled separately with percent germination, shoot biomass, root biomass, total biomass, or reproductive capacity (*H. aurantiacum*- # of stolons; *B. inermis*- # tillers) as the response variable. No F values could be produced for *B. inermis* survival from chronosequence burns because of invariant (100 %) survival rates * $p < 0.05$, ** $p < 0.01$
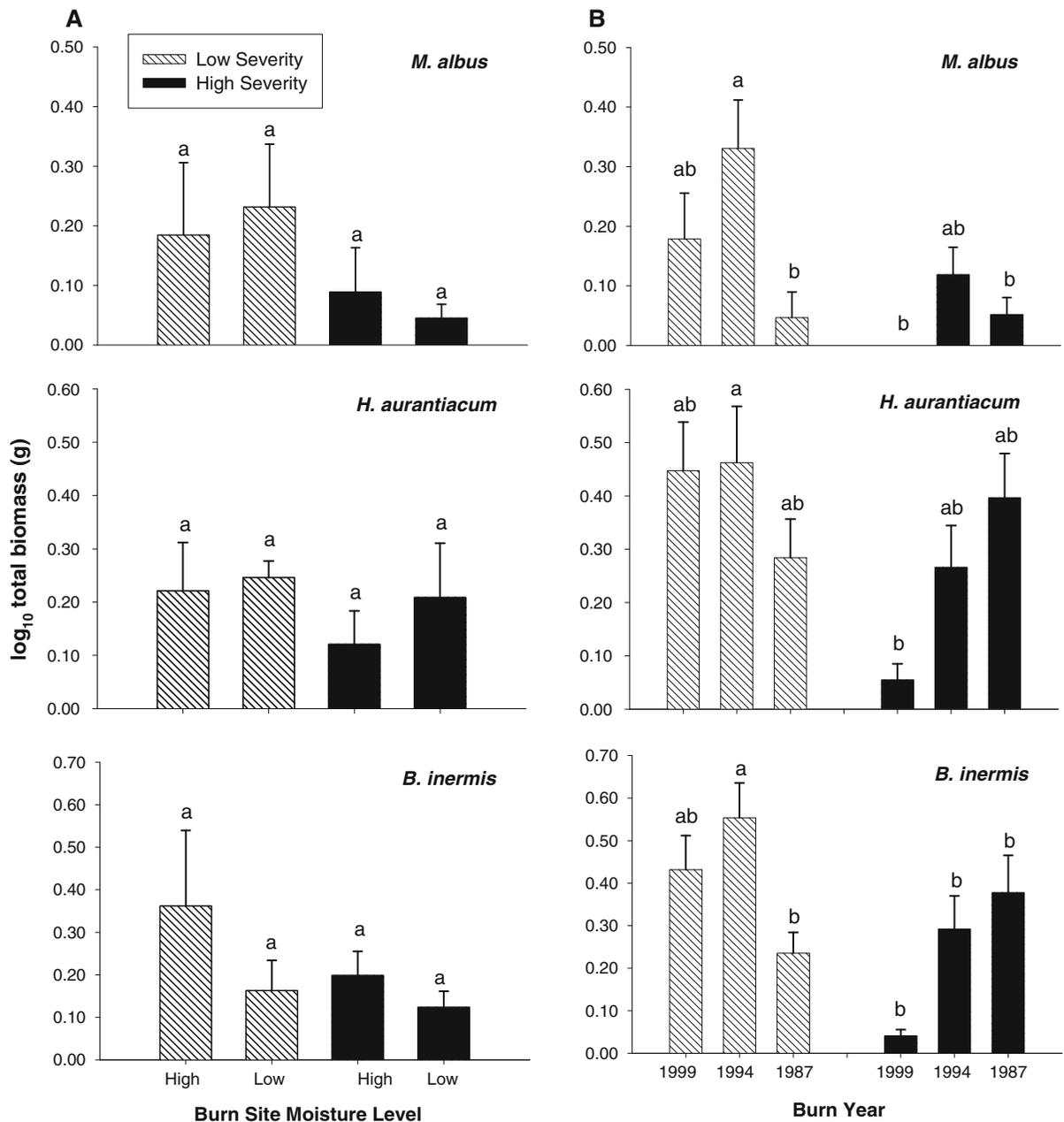
Fig. 3 Mean $\log_{10}$ total biomass ($\pm$ 1SE) of invasive plants grown for 150 days in soil cores taken from sites burned in 2004 (**a**) and from sites in the Delta Chronosequence (**b**). Low severity burn types are indicated by striped bars, and high severity burn types are indicated by *solid bars*. The 2004 values represent the mean biomass across the three sampling regions. *Different letters* indicate significant differences ($p < 0.05$) in total biomass between severity-moisture categories or age-severity categories

maximum native vascular plant heights compared to Taylor or Steese cores (Table 3). Comparing 2004 severity-moisture site types across the three regions, low severity sites tended to have greater lower duff

thickness compared to high severity sites (Table 4). High severity sites, particularly high severity-high moisture sites, tended to have the greater non-vascular plant biomass than low severity sites (Table 4).

Table 2 Average Akaike's Information Criterion parameter estimates ($\bar{b}$) and cumulative parameter weights ($\sum \omega_i$) for candidate variables explaining total biomass of three invasive plant species after 150 days of growth in soil cores from the 2004 burns and the chronosequence burns

Variable	M. albus		H. aurantiacum		B. inermis	
	$\bar{b}$	$\sum \omega_i$	$\bar{b}$	$\sum \omega_i$	$\bar{b}$	$\sum \omega_i$
2004 Experiment						
Moss layer depth (cm)	0.051	0.291	−0.006	0.254	0.022	0.275
Upper duff layer depth (cm)	−0.0004	0.204	0.0002	0.254	0.007	0.388
Lower duff layer depth (cm)	**0.043**	**0.794**	−0.009	0.378	**0.031**	**0.951**
WHC upper duff (g H_2O/g soil)	0.011	0.259	−0.007	0.279	0.020	0.321
WHC lower duff (g H_2O/g soil)	−0.099	0.397	−0.027	0.367	−0.030	0.289
WHC mineral (g H_2O/g soil)	0.264	0.282	−0.185	0.464	**−0.415**	**0.945**
Native plant richness (# spp.)	−0.051	0.379	−0.019	0.424	0.003	0.253
Non-vascular biomass (g)	0.022	0.206	**−0.116**	**0.973**	**−0.056**	**0.918**
Native vascular biomass (g)	−0.126	0.289	**−0.088**	**0.821**	−0.017	0.254
Chronosequence experiment						
Moss layer depth (cm)	−0.013	0.177	−0.017	0.221	**0.069**	**0.841**
Upper duff layer depth (cm)	−0.016	0.371	−0.008	0.241	0.001	0.252
Lower duff layer depth (cm)	0.016	0.365	0.014	0.322	0.000	0.211
WHC upper duff (g H_2O/g soil)	0.012	0.263	−0.095	0.346	0.017	0.257
WHC lower duff (g H_2O/g soil)	−0.107	0.349	**0.206**	**0.535**	**0.191**	**0.689**
WHC mineral (g H_2O/g soil)	**0.290**	**0.784**	−0.151	0.317	0.273	0.433
Native plant richness (# spp.)	**−0.045**	**0.706**	**−0.092**	**0.995**	**−0.051**	**0.989**
Non-vascular biomass (g)	0.029	0.237	−0.051	0.326	**−0.041**	**0.612**
Native vascular biomass (g)	**−0.137**	**0.883**	**−0.177**	**0.975**	**−0.275**	**0.999**

Average parameter values were taken over models with a difference in AICc < 3. Soil water holding capacity is abbreviated as WHC. Bold values indicate well-supported parameters ($\sum \omega_i > 0.5$)

Chronosequence burns: burn age and severity

Burn age and severity did not significantly influence the germination, survival, shoot biomass, root biomass, or reproduction for any of the three focal invasive species in our chronosequence greenhouse experiment (data analyzed using means per site; Table 1). For all three species there was a general pattern toward the greatest invasive plant biomass in soil cores from the 1994 low severity burn site, second greatest biomass in the 1987 low severity soils and lowest biomass in cores from the 1999 high severity burn (Fig. 3b).

Chronosequence burns: small-scale mechanisms

At the within-site level in the chronosequence experiment, native vascular biomass and native plant richness had high cumulative parameter weights and were negatively correlated with final biomass of all three species (Table 2). Water availability may also play an important role in determining invasive plant establishment in the chronosequence burn sites. Water holding capacity of the mineral soil had a high importance value and positively influenced *M. albus* final biomass (Table 2). Similarly, the water holding capacity of the lower duff was positively correlated with the final biomass of both *H. aurantiacum* and *B. inermis* biomass and had high importance values for both species (Table 2).

Soils taken from the 1994 low severity burn chronosequence burns tended to have greater remaining lower duff depth and greater soil water holding capacity for all three soil layers than all the other burn sites, among other soil differences (Table 5). While native vascular and non-vascular biomass

Table 3 Soil and native vegetation characteristics for cores from 2004 burn sites in the Steese, Taylor, and Dalton regions

Variable	Steese	Taylor	Dalton
Moss layer depth (cm)	0.5 (0.1)	0.5 (0.3)	0.4 (0.2)
Upper duff layer depth (cm)	3.0 (1.0)	4.7 (0.8)	3.0 (0.8)
Lower duff layer depth (cm)	3.6 (0.3)	5.2 (0.4)	4.2 (0.8)
WHC upper duff (g H_2O/g soil)	5.04 (0.57)a	4.25 (0.42)ab	2.59 (0.75)b
WHC lower duff (g H_2O/g soil)	2.83 (0.28)	2.18 (0.09)	2.24 (0.38)
WHC mineral (g H_2O/g soil)	0.87 (0.05)a	0.68 (0.05)b	0.65 (0.14)b
Native plant richness (# spp.)	3.4 (0.5)a	1.9 (0.6)b	1.9 (0.4)b
Non-vascular biomass (g)	1.62 (0.13)a	0.85 (0.36)b	1.04 (0.32)b
Native vascular biomass (g)	0.37 (0.08)	0.41 (0.14)	0.25 (0.08)

All values are site-level means with standard error in parentheses. Significant differences ($p < 0.05$) between regions (columns) for each variable are denoted by different letters. Soil water holding capacity (WHC) is abbreviated

varied little between sites, native plant richness was significantly higher in cores from the 1999 high severity site than in cores from any other site, and tended to have greater native vascular plant cover (Table 5).

Discussion

Large scale patterns

Our field survey and greenhouse data suggest that regional effects outweigh the influence of burn site characteristics on invasive plant growth, survival and reproduction in burned areas (Fig. 2; Table 1). In the 2004 burns, greater traffic and propagule pressure along the Dalton Highway could account in part for the higher numbers of invasives (Fig. 2), but our greenhouse study indicated that there were additional factors beyond propagule pressure: all three of our focal species showed greater (though not significant for all species) survival and biomass in soils from the Dalton region than from other regions.

Biotic and abiotic variables that we measured in the greenhouse cannot explain the regional differences we found (Table 3). Soil pH, however, significantly differs between regions at these sites (Hollingsworth et al. 2013) and was an important predictor of non-native plant presence within burns. The higher mineral soil pH along the Dalton Highway compared to the Steese and the Taylor Highways may play a role in the greater field abundances of non-native plants. These results are consistent with the results of a study by Rose and Hermanutz (2004), who found increasing abundances of invasive plants in boreal forest sites with higher pH. The combined effects of higher propagule pressure, lower non-vascular plant cover, and a higher mineral soil pH may have made burns in

Table 4 Soil and native vegetation characteristics for cores from an unburned control site and 2004 burn sites of different severity and moisture levels

Variable	Unburned	Low severity		High severity	
		High moist	Low moist	High moist	Low moist
Moss layer depth (cm)	4.1a	0.2 (0.0)b	0.3 (0.2)b	1.0 (0.2)c	0.4 (0.1)b
Upper duff layer depth (cm)	11.6a	7.6 (1.2)b	4.6 (1.5)c	1.5 (0.6)d	0.6 (0.5)d
Lower duff layer depth (cm)	5.4a	6.2 (0.8)a	5.6 (0.5)a	3.0 (0.2)b	2.6 (1.2)b
WHC upper duff (g H_2O/g soil)	9.48a	6.24 (0.49)b	4.89 (0.42)b	3.07 (1.62)c	1.64 (0.89)c
WHC lower duff (g H_2O/g soil)	3.66a	3.35 (0.46)a	2.76 (0.25)ab	2.06 (0.73)bc	1.49 (0.29)c
WHC mineral (g H_2O/g soil)	0.75	0.65 (0.12)	0.84 (0.12)	0.74 (0.10)	0.70 (0.14)
Native plant richness (# spp.)	3.2ab	1.9 (0.4)ab	1.6 (0.6)a	3.4 (0.5)b	2.7 (1.0)ab
Non-vascular biomass (g)	1.62ab	0.84 (0.36)b	0.76 (0.48)b	1.74 (0.17)a	1.35 (0.11)ab
Native vascular biomass (g)	0.58a	0.50 (0.07)a	0.21 (0.09)b	0.44 (0.14)a	0.22 (0.10)b

All values are site-level means with standard error in parentheses. Significant differences ($p < 0.05$) between burn types (columns) for each variable are denoted by different letters. Soil water holding capacity (WHC) is abbreviated

Table 5 Soil and native vegetation characteristics for cores from the Delta Chronosequence high and low severity sites burned in 1999, 1994, and 1987

Variable	Low severity			High severity		
	1999	1994	1987	1999	1994	1987
Moss layer depth (cm)	1.0 (0.2)ab	0.9 (0.1)ab	2.0 (0.4)c	0.6 (0.1)a	1.3 (0.2)abc	1.5 (0.2)bc
Upper duff layer depth (cm)	5.5 (0.5)b	3.4 (0.6)c	6.6 (0.5)a	0.5 (0.2)d	0.1 (0.1)d	1.3 (0.3)c
Lower duff layer depth (cm)	4.1 (0.5)b	7.3 (0.5)a	4.2 (0.6)c	2.6 (0.3)bc	2.6 (0.3)c	3.2 (0.4)bc
WHC upper duff (g H_2O/g soil)	3.66 (0.21)a	4.95 (0.30)b	3.53 (0.29)c	3.28 (0.53)d	2.54 (0.00)e	2.71 (0.30)f
WHC lower duff (g H_2O/g soil)	2.14 (0.12)a	3.25 (0.23)b	2.08 (0.16)c	1.54 (0.17)d	1.54 (0.08)d	2.04 (0.15)e
WHC mineral soil (g H_2O/g soil)	0.84 (0.17)a	1.70 (0.28)b	0.77 (0.05)a	0.82 (0.07)a	0.73 (0.04)a	0.77 (0.06)a
Native plant richness (# spp.)	3.0 (0.2)a	3.3 (0.2)a	3.2 (0.2)a	4.5 (0.1)b	3.0 (0.2)a	3.0 (0.1)a
Non-vascular biomass (g)	1.57 (0.14)ab	1.32 (0.14)a	1.85 (0.25)ab	2.10 (0.21)b	1.64 (0.10)ab	1.10 (0.23)a
Native vascular biomass (g)	0.53 (0.10)	0.59 (0.11)	0.51 (0.12)	0.50 (0.07)	0.76 (0.12)	0.61 (0.09)

All values are core-level means with standard error in parentheses. Significant differences ($p < 0.05$) between burn types (columns) for each variable, as determined by Tukey tests, are denoted by different letters. Soil water holding capacity (WHC) is abbreviated

the Dalton region more susceptible to invasion than burns in the Steese and Taylor regions. Both the Steese and Taylor sites occurred within the Yukon-Tanana Upland ecoregion while Dalton sites occurred within the Ray Mountian ecoregion (Nowacki et al. 2001). These ecoregions differ primarily in soils and lithography (Nowacki et al. 2001), which may correlate with differences in soil pH and vegetation composition.

Overall, the burned sites within the Delta Chronosequence showed the highest levels of non-native plant invasion of all the field sites we surveyed (Fig. 2). In the greenhouse study, invasive plants grown in soils from the Delta Chronosequence sites had, on average, greater final biomass than the average biomass for plants grown in 2004 burn soils (Fig. 3). This result may also be driven by large-scale differences in soils and geology between ecoregions. These sites occurred within the Tanana-Kuskokwim Lowlands ecoregion, which has plenty of surface moisture and thick organic soils compared to the rocky, well-drained soils of the Yukon-Tanana Uplands and Ray Mountains ecoregions (Nowacki et al. 2001). Both of these characteristics appeared to positively correlate with invasive plant growth in some species when burn age was held constant (Table 2). The differences in the susceptibility of the different regions in interior Alaska suggest that ecoregion delineations (i.e. Nowacki et al. 2001) may be an important tool for prioritizing post-fire invasive plant management, and further research regarding correlations between invasions and ecoregions is warranted.

Contrary to the findings of other studies (Agee and Huff 1987; Turner et al. 1997; Doyle et al. 1998; Keeley et al. 2003; Hunter et al. 2006; Klinger et al. 2006), our focal species did not show a significant response to overarching severity, moisture and age categories at the site level (Table 1). We may have failed to detect any response due to a lack of statistical power, as the number of intensively sampled sites (2004 burn experiment: N = 12; chronosequence burn experiment: N = 6) was limited by the amount of space available in the greenhouse to grow the plants and the logistical challenges of accessing sites spread throughout a large geographic area. Our multiple linear regression analysis, however, suggests that the biomass of all three of our focal species was influenced by small-scale variations in soil and vegetation characteristics within sites that reflect the complex interactions between burn severity, site moisture and time elapsed since burning. These interactions will be discussed in the following section.

Small-scale mechanisms

Burns experiment

The thickness of the lower duff layer was highly important in explaining both *M. albus* and *B. inermis* total biomass (Table 2). Lower duff thickness reflects the amount of time between the most recent fire and

the previous fire, the pre-fire species composition, decomposition rates, environmental conditions, and the post-fire site characteristics (with greater thickness of this layer remaining in low severity, moist sites) (Johnstone et al. 2010a). Sites where fire consumes nearly all of the moss and upper duff layer but a substantial amount of the lower duff layer intact may provide excellent growth substrate for *M. albus* and *B. inermis*. Indeed, the survey site with the highest numbers of *M. albus* (30 reproductive individuals in the burn) fits exactly this description.

In addition, non-vascular plant biomass was one of the most important variables explaining the biomass of *H. aurantiacum* and *B. inermis* (Table 2). The proportion of bryophyte-free area was much greater in our low severity sites than in high severity sites (Table 4; Johnstone et al. 2008; Bernhardt et al. 2011). Quickly establishing liverworts (*Marchantia polymorpha*) and mosses (*Ceratadon purpureus* and *Polytrichum* spp.) may present a buffer to *H. aurantiacum* invasion in high-severity sites. A similar pattern was documented in arctic tundra, where the abundant mosses decreased germination and establishment of a diverse array of native tundra plants (Gough 2006). Non-vascular plant abundance may represent an important barrier to invasive plant colonization and spread in black spruce forest of interior Alaska, and further study is warranted.

Chronosequence burn experiment

Vascular plant species biomass and native plant richness were important covariates for total invasive plant biomass in our chronosequence sites (Table 2). Vascular plant cover and richness tended to be highest in the 1999 high severity burn site (Table 5). We may have seen reduced biomass (Fig. 3b) of our three focal invasive plant species in the soil cores with higher native vascular plant richness and abundance due to higher levels of resource competition and reduced vacant niche space. In other small-scale invasibility studies, sites with greater native plant richness and abundance tend to be more resistant to non-native plant species introductions (Tilman 1997; Naeem et al. 2000; Kennedy et al. 2002).

The higher abundance of native vascular plant biomass in the 1999 high severity burn site compared to the older high severity burn sites may reflect the influence of canopy closure on native plant cover

through time. Reduced light availability associated with higher canopy closure likely caused the reduced abundance of vascular plants in the soil cores from the 1994 and 1987 high severity burns. Other studies in this chronosequence have shown that, as burn age increased, both leaf area index and above ground biomass increased as tree species became larger (Zhuang et al. 2003; Liu et al. 2005). This canopy closure should also presumably reduce invasive plant growth and field abundances, as most invasive plant species in Alaska are early successional species with limited shade tolerance (Carlson et al. 2008). In our greenhouse experiment, the reduced competition from understory plants combined with the absence of shade from dominant deciduous trees and shrubs likely allowed invasive plant biomass and reproduction to be greater than it would be in the field in the 1994 and 1987 sites.

The length of time between fire and canopy closure has been cited as an important parameter for site invasibility (Keeley et al. 2003). While high severity burns in black spruce forest tend to develop into dense, closed canopy deciduous forest relatively quickly (if a seed source is available), low severity burns tend to slowly regenerate into a more open canopy black spruce forest (Johnstone and Chapin 2006). This greater light availability in low severity burns, even as time elapses, may provide ample opportunity for invasive colonization and seed bank establishment. We found some evidence of this in our field survey, where aggressive non-native plants occurred more frequently in low severity chronosequence burn sites than in high severity chronosequence sites.

Mineral soil or lower duff soil water holding capacity also played an important role in explaining the variation in final biomass of all three invasive plant species grown in cores from the chronosequence burns (Table 2). The higher water holding capacity of soils in the 1994 low severity burn site (Table 5), may explain why the three focal species tended to have the greatest biomass in cores from this site (Fig. 3b).

Implications for management

Combining the cross-taxa trends in our greenhouse study with our field survey results, we can provide

some general conclusions that will aid land managers in identifying boreal forest habitats that are particularly vulnerable or resistant to non-native plant invasions. We found that differences in propagule pressure along roadsides and differences in native non-vascular and vascular plant re-establishment are particularly important factors for land managers deciding the regions in which to focus their monitoring efforts. For example, interior Alaska black spruce forests burned within the Dalton region may be particularly vulnerable, while Steese region burns may be more resistant to invasions. Native vegetation rapidly re-establishing in high severity burn sites may provide a level of resistance to non-native plant invasion, while some low severity sites may provide invasive plants ample lower duff soil remaining post-fire and a refuge from intense resource competition. The advantageous soil and light conditions may persist in low severity burns even as succession proceeds, suggesting that invasive plant monitoring and management efforts should not be restricted to recently burned areas. Our greenhouse study and field survey provide support for management plans that focus on burn complexes in regions with the highest amounts of unvegetated ground cover and highest levels of invasive plant propagule pressure.

While boreal forests around the world are changing and fire is becoming a more common occurrence (Gillett et al. 2004; Chapin et al. 2006; Balshi et al. 2009), they still remain some of the least invaded ecosystems on the planet (Sanderson et al. 2012). Continued research and monitoring focused on vulnerable areas such as wildfire burns can aid management decisions and provide hope to prevent invasions in the future.

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