Disturbance impacts on non-native plant colonization in black spruce forests of interior Alaska

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By

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ABSTRACT

While boreal forest habitats have historically been relatively free from invasive plants, there have been recent increases in the diversity and range of invasive plants in Alaska. It is critical that we understand how disturbances influence invasibility in northern boreal forests, to avoid the economic damage other regions have experienced from invasive plants. Black spruce (*Picea mariana*) is the dominant forest type in interior Alaska, and wildfire is the dominant disturbance in these forests. Furthermore, disturbances in the form of management for fire suppression are common in forests close to urban areas. I surveyed recently burned, managed, and undisturbed black spruce forests for invasive plants to determine if fire and management facilitate invasive plant colonization. I also conducted an experimental seeding trial with three invasive plants common to Alaska (bird vetch (*Vicia cracca*), common dandelion (*Taraxacum officinale*), and white sweetclover (*Melilotus officinalis*) in burned and mature black spruce forest to determine if fire facilitates invasive plant germination. To determine the effect of substrate type on invasive plant germination, I planted seeds on a variety of substrates in the burned forest. Results indicate that fire and fire suppression treatments promote invasive plant colonization, as invasive plants were observed in burned and managed areas, but not in mature stands. Analysis of environmental data taken at survey sites indicate that fire mediates invasibility through its effects on substrate quality. In burned stands, invasive plants are most likely to colonize areas of shallow post-fire organic depth. Results from the seeding trials were consistent with results from invasive plant surveys, with reduced germination in mature compared to burned forest, and no germination on the residual organic layer in the burned forest. The highest germination occurred on mineral soil in burned forest, indicating that severe fires that combust the organic layer are likely to increase invasibility. The results of this study suggest that invasive species control efforts should be prioritized to disturbed forests, particularly areas where the disturbance has exposed mineral soil.

ACKNOWLEDGEMENTS

DEDICATION

I would like to dedicate this thesis to the memory of the late Dr. Gary Bortolotti. His passion for teaching ignited my interest in the Biological Sciences, and his mentorship during my Undergraduate Thesis gave me the confidence to continue on in research. I think I can speak on behalf of the whole Department of Biology at the University of Saskatchewan when I say that he was well loved, and is dearly missed.

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CPCRW: Caribou Poker Creeks Research Watershed.

GPS: Global positioning unit.

NMS: Non-metric multidimensional scaling.

PCQ: Point center quarter.

1 GENERAL INTRODUCTION

Invasive species can have negative economic (Pimentel et al. 2005) and environmental (Levine et al. 2003) impacts. Humans often act as transport vectors for invasive species, taking plants with them to new regions for agricultural and ornamental purposes. Many of these species have escaped into natural ecosystems. For example, *Tamarix* species were introduced to the United States as an ornamental and erosion control agent in the early 1900's (Pauchard et al. 2008), and have since invaded over 370,000 ha of land in fifteen states (Zavaleta 2000). Many introductions, however, are unintentional. Seed contamination in crop and grass seed is believed to be responsible for the introduction of many invasive species in Alaska (Conn 2012). Invasive plants have been implicated in the decline of threatened and endangered species by changing ecosystem processes, community structure, and displacing native species (Denslow 2007 and references therein).

Invasive plant species can strongly influence ecosystem functioning. Changes in hydrology (Busch and Smith 1995), nutrient cycling (Drenovsky and Batten 2007), soil conditions (Dukes and Mooney 2004), and fire regimes (D'Antonio and Vitousek 1992), have all been attributed to invasive plants. Invasive plants have also been shown to reduce native biodiversity (Paterson et al. 2011). Aside from ecosystem impacts, invasive plant species also have negative economic impacts. These impacts can be direct impacts on consumptive market-based goods such as urban water supplies, livestock, and crops (Naylor 2000). In the fynbos shrub land of South Africa, native vegetation plays a large role in erosion control and water retention, but invasive tree species have reduced available water for human use (Naylor 2000). It will be very expensive to return the fynbos to its natural state (Naylor 2000). This example emphasizes the need for early detection of invasive plants, and an understanding of invasive plant dynamics in recently invaded ecosystems. Invasive species can also have impacts on non-consumptive values, such as bird watching, hunting, and local subsistence economies (Naylor 2000).

1.1 What is an invasive plant?

There are many definitions of invasive species, and there has been much confusion surrounding the term (Richardson et al. 2000, Colautti and MacIsaac 2004). One point of confusion is that many species are termed invasive if they are considered undesirable and weedy, and this definition is sometimes applied to native plants as well. In this thesis, I define invasive plant species as plants with established populations outside their native range that are expanding into natural ecosystems (Richardson et al. 2000). Invasive plants are often disturbance specialists, which when established can out-compete native vegetation, causing shifts in community composition. Traits such as fast growth rates, high flower and seed production, and high photosynthetic rates, are common in invasive plants (van Kleunen et al. 2010). These traits often provide invasive plants a competitive advantage over native species. Additionally, some invasive species lack natural predators in the regions they are invading, providing them with another advantage.

1.2 Principles of biological invasions and black spruce forest ecology.

In order to mitigate the potential damage invasive plant species might cause in Alaska (Flagstad and Cortes-Burns 2010), we must understand the mechanisms that influence community invasibility (Rew and Johnson 2010). While there has been relatively little work done on invasion biology in Alaskan ecosystems, knowledge of invasive species dynamics in other regions provides a basis for predicting factors most likely to drive patterns of species invasion in interior Alaska. These studies have identified several key factors that affect both the probability of establishment, and the rate of invasive species spread. For example, the probability of establishment is known to be influenced by disturbance-induced changes in native species composition and richness (Kneitel and Perrault 2006), and the rate of invasive spread is influenced by invasive seed sources along roadways (Huebner 2010). Resident plant communities and soil properties such as nutrient levels, however, can increase a community's resistance to invasion (McGlone et al. 2011), and this should hold true for black spruce (*Picea mariana* (Mill.) B.S.P.) forests. Changes in fire regime that impact plant community recovery and composition (Bernhardt et al. 2011), and increased anthropogenic disturbance, however, are likely to change the resistance of black spruce forests to invasive plants.

58   Black spruce is the dominant forest type in boreal Alaska, covering 40% of the Fairbanks

59   region of interior Alaska (Viereck et al. 1983). Black spruce stands are characterized by cool,

60   moist soils, the majority of which are underlain by permafrost (Viereck et al. 1983). These stands

61   have low productivity (Van Cleve et al. 1983b), and a moss dominated understory (Viereck et al.

62   1983). Low temperatures on the forest floor and poor litter quality, combined with high moisture

63   due to poor drainage, restrict decomposition and nutrient cycling, resulting in a thick organic

64   horizon that locks up nutrients (Flanagan and Van Cleve 1983, Viereck et al. 1983). Most fires

65   only partially combust this surface organic layer, generating a poor seedbed characterized by

66   high porosity and dark colour that increase the potential for seedling desiccation (Johnstone and

67   Chapin 2006a). Black spruce overcomes this limitation by producing large quantities of seed

68   with large carbohydrate reserves, that allow rapid root growth to attain moisture (Johnstone et al.

69   2010). These unique properties, and their interactions, have helped keep black spruce forests in a

70   stable succession pattern of stand self replacement for the past 6000 years (Lloyd and Bunn

71   2007).

72   There has only been one study on invasive plants in burned black spruce forests of

73   interior Alaska (Villano 2008). This study suggested that fire can influence invasive plant

74   abundance by reducing moss cover, thereby allowing invasive plants to establish in the

75   understory (Villano 2008). Monitoring studies suggest that time elapsed since burn may have a

76   positive effect on invasive plant abundance in areas where invasive plants have established

77   (Villano and Mulder 2008). The effects of soil pH and active layer depth can play a role in

78   determining invasive plant abundances in burned black spruce forests, but active layer depth has

79   not been measured in previous studies, and only general soil pH data has been available (Katie

80   Villano-Spellman, personal communication, 2011). While there are other factors that influence

81   invasibility (Elton, 1958), here I summarize three principal factors likely to influence invasive

82   plant colonization and spread and describe how they might apply to black spruce forests in

83   AlaskaI

84   *1.2.1   Resource competition*

85   Competition with native plants for resources such as light and nutrients can affect both seedling

86   survival and the subsequent growth of invasive plants (D'Antonio 1993). Disturbances such as

87   fire have been shown to facilitate invasion by increasing the amount of available resources

3

88	(Hobbs and Huenneke 1992, Davis et al. 2000, Cavallero and Raffaele 2010). In a study of

89	protected areas in the boreal forest, natural areas that had been invaded by non-native plants were

90	areas in which limiting resources were already available, or had been made available by

91	disturbance (Rose and Hermanutz 2004). Following a fire there is generally decreased canopy

92	cover. The decreased canopy cover exposes previously shaded micro-sites, allowing colonization

93	of these sites by shade intolerant plant species. In a study on Hemlock stands in the Delaware

94	Water Gap National Recreation Area, there was a strong positive effect of insect induced canopy

95	defoliation on invasive plant success (Eschtruth and Battles 2009). Canopy defoliation induced

96	by fire has similar effects, increasing the potential for exotic plant invasion in some ecosystems

97	(Hunter et al. 2006, Kuppinger et al. 2010). The increased light levels following fire in black

98	spruce forests may allow shade intolerant invasive species to colonize. Furthermore, in black

99	spruce forests in interior Alaska, canopy removal induced by fire causes a warming of the soil

100	due to increased solar radiation (Van Cleve and Dyrness 1983). This soil warming may allow

101	increased colonization of some invasive species intolerant of colder soils.

102	 Increases in soil nutrient availability following a fire (Dyrness and Norum 1983,

103	Cavallero and Raffaele 2010), can give invading plant species an avenue for rapid establishment.

104	In a Mojave Desert shrub land, increased N availability following a fire increased the

105	productivity of an invasive grass, and decreased native plant productivity (Esque et al. 2010).

106	Fluctuations in resource availability after a fire can initially promote invasive plants, but in some

107	ecosystems continued resource fluctuation may act as a filter for invasive plants, restricting them

108	to micro sites in which they maintain a competitive advantage (Davis et al. 2000). Following a

109	fire, black spruce forests in interior Alaska have potential rates of productivity and nutrient

110	cycling similar to warmer ecosystems (Van Cleve et al. 1983a). Over time, however, the system

111	reverts back to low productivity and low nutrient supply (Van Cleve et al. 1983a), which may

112	limit the persistence of invasive species in these forests.

113	*1.2.2 Community diversity*

114	Community diversity is often cited as a mechanism that strengthens a community's ecological

115	resistance to invasion (Levine and D'Antonio 1999, Kennedy et al. 2002). The concept dates

116	back to early work by Elton and MacArthur (Elton 1958, May and Macarthur 1972). Native plant

117	diversity is believed to increase resistance to invasive plants by reducing the amount of available

118   resources (Elton 1958). Greater native species richness, i.e. community diversity, has been

119   shown to significantly decrease survival of invasive plant species (Von Holle and Simberloff

120   2005). The diversity and biomass of invading species have also been shown to be negatively

121   impacted by greater resident species richness (Dimitrakopoulos et al. 2005). In a review of

122   mathematical models relating diversity and invasibility, all models supported the hypothesis that

123   higher community diversity decreases invasibility (Levine and D'Antonio 1999).

124   In a review of empirical studies, however, the relationship between diversity and

125   invasibility was unclear, and many studies indicated that diversity may increase invasibility

126   (Levine and D'Antonio 1999). Diverse native communities indicate a diverse suite of resources,

127   which may increase the probability that invasive plant species are able to establish. The spatial

128   scale of the diversity-invasibility relationship is also important. On a small scale, community

129   diversity appears to foster resistance to invasion. However, on a broad spatial scale, covariation

130   in diversity and ecological factors such as propagule supply, may make the most diverse

131   communities the most invasible (Levine and D'Antonio 1999, Levine 2000).

132   When relating community diversity to invasion resistance, a simple measure of species

133   richness is not sufficient, and the functional traits of the species present must be taken into

134   consideration (Davis 2009). Plant functional traits will govern competitive interactions for

135   resources, such as light and nutrients. Plants can be placed into functional groups based on traits

136   such as resource use and growth form. Functional group diversity can increase an ecosystem's

137   resistance to invasive species. For example, in an experimental manipulation of functional group

138   diversity in grasslands, a negative relationship was found between functional group diversity and

139   invasibility (Symstad 2000). In a similar study, the functional diversity of the native plant

140   assemblage appeared to have a greater influence on invasive plants through competitive effects

141   and suppression of adult plant growth, than it did on seedling establishment (Hooper and Dukes

142   2010). Changes in plant community composition, both at the species and functional group level,

143   may influence invasibility in Alaskan black spruce forests. Whether generalizations on the

144   effects of species and functional group diversity on invasibility in other regions will hold true in

145   Alaska, however, is unknown.

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148 *1.2.3   Propagule pressure*

149 Propagule pressure can be defined as a composite measure of individuals released into a region

150 to which they are not native, incorporating the number of individuals involved in a release event,

151 and the number of release events (Lockwood et al. 2005). Release events are the release of

152 mature seeds from the parent plant. Distance from propagule source is also an important aspect

153 of propagule pressure, but is an aspect seldom considered in studies addressing propagule

154 pressure.

155   Gradients of propagule pressure are thought to influence the susceptibility of a given

156 community to invasion (Lockwood et al. 2005, Eschtruth and Battles 2009). Propagule pressure

157 has been recognized as a factor influencing colonization and establishment of new species since

158 the writings of Drude in 1896 (Davis 2009). While it is unusual to find consistency in the effects

159 of different factors on invasion, propagule pressure has been shown to outweigh other factors

160 influencing community invasibility in many ecosystems (Lockwood et al. 2005). In a review by

161 Colautti and others (2006), propagule pressure was a significant predictor of plant invasiveness

162 and community invasibility in 55 out of 64 studies reviewed. Propagule pressure was also the

163 only factor that significantly predicted community invasibility in an experimental manipulation

164 of forest understory vegetation by Von Holle and Simberloff (2005). In interior Alaska,

165 propagule pressure from the roadsides likely plays a large role in invasive plant establishment in

166 black spruce forest interiors, however this relationship has not been directly tested (Villano and

167 Mulder 2008).

168   The timing of a propagule release event is very important for invasive plant

169 establishment. The release must correspond with favourable conditions in the habitat being

170 invaded. Recent research suggests that in black spruce forests, moss acts as a barrier for invasive

171 seed germination (Villano 2008). Wildfires in northern boreal forests that combust the thick

172 organic layer have been shown to increase seedbed quality for black spruce (Brown and

173 Johnstone 2012). If an invasive plant has a seed source that remains intact following fires which

174 expose better seedbeds, they may have the potential to colonize these recently burned areas.

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177

1.3 General objectives

The objectives of this thesis are to test the hypothesis that disturbance facilitates invasive plant colonization in black spruce dominated forests of interior Alaska. Specifically, I aimed to examine whether invasive plants were more likely to be found in recently burned compared to mature forest stands, to explore what post fire characteristics best predict invasive plant presence, and to experimentally determine the effect of disturbance and substrate types on invasive plant germination. To accomplish these objectives, I surveyed the current distribution of invasive plants in mature, recently burned, and managed black spruce forests in interior Alaska, and conducted a detailed field experiment of invasive plant germination at a single location. This is the first study I am aware of to systematically survey an equal number of burned and mature stands for invasive plants in interior Alaska, and also the first study to experimentally test the effects of substrate type on germination of invasive plants in a field based setting in interior Alaska. In answering the objectives listed above, I will be able to determine whether fire facilitates invasive plant colonization, and whether there is a germination barrier preventing colonization of mature forests. Determining what post fire characteristics best predict invasive plant presence will allow land managers to prioritize invasive species control efforts in forested areas of interior Alaska.

2 EFFECTS OF WILDFIRE AND FORESTRY MANAGEMENT ON INVASIVE PLANT COLONIZATION

2.1 Introduction

Northern habitats have historically been relatively free from invasive plant species (Conn et al. 2008), and populations of invasive plants in Alaska have generally been restricted to areas of human disturbance (Carlson and Lapina 2004, Cortes-Burns and Flagstad 2010). The cold climate of Alaska, as well as its isolation and low levels of human disturbance, have limited the establishment and spread of many invasive species (Wurtz et al. 2006). There has, however, been a recent expansion of invasive plants into natural habitats in interior Alaska (Carlson and Lapina 2004, Wurtz et al. 2006, Cortes-Burns et al. 2007, Lapina et al. 2007). As the northern climate warms, and anthropogenic disturbances increase, invasive plant diversity and abundance are likely to continue increasing.

Areas where human disturbances intersect with natural disturbances provide can an entry point for invasive species into natural ecosystems (Carlson and Lapina 2004). Disturbances from road construction can create soils that are favourable for invasive plant colonization and growth (Greenberg et al. 1997). Once non-native plants are established along the road verge, high propagule pressure can threaten the invasion of adjacent ecosystems (Lockwood et al. 2005). There are several examples of invasive plants moving from human disturbed areas into natural ecosystems in Alaska (Cortes-Burns et al. 2007, Lapina et al. 2007, Villano 2008). Invasive plants have been found in burned forests that also serve as campgrounds (Cortes-Burns et al. 2007). Only one study, however, has addressed movement of invasive plants from human disturbed areas into burned forests that are relatively free of anthropogenic disturbance (Villano 2008, Villano and Mulder 2008).

The prevalence of non-native plant infestations on roadways of interior Alaska has allowed some non-native species to infiltrate into naturally disturbed (burned) black spruce forests (Villano and Mulder 2008) that have historically remained relatively free from invasive plants. The frequency of non-native plants in burned forests and the effects of prescribed fire and other fuel treatments on invasive plant abundances, however, have not been assessed. The one study that was conducted on invasive plant movement into burned forests (Villano 2008) only

225   assessed broad scale environmental variables such as region, site moisture, and latitude. This

226   study found patterns of invasive colonization within burned stands that were best explained by

227   regional differences, however it only had one mature stand to compare to the burned stands, thus

228   it remains unclear if mature forests differ from recently burned forests in terms of resistance to

229   invasive plant colonization. Villano (2008) also collected soil cores from burns of different

230   severity and age, and found that soils from older, lower severity burns, supported the greatest

231   invasive plant growth. The inferences made in her study with respect to invasive plant growth,

232   however, were conducted in a greenhouse setting, and knowledge of how invasive plants will

233   perform in a natural setting is lacking. It is also unclear how far into the forest interior non-native

234   plants are able to establish. In other forested ecosystems of Indiana and Arizona, invasive plant

235   abundances decrease as distance to road verges increase (e.g. Flory and Clay 2006, Fowler et al.

236   2008). If invasive plants are concentrated near the forest edge in forests of Interior Alaska, land

237   managers can focus invasive plant control efforts to the forest edge.

238   The increase of invasive plant species diversity in interior Alaska, and the spread of these

239   species into natural habitats, illustrate the need for more studies on the relationships between

240   environmental conditions and disturbance, and how these factors influence community

241   invasibility. Understanding how environmental conditions and disturbance affect invasibility is

242   especially important as Alaska is currently seeing an expansion of population, commercial

243   development, gardening, and outdoor recreation activities (Carlson and Shephard 2007), all of

244   which have been implicated in the introduction and range expansion of non-native plants.

245   Understanding how frequently invasive plants are migrating into forested areas, and what factors

246   are influencing invasive plant migration, can be used to prevent the ecological and economic

247   damage that invasive species have caused in other regions (e.g. Naylor 2000, Paterson et al.

248   2011).

249   The objectives of this chapter are: 1) to determine if fire facilitates invasive plant

250   colonization, 2) to assess what post fire environmental variables best predict invasive plant

251   presence, 3) to determine if understory plant functional composition influences invasibility, 4) to

252   assess if propagule pressure influences invasive plant abundances in burned stands, and 5) to

253   determine if patterns of invasive plant abundance within burned stands show an edge effect. To

254   answer these questions I surveyed an equal number of burned (n=33) and unburned (n=33)

255 stands for invasive plants, and measured environmental characteristics and native plant

256 functional group compositions.

2.2   Methods

2.2.1   Study area

259 This study took place in interior Alaska, which is bounded by the Brooks mountain range

260 (~67°N) to the north, and the Alaska mountain range (~63°N) to the south. The region is

261 characterized by mountain ranges and gently sloping uplands, braided rivers with large

262 floodplains, and extensive areas of flat lowlands (Van Cleve et al. 1983a). The dominant forest

263 type in interior Alaska is black spruce (*Picea mariana* (Mill. B.S.P.), and is characterized by

264 extensive moss cover, a sparse layer of tall shrubs, and a well-developed layer of low shrubs

265 (Viereck et al. 1983). Other forest types are found throughout the landscape, including forests

266 dominated by white spruce (*Picea glauca* (Moench) V.), and deciduous species such as

267 trembling aspen (*Populus tremuloides* (M.), balsam poplar (*Populus balsamifera* L.), and

268 Alaskan paper birch (*Betula neoalaskana* (S.) (Van Cleve et al. 1983a). Study sites were located

269 in black spruce dominated forests along major roadways in interior Alaska.

270   Interior Alaska experiences a continental climate with large annual temperature

271 fluctuations. At the southern extent of our study sites, in Nenana, mean annual temperature is

272 -3°C, while mean January and July temperatures are -22°C and 16°C, respectively. Annual

273 precipitation in Nenana averages 235mm, 54% of which falls from June to August. At the Bettles

274 airport, north of the Yukon River, mean annual temperature is -5°C, and temperatures range from

275 -24°C in January to 16°C in July. Mean annual precipitation at the Bettles airport is 355mm,

276 43% of which falls from June to August (Shulski & Wendler 2007). My study region falls within

277 the discontinuous permafrost zone of interior Alaska, and the majority of which is underlain by

278 permafrost (Osterkamp and Romanovsky 1999).

2.2.2   Site selection

280 Fifty sites were surveyed adjacent to the Dalton highway (25 burned sites, 25 mature sites, burn

281 year 2004), and sixteen sites (8 burned sites, 8 mature sites, burn year 2006) were surveyed

282   adjacent to the Parks highway in the Nenana burn complex (Figure 2.1). Surveys were conducted

283   between June 19th 2012 and July 28th 2012. Whereas the sites adjacent to the Dalton highway

284   were mostly black spruce dominated, the sites adjacent to the Parks highway were often a

285   mixture of larch, black spruce, and trembling aspen. Burn patches were identified and sites were

286   randomly selected from burn scars using random numbers to represent starting points along the

287   road and within the burn scar. Survey sites required road access, a safe spot to park the vehicle

288   within walking distance of the sites, and a minimum distance of 100 m between sites. For burned

289   stands, the fire scar had to extend 100 m into the forest from the road corridor edge. Four of the

290   Dalton burned sites were within 50m of the Trans Alaska pipeline at the end of the transect

291   furthest from the road. For mature stands, the unburned portion of the stand had to extend 100m

292   from the forest edge when possible. Due to the patchy nature of mature forests and adjacent fire

293   scars, transects in three mature stands were only 85m in length.

294   *2.2.3   Sampling protocol for invasive plant surveys*

295   In each site, a 100 m belt transect was run into the forest from the forest edge, perpendicular to

296   the road. The forest edge was located by visually assessing a shift from the disturbed roadside to

297   typical forest understory plant communities. Vegetation in the ditches of these highways is

298   regularly cut and in some cases the cutting overlapped with the shift to forest plant communities.

299   When cutting was present, the transect was started where the disturbance from cutting stopped.

300   Along the transect, 0.5 m X 0.5 m quadrats were placed at the following distances from the forest

301   edge: 1 m, 5 m, 10 m, 15 m, 20 m, 25 m, 30 m, 50 m, 70 m and 100 m. Within each quadrat,

302   percent cover estimates were made for the following ground cover types: exposed mineral soil,

303   moss, *Marchantia*, leaf litter, lichens, grass, dead wood, residual organic layer, rock, and sedges.

304   Exposed mineral soil represented patches of bare mineral soil void of vegetation, moss

305   represented regenerating mosses, *Marchantia* represented the liverwort *Marchantia*, leaf litter

306   represented deciduous broadleaf and grass litter, lichens represented lichens, grass represented

307   live grass, dead wood represented downed woody debris with a diameter >1 cm, residual organic

308   layer represented charred organic layer uncolonized by plants, rock represented rocks with a

309   diameter > 1 cm, and sedges represented live sedges. The same observer performed all percent

310   cover estimates to avoid observer bias. To obtain some information on plant community

11

311 composition, a presence list of all plant genera was generated by recording any genera present on

312 the belt transect regardless of whether they were in the quadrats used for ground cover sampling.

313   The transects were also used to sample site level variables, including: invasive plant

314 density, understory plant composition, absolute density of all trees in the stand, absolute densities

315 for individual tree species within the stand, estimates of seedling density for dominant tree

316 species, soil pH, soil moisture, soil texture, and active layer depth. For assessing invasive plant

317 density, the whole belt transect was surveyed (100 m X 2 m) and any occurrences of invasive

318 plants were documented and the distance on the transect was recorded. To speed up sampling,

319 the densities of invasive plant stems were grouped into one metre classes (e.g. 0-1 m, 1-2 m ...

320 99-100 m). The transects were surveyed twice to increase the detection of invasive plants. The

321 presence of all understory plants along the transect were recorded (to the genus level, and to

322 species level for a few plants), and dominant understory genera were indicated. For a description

323 of how tree density was measured and calculated, see point center quarter (PCQ) methods below.

324 Seedling estimates of black spruce, paper birch, and trembling aspen were recorded in five 1 m X

325 1 m plots placed randomly along the transect. Estimates were grouped into five ordinal

326 categories: 0 (0 seedlings), 1 (0-5 seedlings), 2 (6-10 seedlings), 3 (11-20 seedlings), and 4 (>20

327 seedlings). Soil measurements were conducted at three randomly selected points along the

328 transect. Mineral soil was diluted with deionized water and pH was measured using the Hanna

329 HI 98128 handheld pH metre (Hanna instruments, USA, Carrolton, TX). Soil moisture was

330 measured using a Hydrosense CS620 moisture probe inserted at a 45° angle to the soil surface

331 (Campbell Scientific, Canada, Edmonton, AB) using 12cm probes. Mineral soils were hand

332 textured using a chart from Thien (1979). Active layer depth was measured by pushing a 120cm

333 thaw probe into the ground perpendicular to the surface until it hit ice or rock. While it was our

334 intention to hit ice, if ice could not be reached within three tries this failure was noted and the

335 depth to rock/gravel was recorded. Thaw depth in sample points where the thaw depth was

336 greater than the length of the probe were recorded as exceeding 120cm. Active layer depth

337 measurements were all taken within one week at the end of the summer to minimize variation

338 due to thawing. A site moisture classification based on topography and drainage was also

339 conducted for each site following the methods of Johnstone and colleagues (2008).

340

341   *2.2.4   Point Center Quarter (PCQ) sampling*

342   The sampling protocol for PCQ sampling of tree density were modified from Mitchell (2001).

343   The same transect that was used for other measurements was used for PCQ sampling. Along

344   each transect, a sampling point was placed every ten metres (n=10). A line was run perpendicular

345   to the transect at each point. The line and the transect created four quarters for sampling. In each

346   quarter, the tree nearest to the sampling point (within five metres of the sampling point) was

347   selected and distance from the sampling point, diameter at breast height (DBH) and tree species

348   were recorded. Absolute density of all tree species and absolute density of individual tree species

349   were calculated following the methods outlined in Mitchell (2001).

350   *2.2.5   Roadside sampling*

351   A 1 m^2 plot adjacent to the road was used to visually estimate roadside invasive plant

352   abundances. Any invasive plants present were recorded as having zero (0 individuals/m^2), low

353   (<25 individuals/m^2), medium (25-50 individuals/m^2), or high (>50 individuals/m^2) levels of

354   infestation. These estimates of abundance were used as an indicator of propagule pressure.

355   *2.2.6   Sampling protocol for managed areas*

356   Twelve sites were sampled for invasive plant presence in shear bladed (n=11) and thinned (n=1)

357   forests within 150 km of Fairbanks, Alaska. Shearblading mechanically removes all vegetation

358   and piles the debris in windrows. Thinning treatments remove only some trees, leaving live trees

359   present. Each managed forest had a nearby undisturbed control. Within each site, two 20 m X 2

360   m transects were placed parallel to each other within the treatments (or mature forests) in a

361   position meant to capture the dominant features of the disturbance. These transects were

362   surveyed for invasive plant presence, and native plant community was measured by recording the

363   presence of all genera that occurred on the transects. The presence of invasive plants that were

364   not on the transects was noted, but density estimates were not made. The two transects were also

365   used to visually estimate dominant ground cover types (for a description of ground cover types

366   see sampling protocol for invasive plant surveys above) at ten points on each transect (n=20).

367

2.2.7   Statistical analysis

369   I used contingency table analysis with the chi-square test statistic to determine whether fire

370   increases invasive plant occurrences (Marques de Sá 2007). The response variable was coded as

371   the number of sites with invasive plants present, and the explanatory variable was forest type

372   (mature or burned). To test for differences in organic layer depth between burned and mature

373   sites, a Welch two sample t-test was used because organic layer depth showed a normal

374   distribution. To test for differences in thaw depth between burned and mature sites, a Wilcoxon

375   rank sum test was used because thaw depth did not follow a normal distribution, and

376   transformations were unsuccessful at making the data approximate a normal distribution. All

377   analyses were conducted in R 2.14.1 (R Development Core Team 2011).

378   *2.2.8   Multi-model inference*

379   General linear models were used to assess the effects of measured variables on invasive plant

380   presence, including 1) the effect of *Taraxacum officinale* G.H. Weber ex Wiggers (hereafter

381   referred to as *Taraxacum*) roadside density, 2) the effect of tree seedling regeneration, 3) the

382   effect of soil characteristics, and 4) the effect of plant functional group diversity and diversity

383   within plant functional groups. It should be noted that these models were largely predicting the

384   presence of *Taraxacum*, as it was present at every site that invasive species were observed, and

385   occurrences of other invasive species at sites were rare (see Results). All models were run as

386   binomial general linear models (GLM). The binomial GLM is an extension of logistic regression

387   that uses the Bernoulli (binomial) error family rather than the Gaussian (normal) error family

388   (Zuur et al. 2009). I chose the complementary log-log (clog-log) link function as it is more

389   suitable for binomial data that have an unequal number of zeroes and ones than the other two

390   commonly used (logit and probit) link functions (Zuur et al. 2009). The response variable in all

391   models was the presence (1) or absence (0) of invasive plants within a site.

392   To test what factors best predict invasive plant presence within burned stands, I used

393   multi model inference, an information theoretic approach to model selection and inference

394   (Burnham and Anderson 2002). The advantage to this approach over traditional stepwise model

395   selection procedures is the ability to test multiple hypotheses and make inferences from multiple

396   models. The information theoretic approach also allows one to determine which of the models in

397 a candidate set best fit the data. Furthermore, if a given explanatory variable occurs in many of

398 the top models from the candidate set, it provides further evidence that it has a strong influence

399 on the response variable.

400   For each question, a maximal model was run using all explanatory variables related to the

401 question. To test for the effect of propagule pressure on invasive plant presence, I used the

402 roadside density of *Taraxacum* as the explanatory variable. Other invasive plant roadside

403 densities were not used because every site that had invasive plants present had *Taraxacum*

404 present, and of the sites with invasive plants, *Melilotus officinalis* (L.) Lam. (hereafter referred to

405 as *Melilotus*) and *Crepis tectorum* L. (hereafter referred to as *Crepis*) were only present at one

406 site each. To test for the effects of seedling regeneration of dominant tree species on invasive

407 plant presence, the maximal model included seedling counts for black spruce, paper birch, and

408 trembling aspen. Seedling regeneration was recorded as an ordinal variable (see above) and

409 seedling counts for the model were calculated by taking the midpoint of the seedling classes for

410 each species and totaling them for each site. To test the effects of soil characteristics on invasive

411 plant presence, a model including residual organic layer depth, soil moisture, and mineral soil pH

412 was also fit. Neither the seedling model nor the soil model differed from the null model, so

413 seedling regeneration and soil characteristics were combined into one model, which did differ

414 from the null model. This model contained residual organic layer depth, mineral soil pH, soil

415 moisture, and seedling counts for black spruce, paper birch, and trembling aspen. Hydrosense

416 moisture probe values were used in the model rather than site moisture classification, because the

417 model would not run using moisture class. The Hydrosense moisture values showed a significant

418 positive correlation with moisture class ($p<0.001$, $R^2=0.85$), justifying the use of these values in

419 the model. To test for the effect of functional group richness and richness within functional

420 groups on invasive plant presence, a maximal model was fit using functional group richness,

421 deciduous shrub richness, ericaceous shrub richness, forb richness, *Equisetum* presence/absence,

422 lichen presence/absence, and sedge presence-absence.

423   Each maximal model was simplified following a stepwise model simplification procedure

424 using Akaike's information criterion (AIC) (Crawley 2007). In model simplification procedures

425 a drop in AIC is desirable, and the model with the lowest AIC is usually considered the "best"

426 model (Crawley 2007). Following model simplification for all maximal models, each simplified

15

427   model, maximal model, and every model from stepwise simplification were included in a set of

428   candidate models to rank using multi-model inference (Table 2.1). I also chose to include one

429   term models for each of the environmental variables (residual organic layer depth, mineral soil

430   pH, and soil moisture) to test the effects of these factors independently. For each candidate

431   model, corrected AIC (AIC_c) were calculated, and from this value each model was assigned an

432   Akaike model weight (w_i) (Burnham and Anderson 2002). I chose to use AIC_c because it is

433   better than AIC for small sample sizes (Burnham and Anderson 2002). Calculations were done in

434   the multi-model inference package (Barton 2013) in R (R Development Core Team 2011).

435   Models with a higher w_i indicate a better model fit to the data set, as w_i is analogous to the

436   probability that the model best fits the data. From the set of models, a 95% confidence set was

437   created by selecting models whose summed w_i was <0.95.

438   *2.2.9   Ordination analysis*

439   Non-metric multidimensional scaling (NMS) was used to look for patterns in ground cover types

440   related to invasive plant presence in burned sites (n=33). NMS is an unconstrained multivariate

441   ordination technique that places sample units along a chosen number of axes based on the

442   similarity of the variables put into the ordination (McCune and Grace 2002). The dimensions of

443   the matrices for the ordination were 10 X 33, and represented ground cover types (10) and sites

444   (33). The ordination was run on average values for ground cover (averaged from ten points)

445   within sites. The Sorensen coefficient was used because it is suitable for community data

446   (McCune and Grace 2002). The number of axes to use was determined using a Shepard plot,

447   which plots the stress of the ordination solution against the number of axes. I chose to use two

448   axes for the ordination, with a final stress of 0.16. The addition of further axes continued to

449   reduce stress, however the complication of interpretation generated by adding additional axes did

450   not justify the drop in stress. I also conducted a post-hoc test to determine the correlation

451   between ordination and original distance in the dissimilarity matrix, which gives an

452   approximation of the variance captured by each axis. The ordination analyses were conducted in

453   the vegan package (Oksanen et al. 2012) in R 2.14.1 (R Development Core Team 2011).

454

2.3   Results

2.3.1   *Distribution of invasive plants*

455

456

457   Fire had a strong influence on invasive plant presence. Invasive plants were never observed in

458   unburned stands, whereas 11 of the 33 burned stands had invasive plants present (χ^2=12.32,

459   d.f.=1, p<0.001). Mature stands had significantly greater organic layer depth (t=-4.4399, d.f.=63,

460   p<0.001) and significantly lower thaw depth (W=1019.5, p<0.001) (Figure 2.2).

461   Comparisons of models predicting invasive plant presence in burned stands resulted in

462   the top weighted (w_i) model having residual organic layer depth and regenerating paper birch

463   seedlings as model parameters (Table 2.1). All three top models contained residual organic layer

464   depth, indicating that it is a strong predictor of invasive plant presence (Table 2.1). Residual

465   organic layer depth was lower in sites where invasive plants were present (Figure 2.3), and the

466   density of paper birch seedlings was highest in sites where invasive plants were present. While

467   the median value for paper birch seedling density was lower in sites where invasive plants were

468   present, in sites where paper birch seedlings were present the density was high (Figure 2.4).

469   Because the median represents the middle data point in the data set, invaded sites with no paper

470   birch seedlings brought the median value down, while invaded sites that did have paper birch

471   seedlings present tended to have high densities which increased the range of the upper quartiles.

472   We found no evidence of mineral soil pH influencing invasive plant presence as it was

473   not present in any of the models in the 95% confidence set, and there was little difference in

474   mineral soil pH in sites where invasive plants were present versus sites where they were absent

475   (Table 2.1, Figure 2.3). Roadside density (propagule pressure) of *Taraxacum* did not

476   significantly influence invasive plant presence (Table 2.1). We found no strong evidence that

477   functional group diversity and diversity within functional groups influence invasive plant

478   presence. While some measures of functional group diversity were retained in the 95%

479   confidence set of models, the model weights were extremely low (Table 2.1). Soil moisture had a

480   significant effect on invasive plant presence in one of the models, however the model weight was

481   very low (Table 2.1).

482

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2.3.2   Species specific responses of invasive plants

484   High roadside densities of some invasive plants did not result in high presence within burned

485   stands. While *Melilotus* was present along the roadside for all sites surveyed, it was only

486   observed in one of the burned stands along the Dalton highway. *Taraxacum*, however, was

487   observed in eight sites (33%) on the Dalton highway and three (37.5%) along the Parks highway

488   despite having a lower roadside density than *Melilotus* (Table 2.2). Overall infestations of

489   *Taraxacum* and *Melilotus* were higher along the Dalton highway than the Parks highway (Table

490   2.2). *Crepis* was only present in one site along the Dalton highway, and was seldom encountered

491   in the roadside (Table 2.2). Other species that are considered to be invasive plants of concern in

492   Alaska (Carlson et al 2008), such as *Hordeum jubatum, Matricaria discoidea, Chenopodium*

493   *album, Plantago major,* and *Vicia cracca* were infrequently encountered in the roadside (Table

494   2.2), and were never observed colonizing burned stands. Invasive plant presence was unrelated to

495   dominant patterns in species ground cover composition expressed in the NMS ordination (Figure

496   2.5; Appendix C3). Axes 1 and 2 were able to capture approximately 46% and 26% of the

497   variation in the data, respectively. The variation in axis one was most strongly driven by the

498   presence of rock, sedge, and leaf litter, while the variation in axis two was most strongly driven

499   by mineral soil (Table 2.3). There was no apparent separation of sites with invasive plants

500   compared to those without along the axes of this ordination, indicating no systematic differences

501   in ground cover between invaded and non-invaded sites.

502   *2.3.3   Management effects on invasive plant colonization*

503   Four of the twelve managed sites had invasive plants present, and none of the undisturbed

504   controls had invasive plants present. Ground cover in the undisturbed control sites was

505   predominantly moss, leaf litter, and lichen, whereas managed sites had a variety of substrates

506   present (Table 2.4). *Crepis* was present in four sites and *Taraxacum* was also present at one of

507   those sites. All of the sites with invasive plants present had been treated by shear blading. Some

508   of the shearbladed sites had exposed mineral soil present, whereas the thinned site did not have

509   mineral soil present. In the thinned site the ground cover was predominantly moss (Table 2.4).

510

511   *2.3.4   Edge effects*

512   Plotting the number of *Taraxacum* individuals as a function of distance from the forest edge did

513   not reveal any edge effects, however this was not tested statistically. *Taraxacum* density was

514   similar at all distances, with the exception of one site that had a cluster of rosettes at 80m (Figure

515   2.6).

516 **Table 2.1:** Summary of models selected within the 95% confidence set of binomial logistic regression models predicting invasive
517 plant presence in burned survey sites from covariates representing soil properties, tree seedling regeneration, *Taraxacum* roadside
518 density (propagule pressure), functional group diversity and diversity within functional groups.

Model parameters	d.f.	Log likelihood	AIC_c	ΔAIC_c	$ɯ_i$	Summed $ɯ_i$
Residual organic layer depth* Paper birch seedlings	3	-14.829	36.50	0.00	0.310	0.310
Residual organic layer depth*	2	-16.803	38.00	1.50	0.146	0.456
Residual organic layer depth** Paper birch seedlings* Trembling aspen seedlings	4	-14.410	38.30	1.79	0.127	0.583
Taraxacum roadside density	4	-14.615	38.70	2.20	0.104	0.687
Deciduous shrub diversity* Equisetum presence/absence* Lichen presence/absence*	4	-14.966	39.40	2.90	0.073	0.760
Soil moisture*	2	-17.543	39.50	2.98	0.070	0.830
Deciduous shrub diversity** Equisetum presence/absence* Lichen presence/absence Functional group diversity	5	-13.612	39.50	3.02	0.069	0.899
Residual organic layer depth* Paper birch seedlings* Trembling aspen seedlings Black spruce seedlings	5	-14.043	40.40	3.88	0.045	0.944

519

520 **Note:** For model parameters: residual organic layer depth was measured in centimetres, seedlings for trees were transformed ordinal categories
521 representing the number of individuals/m^2, *Taraxacum* roadside density represents an ordinal category indicating the number of individuals/m^2,
522 soil moisture represents Hydrosense % volumetric soil moisture readings. Degrees of freedom = d.f., corrected Akaike's information criterion =
523 AIC_c, change in AIC_c from the top model = ΔAIC_c, Akaike model weight = $ɯ_i$. *p<0.05, **p<0.01.

524 **Table 2.2:**.Proportion of sites with low, medium, and high roadside densities for all invasive plants encountered in road surveys.

Density	Region	Taraxacum officinale	Melilotus officinalis	Crepis tectorum	Hordeum jubatum	Matricaria discoidea	Chenopodium album	Plantago major	Vicia cracca
Absent	Both	0.15	0.00	0.88	0.89	0.98	0.98	0.92	0.91
Low		0.59	0.41	0.12	0.08	0.02	0.02	0.08	0.06
Medium		0.20	0.33	0.00	0.03	0.00	0.00	0.00	0.00
High		0.06	0.26	0.00	0.00	0.00	0.00	0.00	0.03
Absent	Dalton	0.04	0.00	0.84	0.86	0.98	0.98	0.94	0.88
Low		0.62	0.26	0.16	0.10	0.02	0.02	0.06	0.08
Medium		0.26	0.40	0.00	0.04	0.00	0.00	0.00	0.00
High		0.08	0.34	0.00	0.00	0.00	0.00	0.00	0.04
Absent	Parks	0.50	0.00	1.00	1.00	1.00	1.00	0.88	1.00
Low		0.50	0.88	0.00	0.00	0.00	0.00	0.13	0.00
Medium		0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00
High		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

525

526 **Note:** For density categories: low <25 individuals/m^2, medium=25-50 individuals/m^2, high>50 individuals/m^2. For region, "both" represents the
527 combined set of sites adjacent to the Dalton highway and Parks highway.

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535 **Table 2.3:** Axis scores for the ground cover variables used in NMS ordination. The sign value represents the direction of influence,
536 and the absolute value of the number indicates the strength of the influence.

Ground cover type	Axis 1	Axis 2
Mineral soil	-0.25	0.67
Moss	0.19	0.09
Marchantia	0.04	0.07
Leaf litter	0.39	0.02
Lichen	0.15	0.00
Grass	0.29	0.17
Downed woody debris	0.11	0.06
Burned organic layer	0.02	0.04
Rock	0.45	0.30
Sedge	0.36	0.32

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539 **Table 2.4:** Ground cover values and invasive plant presence (1= present, 0= not present) recorded at managed and disturbed sites.
540 Values represent percent cover estimates averaged from twenty points in each site.

Site	Treatment	Invasive presence	Mineral soil	Moss	Marchantia	Leaf litter	Lichens	Grass	Dead wood	Residual organic layer
CCRM1	Shearbladed	1	0.75	9.30	0.05	34.55	0	10.00	4.00	41.5
CCRM2	Shearbladed	0	0	45.50	0	9.00	2.00	1.50	3.25	38.75
CCRM3	Shearbladed	0	0	25.25	0	13.25	0	28.25	0	33.25
OMDWM1	Shearbladed	0	0	22.75	0	8.25	2.05	2.75	0.50	63.75
OMDEM1	Shearbladed	0	0	21.55	0	50.75	0	0	5.75	21.50
CHSRNM1	Shearbladed	1	0	18.25	0	0	0	43.25	8.75	29.75
CHSRSM1	Shearbladed	1	0	23.50	0	0	1.25	2.25	2.00	71.00
HDLCM1	Shearbladed	0	6.25	17.50	3.5	5.50	0	1.00	4.00	62.25
HDLM2	Shearbladed	0	5.50	7.25	0	0	0	1.00	7.75	78.50
HDLM3	Thinned	0	0	83.00	0	8.05	2.35	0	6.75	0
HDLM4	Shearbladed	0	8.50	19.50	0	0	0.25	0	8.00	63.75
FTGM1	Shearbladed	1	33.75	24.50	0	11.50	0	21.30	9.00	0
CCRC1	Undisturbed	0	0	13.50	0	86.50	0	0	0	0
CCRC2	Undisturbed	0	0	42.00	0	23.00	22.00	13.00	0	0
CCRC3	Undisturbed	0	0	53.50	0	46.50	0	0	0	0
OMDWC1	Undisturbed	0	0	95.50	0	4.50	0	0	0	0
OMDEC1	Undisturbed	0	0	94.50	0	5.50	0	0	0	0
CHSRNC1	Undisturbed	0	0	96.50	0	0	5.50	0	0	0
CHSRSC1	Undisturbed	0	0	100.00	0	0	0	0	0	0
HDLCC1	Undisturbed	0	0	94.00	0	6.00	0	0	0	0
HDLC2	Undisturbed	0	0	97.50	0	0	2.50	0	0	0
HDLC3	Undisturbed	0	0	96.50	0	0.50	3.00	0	0	0
HDLC4	Undisturbed	0	0	96.00	0	0	4.00	0	0	0
FTGC1	Undisturbed	0	0	98.00	0	0	2.00	0	0	0

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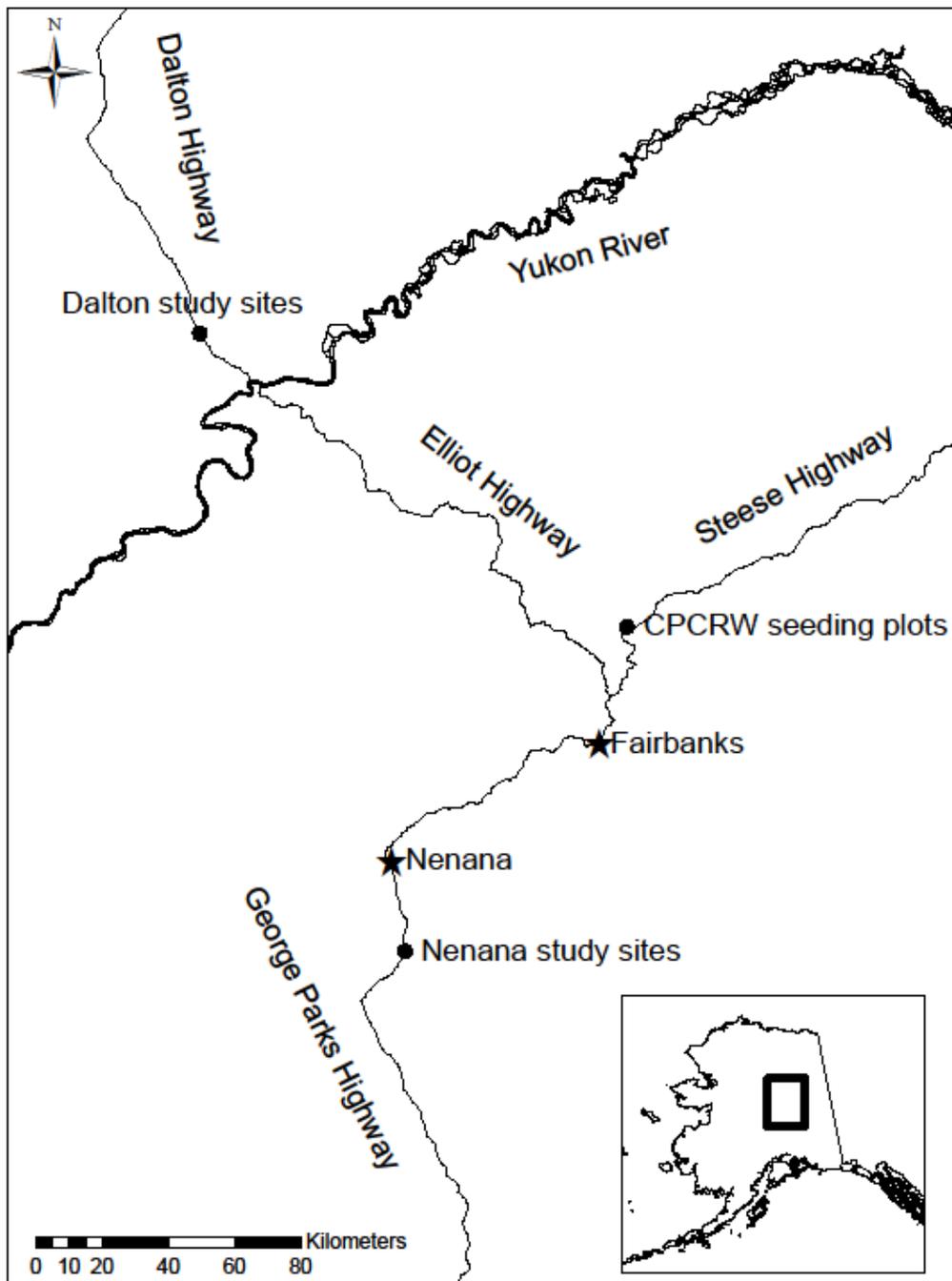
Figure 2.1: Map of interior Alaska showing the general locations of study sites.
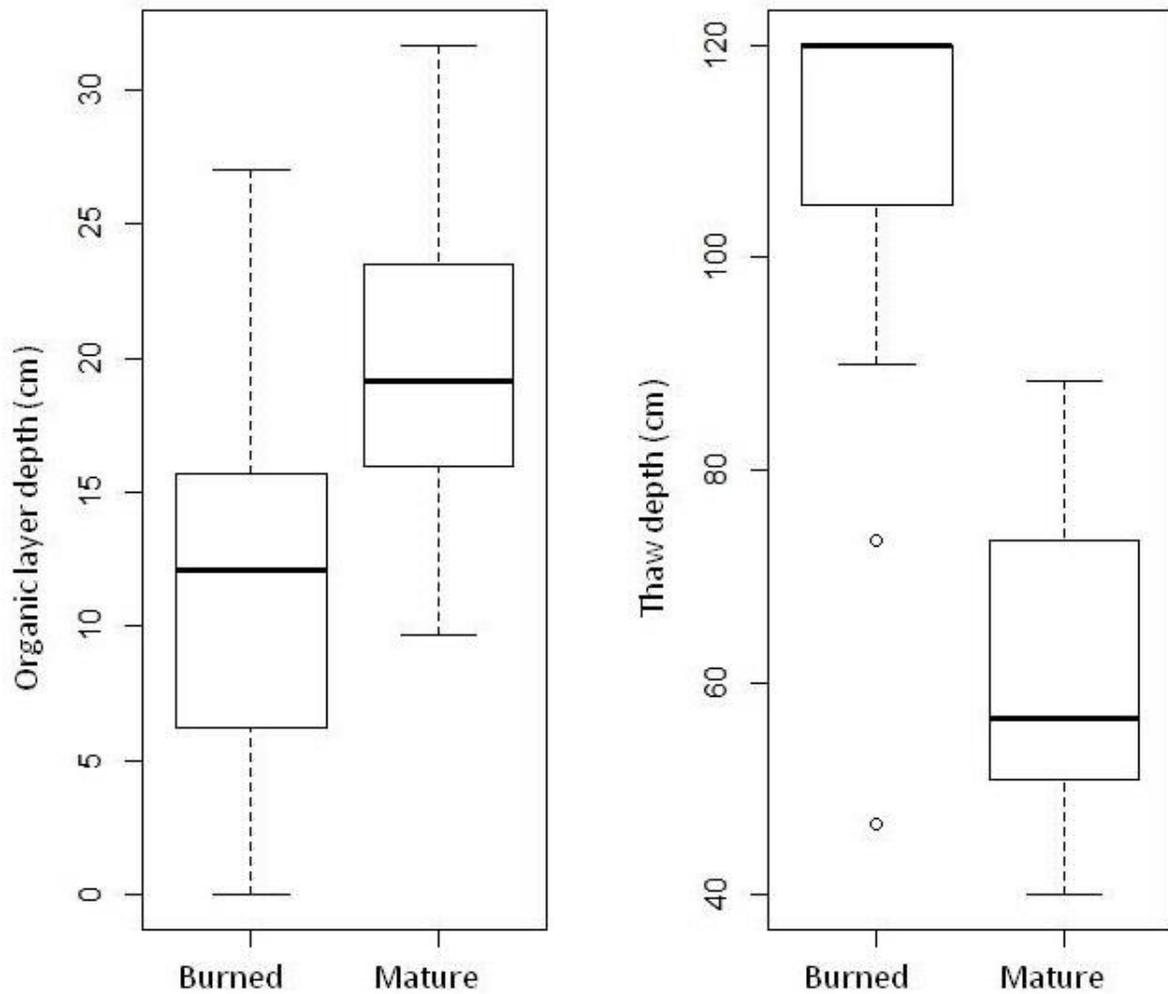
Figure 2.2: Distribution of organic layer and thaw depth observed in burned versus mature stands. Thaw depth values <120cm for burned stands represent rock rather than actual thaw depth. The organic layer depth for burned stands represents residual organic layer depth after fire. The horizontal line within each box represents median value, the box encloses the median 50% of data points, and whiskers represent upper and low quantiles. Circles represent data points that fall outside of the 95th percentile.
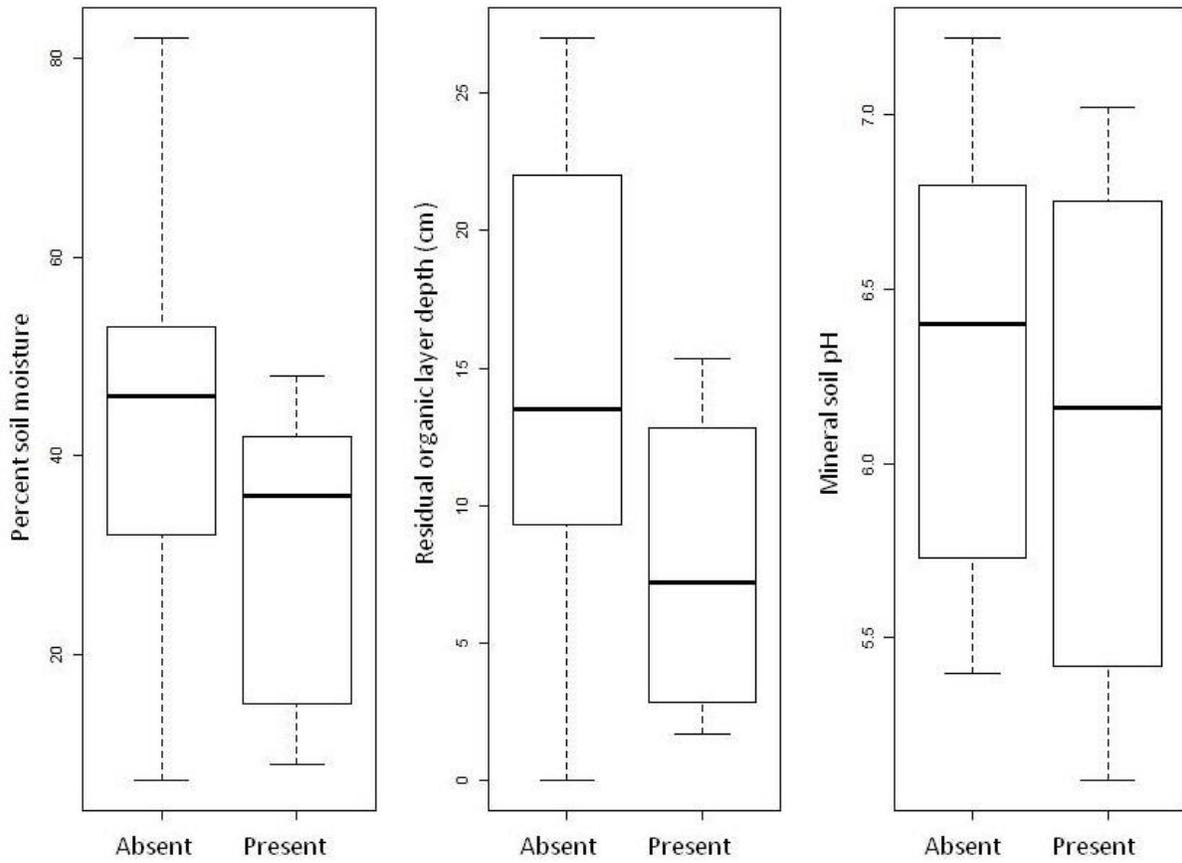
Figure 2.3: Distribution of soil moisture, residual organic layer depth (cm), and mineral soil pH in burned sites where invasive plants were absent vs. present. The horizontal line within each box represents median value, the box encloses the median 50% of data points, and whiskers represent upper and low quantiles.
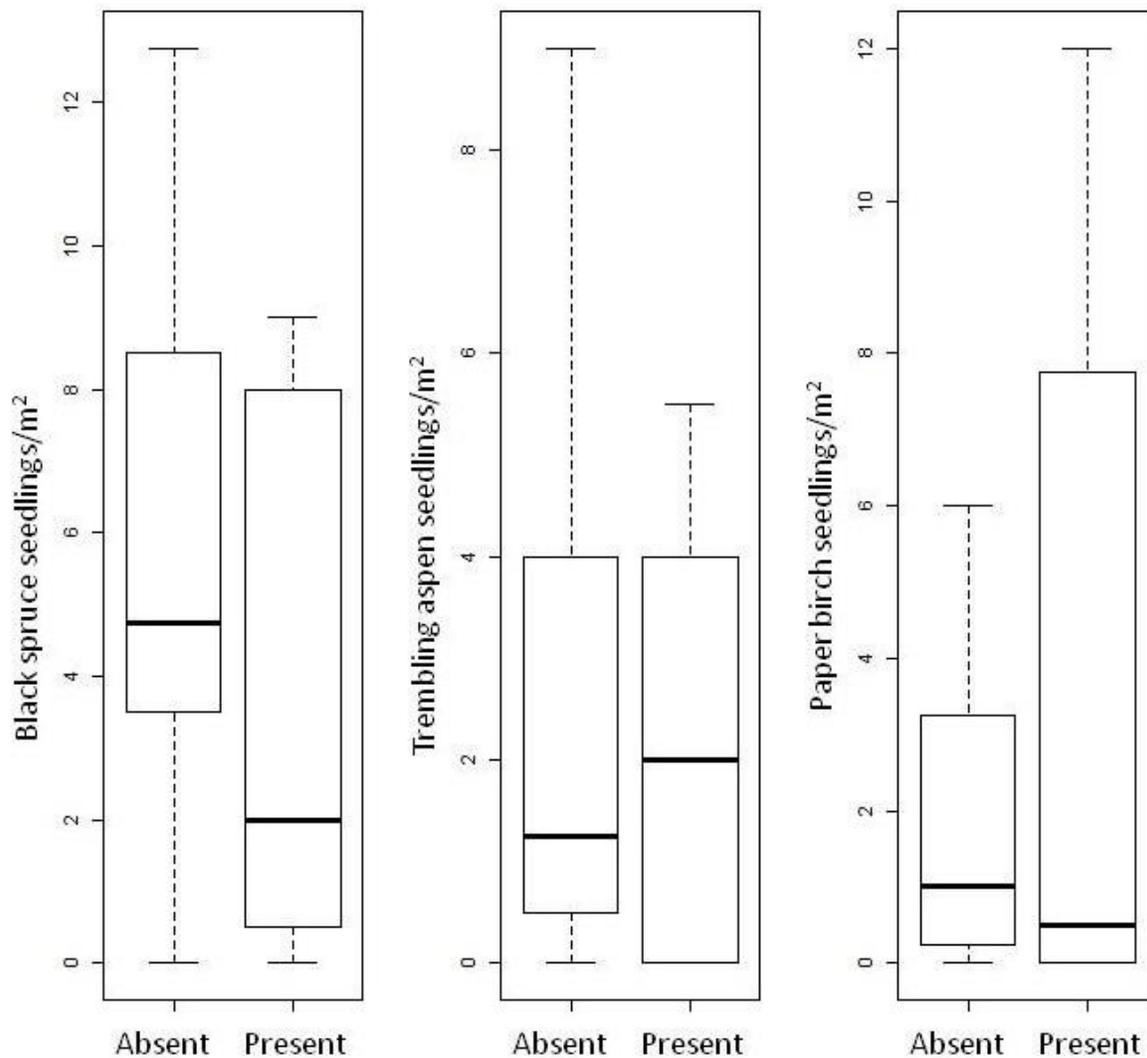
Figure 2.4: Distribution of tree seedling densities for black spruce, trembling aspen, and paper birch, in sites where invasive plants were absent vs. present. The horizontal line within each box represents median value, the box encloses the median 50% of data points, and whiskers represent upper and low quantiles.
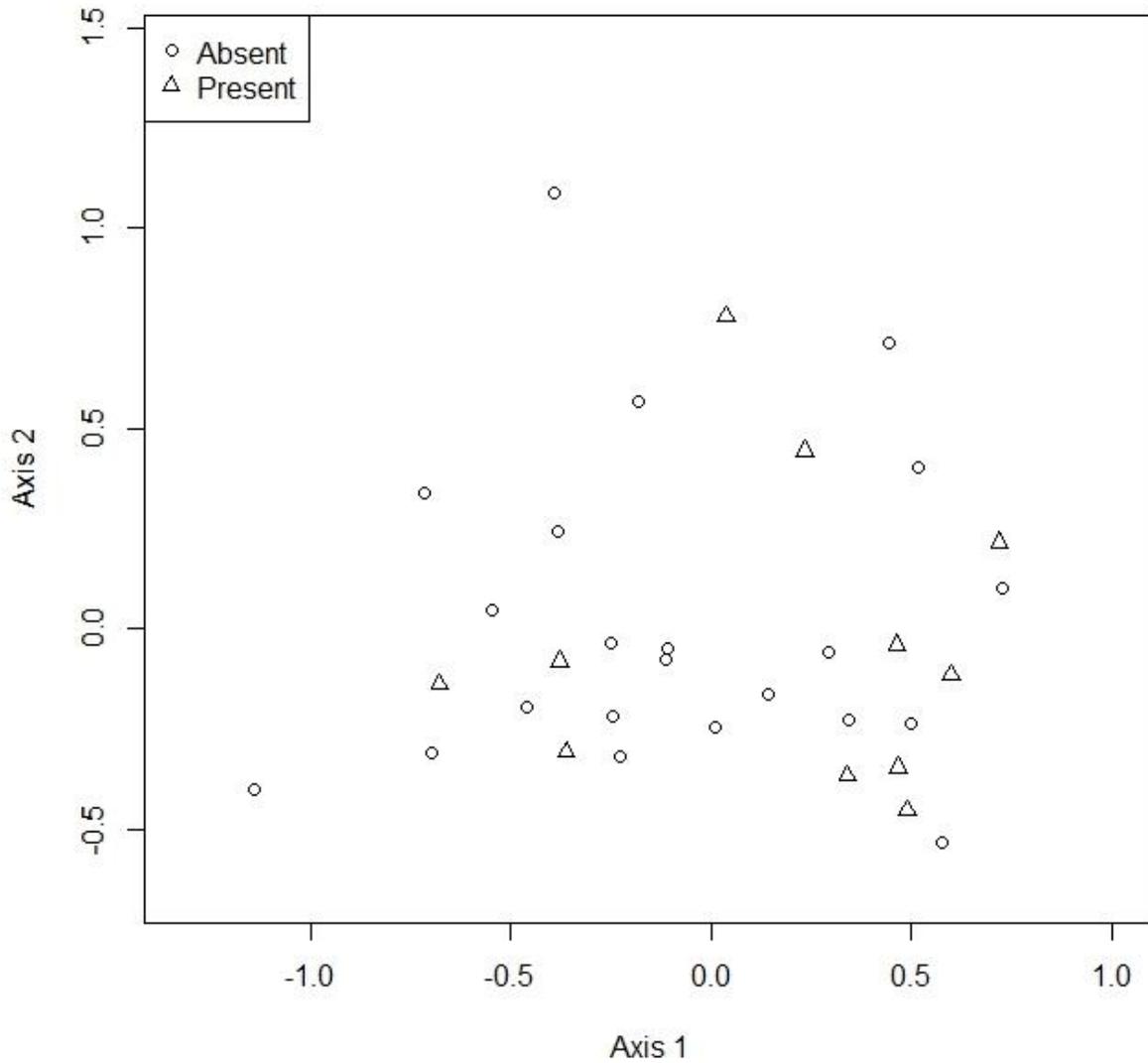
Figure 2.5: NMS Ordination of burned stands based on ground cover types using the Sorensen similarity coefficient. Points that are close to each other indicate similar ground cover composition within a stand. The final stress of the ordination was 0.05, and the number of dimensions was two. Post hoc regression of ordination and original distance in the dissimilarity matrix showed that Axes 1 and 2 had an r^2 of 0.46 and 0.26, respectively. The legend refers to presence-absence of invasive plant species.
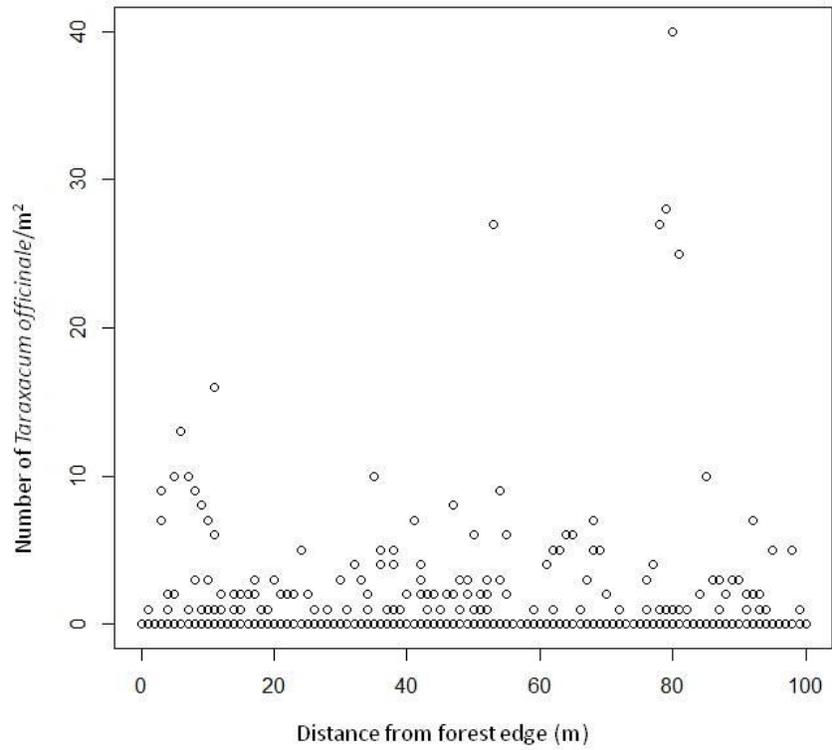
Figure 2.6: Observed density of *Taraxacum officinale* as a function of distance from forest edge (n=33). Sites with no *Taraxacum* were included in the plot. The distance effect was not tested statistically.

2.4 Discussion

2.4.1 *Wildfire and management effects on invasive plant colonization*

This study provides strong evidence that fire facilitates non-native plant colonization in black spruce forests in interior Alaska. Invasive plants were observed in burned stands, but not mature stands, indicating that mature forests are resistant to invasive plant colonization. This result agrees with a study in a ponderosa pine forest, where exotic plant cover increased from 0% in unburned stands to up to 116% cover in severely burned stands (Crawford et al. 2001). In a similar study in the southern boreal forest of Saskatchewan, invasive plants were observed in mature stands (Sumners and Archibold 2007). In the Saskatchewan study, however, it was noted that invasive plants were only observed in mature stands that were in close proximity to a resort village (Sumners and Archibold 2007). Thus, in this case, it may be disturbance caused by anthropogenic activities in the forest that are causing the invasive plant occurrences.

The lack of invasive plant presence in mature stands might be due to several factors that relate to resource availability. Although light levels were not directly measured in this study, canopy shading could be one mechanism that lowers a mature forest's invasibility. Fire induced canopy defoliation may increase a forest's invasibility by increasing both the quality of light, and the amount of light. Light is an essential resource for plants and without the proper quality of light, many species will fail to germinate. Canopy light interception can reduce the red/far-red light ratio (Federer and Tanner 1966), which can inhibit germination in many plants (Baskin and Baskin 1998). Even if a seed is able to germinate under low red/far-red light ratios, the reduced amount of photosynthetically active radiation (PAR) may have a negative effect on seedling growth and establishment. In boreal forests, increased light levels induced by disturbance facilitate plant invasions (Rose and Hermanutz 2004). Most invasive species are disturbance specialists adapted to high light environments. Competition with the resident understory vegetation, which is adapted to lower light conditions, may lead to competitive exclusion of non-native plants. While germination and growth are likely inhibited by light limitations, they may also be reduced by other unfavourable characteristics of mature black spruce forests.

In black spruce forests, a thick organic layer of mosses and accumulated plant litter carpet the forest floor. The organic layer has many properties that offer resistance to non-native

plant colonization. First, mosses are a poor substrate for seedling establishment. In the mature stands surveyed, tree regeneration from seed was never observed. If the resident tree species are unable to establish from seed in mature forests, then it is highly unlikely that non-native disturbance specialists will be able to establish from seed. Moss prevents the seedling radicle from contacting mineral soil (Jeschke and Kiehl 2008), thereby restricting access to nutrients and moisture in the mineral soil layer. In boreal forests, disturbances that expose mineral soil favour colonization of non-native plants (Rose and Hermanutz 2004). Second, the thick moss layer provides insulation for the mineral soil layer, resulting in frozen soil for much of the growing season (Van Cleve et al. 1983a). In many of the mature stands surveyed, we observed shallow thaw depths. In some cases, the surface of the mineral soil was still frozen when moss was excavated. Thus, even if the radicle does make soil contact it may contact frozen mineral soil, preventing the uptake of moisture and resulting in seedling mortality. Third, phenolic compounds released into the organic layer by the litter of ericaceous shrubs (Castells et al. 2005), may be inhibiting non-native plant germination and establishment. Phenolic compounds are considered to be a form of allelopathy for some plants, and have been shown to have negative effects on both germination (Nilsson and Zackrisson 1992) and growth (Guenzi and McCalla 1966). In some cases, it is not the direct affects of phenolics on plant physiology that cause growth difficulties, but reductions in soil-available nitrogen by phenolic compounds (Castells et al. 2005). Many barriers to establishment from seed exist in mature black spruce forests, and the lack of invasive plants in mature forests is likely influenced by the thick organic layer and low light conditions.

The thick organic layer found in mature stands appears to offer resistance to colonization by invasive plants, and its legacy effect following fire also influences site invasibility. Sites with low average residual organic depth were the most likely to have non-native plants present. The residual organic layer presents a barrier between the seed and soil, and its physical properties are unfavourable for seed germination. The porous nature of the residual organic layer results in lower moisture content than mineral soils (Johnstone and Chapin 2006a), and its dark colour results in very warm soil temperatures and drying of the surface organic material (Coyea 1988). These warm dry conditions may inhibit germination entirely, or in cases where seeds do germinate, result in seedling desiccation and mortality (Johnstone and Chapin 2006a). Lower average residual organic layer depth within a site may also indicate more exposed mineral soil at

the site, which is the most favourable substrate for germination among post-fire substrate types (see Chapter 3). The other strong predictor variable for invasive plant presence was paper birch regeneration from seed. Sites with the highest densities of paper birch seedlings were more likely to have invasive plants present. Paper birch seedling abundance may be a proxy for site substrate quality, as paper birch is a small seeded species with few carbohydrate reserves in the seed, and favours exposed mineral soils over residual organic soils (Johnstone and Chapin 2006a). The fact that both paper birch regeneration and residual organic layer depth were the strongest predictors of invasive plant presence within a site indicates that fire severity has a strong influence on site invasibility. High severity fires generally result in greater combustion of the organic layer within a site relative to lower severity fires, which increases the probability that plant regeneration will occur from small seeded species arriving from offsite such as paper birch and fireweed (Dyrness and Norum 1983, Hollingsworth et al. 2013, Johnstone and Chapin 2006a). While I did not directly measure fire severity, a comparison to other literature on the effects of fire severity on invasibility suggest that fire severity played a role in invasibility in my study area. In ponderosa pine stands, greater exposure of bare ground from high severity fires causes higher site invasibility (Crawford et al. 2001), and other studies have also shown that fire severity positively influences invasibility (Crawford et al. 2001, Fornwalt et al. 2010, Kuppinger et al. 2010).

The surveys of managed areas indicate that disturbance induced by management also facilitates invasive plant colonization. Because there were only two sites that were thinned, I am unable to make inferences about what management types facilitate invasion. It is likely that the shearblading creates favourable conditions for invasive plant colonization by exposing mineral soil and causing substrate disturbance. Neither of the two thinned sites had invasive plants present, which may be due to lower substrate disturbance from this treatment. Alternatively, it may be that there were not enough thinned sites surveyed to detect invasive plant colonization.

2.4.2 Species-specific responses to fire

Differences in occurrence of invasive plants found in burned stands can be attributed to seed architecture. Despite having *Melilotus* present in the roadside at most sites, it was only observed colonizing one burned site. *Taraxacum*, however, occurred in every site where other invasive species were observed colonizing the forest. This result is similar to a trend observed by Sumners

and Archibold (2007), where exotic species adapted for wind dispersal, including *Taraxacum* and *Crepis*, were the most common non-native plants found in the forest. The feathery pappus on *Taraxacum* seeds makes them well adapted for wind dispersal, whereas the seeds of *Melilotus* have no adaptations for wind dispersal. In order for *Melilotus* to colonize a burned forest, it requires a vector to transport it from the roadside to the forest interior. Herbivores such as moose may act as transport vectors for *Melilotus*, as seeds of *Melilotus* remain viable after passing through the moose digestive tract (Seefeldt et al. 2010).

No edge effect was detected with respect to *Taraxacum* density in burned stands. It was expected that as the distance from the forest edge increased, that invasive plant density would decline. The lack of an observable edge effect is probably due to wind dispersal adaptations mentioned above. Because of this dispersal ability, it is likely that microsite limitations rather than propagule limitations were influencing *Taraxacum* colonization patterns. The clumped distribution of high *Taraxacum* densities around 80m at one site, likely represents a favourable microsite where many seeds landed. Because *Melilotus* and *Crepis* were only present in one site each, I was unable to assess edge effects for these species. I would expect, however, that in a larger study *Melilotus* density might decrease further into the forest, as it does not have seeds adapted for wind dispersal. *Crepis* would likely show a trend similar to *Taraxacum*, due to the similar fruits adapted for wind dispersal.

2.4.3   Ground cover effects on invasibility.

In the ordination using ground cover types, I was expecting to find a pattern where mineral soil would drive patterns of invasive plant presence along one of the principal axes. Such a pattern would show a distinct separation of invaded and uninvaded sites. While mineral soil did have a strong effect on axis two no distinct separation of invaded and uninvaded sites was present on this axis. This result may be due to the relatively low occurrence of mineral soil in surveys. The low occurrence of mineral soil would influence the axes as there was high variation in mineral soil due to zero values. Mineral soil that was exposed by fire has likely been partially colonized by mosses, or covered by leaf litter, in the time that has elapsed since the 2004 fires. I would expect that had this study been conducted in the earlier years following fire that mineral soil variation would drive a pattern of separation between invaded and uninvaded sites. Furthermore,

variations in other stand characteristics may interact with groundcover type to influence invasibility, and an ordination incorporating more data may bring out more distinct patterns of site separation.

2.5   Conclusions

Disturbances, in the form of wildfire and management, facilitate invasive plant colonization. Mature stands appear to be resistant to invasive plant colonization, and while there are many possible factors inhibiting invasive plant colonization, there is evidence that the thick organic layer is the primary factor. Following fire, and combustion of the organic layer, invasive plants have a tendency to colonize sites with greater organic layer combustion and more paper birch seedlings. Residual organic layer depth and paper birch seedlings are both indicative of fire severity and substrate quality, suggesting that fire severity mediates site invasibility via its effects on substrate. Whereas *Melilotus* was less common than *Taraxacum* in burned stands, it may have the potential to colonize given a suitable dispersal vector. Due to the limited number of sites with non-native species other than *Taraxacum*, more research is required to make strong inferences about site invasibility by other non-native plants. I recommend that severe fires are closely monitored for invasive plant colonization.

3   SUBSTRATE EFFECTS ON INVASIVE PLANT GERMINATION

3.1   Introduction

Invasive plants impact ecosystem functioning at a global scale, by displacing native species, altering soil nutrient cycles, and changing local fire regimes (Pysek et al. 2012). Impacts and control of invasive plants have been estimated to cost up about $35 billion annually in the United States (Pimentel et al. 2005). This damage has been largely avoided in northern habitats, as they have historically been relatively free from invasive plant species (Carlson et al. 2008), mostly due to low population density, limited agriculture, and cold climate (Wurtz et al. 2006). Populations of invasive plants in Alaska generally have been restricted to areas of human disturbance (Carlson and Lapina 2004, Cortes-Burns and Flagstad 2010). Unfortunately, there have been signs of a recent increase in the expansion of invasive plants into natural habitats in interior Alaska (Carlson and Lapina 2004, Wurtz et al. 2006, Cortes-Burns et al. 2007, Lapina et al. 2007). For example, *Melilotus* has been observed establishing in glacial river floodplains (Conn et al. 2008). If invasive plants are able to establish and persist in other natural habitats, they could have negative consequences for ecosystem structure and function in Alaska.

Disturbance caused by fire has been observed to increase exotic plant invasions in some ecosystems. Fire is the dominant disturbance in black spruce forests of interior Alaska, and black spruce is the main forest type in interior Alaska (Viereck et al. 1983). Canopy defoliation as a result of fire has been shown to increase invasive plant abundances (Hunter et al. 2006, Kuppinger et al. 2010) as it exposes previously shaded microsites, allowing shade intolerant plant species to colonize post fire. Canopy defoliation may increase invasibility in black spruce forests, however there are other fire induced changes that may also promote invasive species colonization. In black spruce forests, wildfire creates a mosaic of ground cover types, ranging from lightly burned residual organic layers to complete combustion of the organic layer that exposes mineral soil (Dyrness and Norum 1983). This mosaic of ground cover types influences whether plant regeneration will occur from underground plant parts, or from incoming seeds.

Disturbance induced changes in microsite availability, and quality, mediate community assembly through their effects on seed germination and seedling establishment (Davis et al. 2000). The success of a seed arriving from offsite ultimately depends on the availability of safe

sites for seed germination (Grubb 1977). In forested systems, microsite limitation is particularly prevalent (Crawley 1990). Furthermore, it has been suggested that microsite limitation is more common in coniferous than deciduous forests (Eriksson and Ehrle'n 1992). In mature black spruce forests, the dominant groundcover is a thick moss layer (Viereck et al. 1983), which can inhibit seed germination (Jeschke and Kiehl 2008). In addition to negative effects on germination from mosses, bryophytes also have negative effects on seedlings until they are able to grow above the moss layer (Zamfir 2000). Thus, it would be expected that wildfire in black spruce forests might increase invasive plant colonization by removing the inhibitory effects of moss on germination, and exposing better microsites for germination.

Fire should increase invasive plant colonization, however its effects may be highly variable due to the mosaic of ground cover types following a fire. In patches where the fire exposes the underlying mineral soil, seed germination should be higher than on microsites containing regenerating moss or plant litter, both of which can inhibit germination (Donath and Eckstein 2010). Litter accumulation negatively affects plant germination by creating a barrier that can prevent seedlings from piercing through the litter and reaching the light required for growth (Rotundo and Aguiar 2005). Lightly burned microsites with a partially combusted organic layer should also have lower seed germination than exposed mineral soil. Partially combusted organic layers are a poor seedbed due to their high porosity and relatively high temperature due to the dark colour, both of which increase seedling desiccation (Johnstone and Chapin 2006b). While exposed mineral soil should show the highest seed germination, differences in germination between other post-fire substrates remain unclear.

This chapter seeks to determine whether burned forests are more susceptible to invasive plant colonization by seed than unburned forests, and whether different substrate types characteristic of recently burned forests will show different susceptibilities to invasion. To test the effects of fire on invasive plant germination, and whether germination differs among forest substrates, I conducted seeding trials in burned and unburned forests, on a variety of substrate types. If fire promotes invasive plant colonization in boreal forests, then germination should be highest in burned forests. Furthermore, if some substrates characteristic of burned forests provide safe micro sites for germination, there should be differences in germination amongst substrate types. An understanding of the role of fire in invasive plant movement into black spruce forests,

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as well as species-specific responses to fire, can be used to prevent the ecological and economic impacts that invasive species have caused in other regions (Naylor 2000, Paterson et al. 2011). Understanding the role of fire in exotic plant invasions is particularly important in Alaska, as fire activity has doubled over the last decade (Barrett et al. 2010) and is expected to continue increasing (Bachelet et al. 2005). By gaining an understanding of substrate preference, we can prioritize invasive plant control efforts to highly vulnerable areas. The knowledge gained from this study can also be used to direct invasive plant control efforts in other northern boreal regions.

3.2 Methods

3.2.1 Study Area

The Caribou-Poker Creeks Research Watershed (CPCRW) is located approximately 31 miles North of Fairbanks, Alaska, in the Yukon Tanana Uplands (Figure 2.1). CPCRW falls within the discontinuous permafrost zone. It is a 104km^2 basin used for ecological research. The area is characterized by round-topped ridges with gentle slopes. Our plots were located in a recently burned (2004) and a mature black spruce forest on a southwest-facing slope. The nearest climate station to CPCRW is at the Fairbanks international airport. Mean annual temperature in Fairbanks is -2.94°C, and ranges from -23.16 in January to 16.74°C in July. Annual precipitation amounts to 262 mm, 47% (124 mm) of which falls between June and August (Shulski and Wendler 2007).

3.2.2 Seed collection and treatment

Three invasive plants commonly found in interior Alaska were chosen for seeding: *Vicia cracca* L. (hereafter referred to as *Vicia*)*, Taraxacum officinale* G.H. Weber ex Wiggers (hereafter referred to as *Taraxacum*)*, and *Melilotus officinalis* (L.) Lam. (hereafter referred to as *Melilotus*). These species were chosen to look for species-specific responses in germination, and to capture a range in seed size. The seeds were collected in September 2011 near Fairbanks, Alaska. Seeds were stored in a freezer prior to planting. Average seed weights were determined from a sample of 100 seeds per species (Table 3.1). To determine seed viability, germination trials were conducted in a laboratory setting. Seeds were incubated in covered Petri dishes with

moist filter paper for one week (April 24-May 01 2012) at 20°C using natural sunlight. To improve germination, two different treatments were applied to the seeds. Mechanical scarification and percussive scarification (Baskin and Baskin 1998), and a control treatment (no manipulation) were applied to ten seeds of each species. Percussive scarification is achieved by placing seeds in a vessel, such as an Erlenmeyer flask, and vigorously shaking the vessel so the seeds bounce off the sides (Baskin and Baskin 1998). The mechanical scarification treatment was achieved by gently rubbing seeds between two pieces of sand paper. Because of limited seed there were only two replicates of ten seeds for each of the three treatments. Percussive scarification resulted in the highest germination for *Vicia,* while mechanical scarification resulted in the highest germination for *Melilotus* and these treatments were applied prior to planting in the field. Neither of the treatments enhanced germination of *Taraxacum*; thus, the seeds were not treated before planting in the field (Table 3.1).

3.2.3   Substrate types

Seeding plots were all located within the CPCRW (Figure 2.1). Seeding trials were conducted on a variety of substrate types nested within disturbance classes (Figure 3.1). There were three disturbance classes: a gravel pit was used to represent a high disturbance class (65.13665 °N, 147.45486 °E), a recently burned (burn year 2004, 65.14230 °N, 147.46828 °W) forest was used to represent a mid-level disturbance class, and an unburned forest (65.14197 °N, 147.46829 °W) was used as a low disturbance class. Within the burned forest, five substrate types characteristic of recently burned forests were selected: leaf litter, regenerating moss, grass litter, burned organic layer, and exposed mineral soil. Within the unburned forest, moss was chosen as the representative substrate type, and a moss removal substrate was also used to control for potential competitive effects of live moss. Within the gravel pit there was only one substrate type present, gravel (Figure 3.1).

3.2.4   Plot selection and measurements

 In the burned and mature forests, seeding plots were placed in a randomized blocked design, with ten replicates for each substrate type. In both the burned and the mature forest, a 100 m transect was run parallel to the road (approximately 10m from the road) to control for any potential edge effects. The burned and mature forests were separated by a road that acted as a fire

break. In the gravel pit, a 100 m transect was run using a random compass bearing. Ten random numbers were selected along each transect, and plots were placed on the nearest occurrence of each substrate type to the random points. Because there was no exposed mineral soil present in the burned forest, plots were excavated down to the mineral soil for this treatment. Plots were 15 cm X 15 cm. Each plot was covered by a hardware cloth (mesh size = 1 cm) cage to prevent small mammals or birds from removing seeds or grazing on seedlings. All regenerating tree saplings were removed if they were within 50cm of the plots to control for potential effects of shading. Ten seeds of each species per plot were planted on June 4th 2012, and final germination counts were taken on July 30th 2012. Following final germination counts, all seedlings were excavated, visible seeds were removed, and the substrate was dug out and removed from the site to prevent any invasive plants remaining.

3.2.5   Statistical analysis

The sample design within the burned and mature stands was blocked, so Fisher's exact test was used to test for any significant blocking effects. No significant blocking effects were detected, thus analysis proceeded without considering blocking effects.

The germination results cannot be considered as continuous variables, because only ten seeds of each species were planted on each substrate type. Thus, contingency table analysis was used to test whether germination levels were different between the disturbance classes, and between substrate types within the burned forest. Chi-square contingency analysis was initially used, but because many of the expected values were small, Fisher's exact test was used as it is more appropriate when expected values are small (Yates 1984, Marques de Sá 2007). I used Fisher's exact test to compare germination: between disturbance classes, between the moss and moss removal substrate in the mature forest, and between all substrate types in all disturbance classes. The application of a G-Test to the data was also investigated, however, like the chi-square test, it performs poorly when expected values are small (Crawley 2007). The analyses were performed in R 2.14.1 (R Development Core Team 2011).

Table 3.1: Total germination counts and average seed weights for three seed treatments (n=20 seeds/treatment).

	Vicia cracca	*Melilotus officinalis*	*Taraxacum officinale*
Control	3	1	12
Mechanical scarification	7	13	5
Percussive scarification	13	5	9
Average seed weight	0.012 g	0.0018 g	0.00081 g

Note: There were two replicates of each treatment, and ten seeds per replicate.
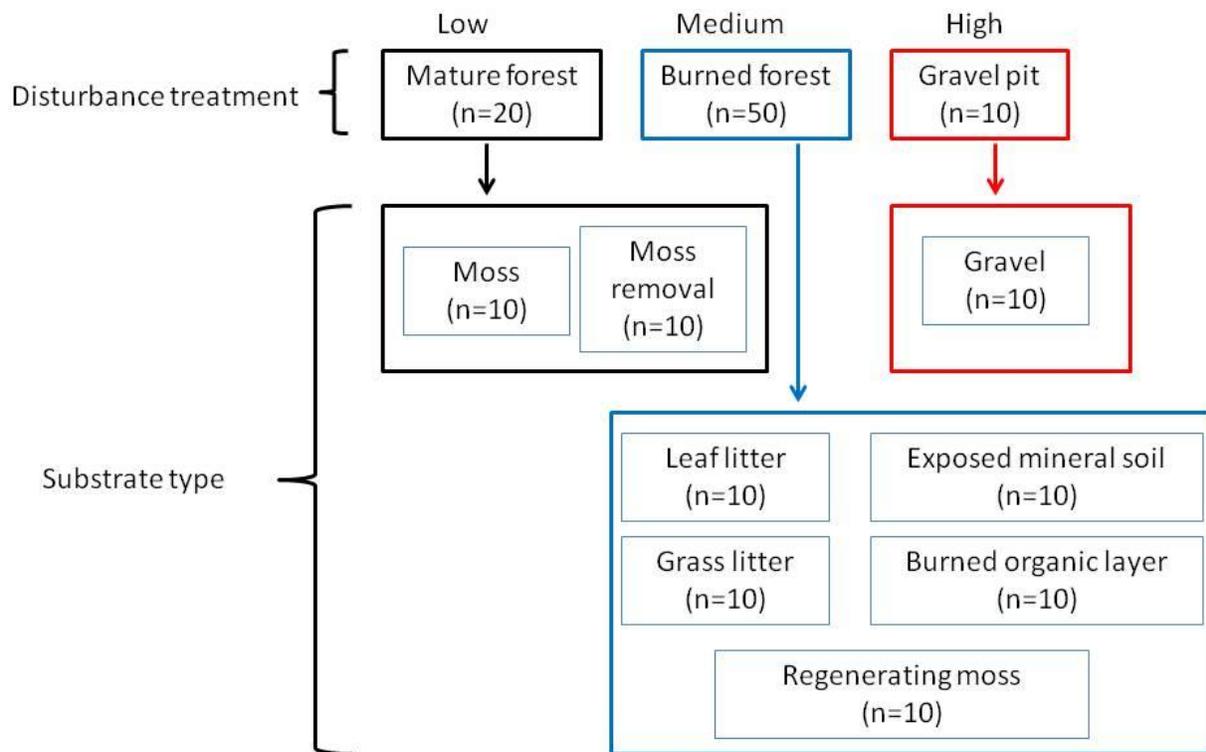
Figure 3.1: Conceptual diagram of seeding plot experimental design. Substrate types are nested within disturbance treatments.

3.3   Results

3.3.1   Differences among disturbance classes

Germination was higher for *Melilotus* in the burned forest compared to unburned forest, but not for *Vicia* (Figure 3.2). *Taraxacum* showed a trend towards higher germination in the burned forest, however this trend was not statistically significant (Figure 3.2). There was no germination of *Melilotus* in the unburned forest (n=200) while 35 out of 500 (7%) seeds germinated in the burned forest (Figure 3.2). Only one of 200 (0.5%) *Taraxacum* seeds germinated in the unburned forest, while 19 of 500 (3.8%) germinated in the burned forest (Figure 3.2). For *Vicia*, the difference between unburned and burned germination was not as pronounced, with 22 of 200 (11%) seeds germinating in the unburned forest compared with 76 of 500 (15.2%) in the burned forest (Figure 3.2). Both *Melilotus* and *Taraxacum* performed best on the gravel pit (high disturbance) treatment (Figure 3.2). In the gravel pit 3 of 100 (3%) *Vicia* seeds germinated. 15 of 100 *Melilotus* seeds germinated (15%), and 15 of 100 (15%) *Taraxacum* seeds germinated (Figure 3.2). The disturbance treatment effect was only significant for *Melilotus* (p=0.02). Despite large differences in germination between disturbance classes for *Taraxacum*, the treatment effect was not significant.

3.3.2   Performance on different substrate types

There were strong differences between germination rates across the experimental substrate types for all species (p<0.001 for all species). Germination was consistently higher on the mineral soil substrate, and germination never occurred on the burned organic substrate (Figure 3.3). *Melilotus* and *Taraxacum* performed better on the gravel pit substrate than on substrates other than mineral soil, however this trend was not observed for *Vicia*, which had its lowest germination on the gravel pit substrate (with the exception of burned organic). *Vicia* performed better on the leaf litter and all moss substrates than *Melilotus* and *Taraxacum*. Overall, *Vicia* had the highest germination levels totaled across all substrate types. Within the mature forest, there was no effect of the moss removal treatment relative to the moss treatment (p > 0.5 for all species).

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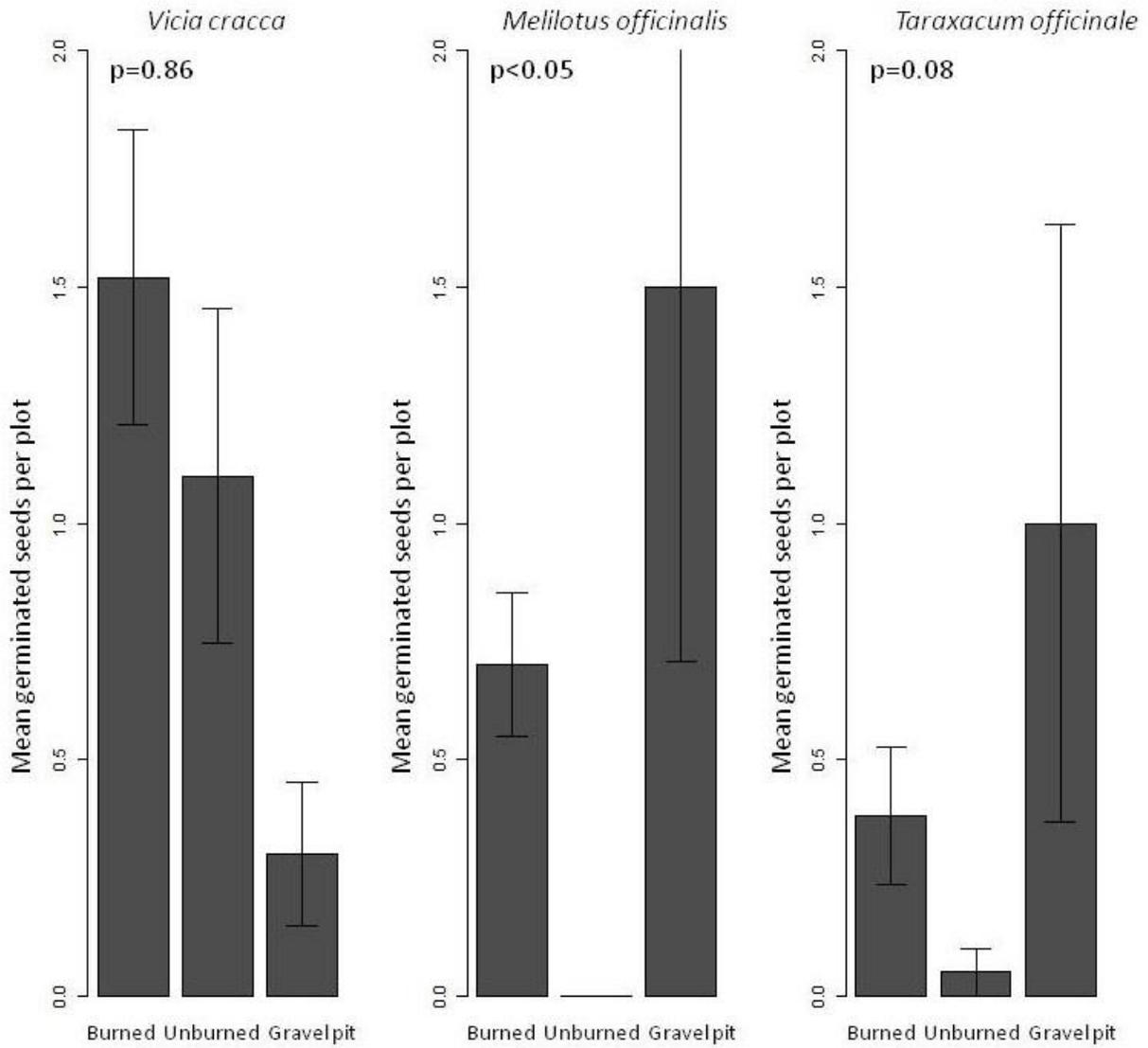
Figure 3.2: Mean germination of *Vicia cracca, Melilotus officinalis,* and *Taraxacum officinale* across all sampled substrate types in a burned forest (n=50), an unburned forest (n=20), and a gravel pit (n=10). Error bars represent one standard error. The p-values are from Fisher's exact test Plots were seeded with 10 seeds of each species.
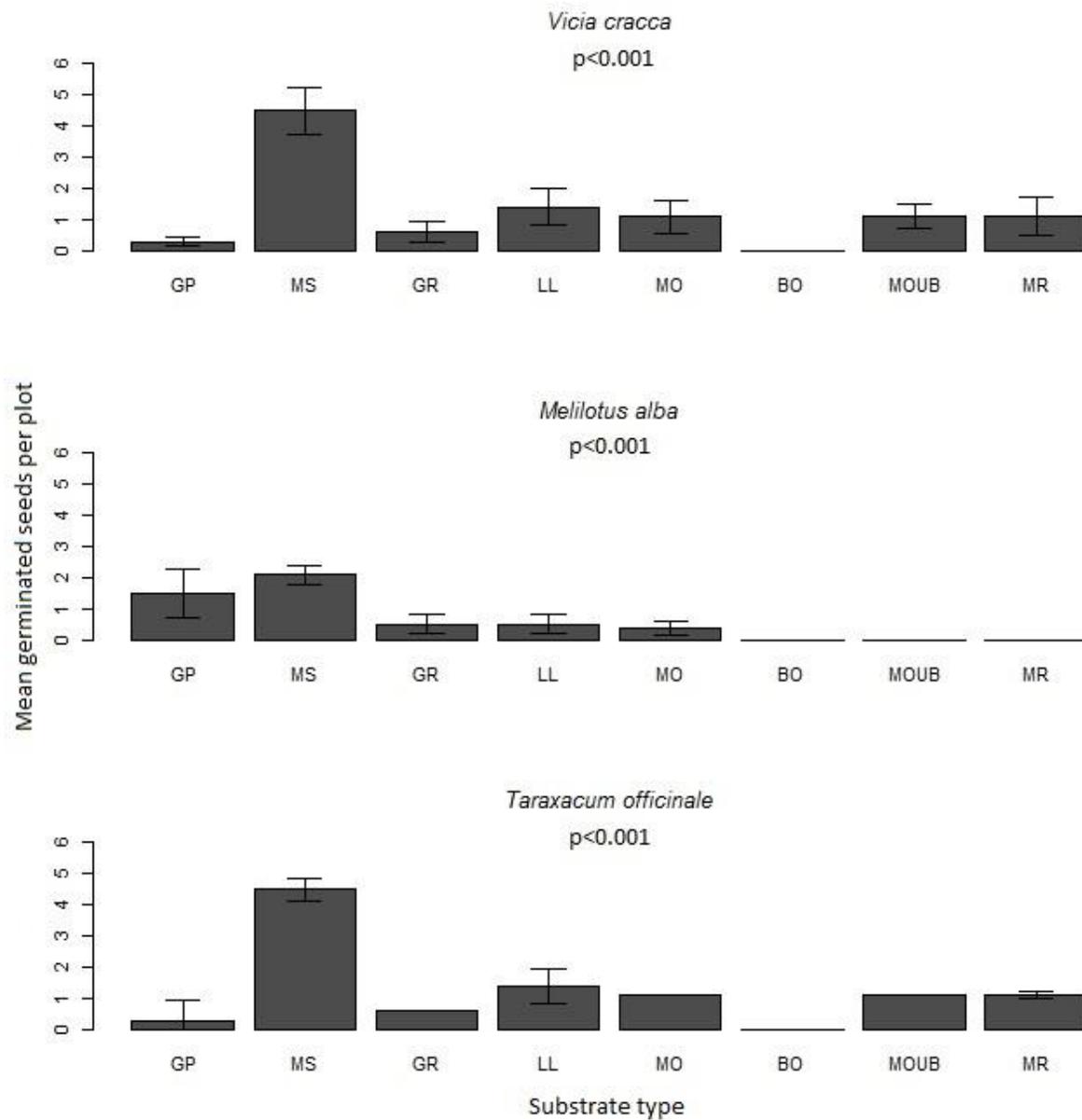
Figure 3.3: Mean germination of *Vicia cracca, Melilotus officinalis,* and *Taraxacum officinale* on eight substrate types (n=10, GP= gravel pit, MS= exposed mineral soil, GR= grass litter, LL= leaf litter, MO= regenerating moss, BO= burned organic layer, MOUB= moss unburned, MR= moss removal). Error bars represent one standard error. The p-values are from Fisher's exact test. Plots were seeded with 10 seeds of each species.

3.4   Discussion

The high levels of germination in the burned forest and the gravel pit, relative to the unburned forest, suggest that disturbance allows invasive plants to colonize the forest by creating more favourable substrates and increasing light levels. High levels of disturbance in the gravel pit seem to favour *Melilotus* and *Taraxacum* over lower disturbance levels. *Vicia* had lower performance in the gravel pit and this trend is discussed below. The higher germination in the burned forest and gravel pit for *Melilotus* and *Taraxacum*, can be attributed to safe micro-sites for seed germination. Community invasibility is heavily influenced by the presence of suitable micro sites for germination (Grubb 1977), and micro-site limitation is common in coniferous forests (Eriksson and Ehrle'n 1992). Disturbance induced changes in micro-site availability are known to influence community assembly and invasibility by affecting germination, and seedling emergence (Davis et al. 2000). In black spruce forests, fire often results in combustion of the mossy organic layer. Moss has been shown to negatively affect seedling germination (Jeschke and Kiehl 2008), which is consistent with our findings as moss was the only substrate present in the mature forest.

Whereas substrates in the mature forest appear to have prevented germination of *Melilotus* in the unburned forest, and inhibited germination of *Taraxacum*, they did not substantially inhibit germination of *Vicia.* It should be noted, however, that there was no statistically significant disturbance treatment for *Taraxacum.* This is likely due to the low number of seeds sown in each plot combined with the small seed weight of this species. I would expect that with more seeds sown a significant effect might be detected. The moss removal treatment in the mature forest exposed underlying fibric soil which is has a structural composition similar to live moss. Thus, it is likely the physical characteristics of the substrates in the mature forest that inhibited germination for some species, rather than competition from mosses. There are three possible reasons why germination of *Vicia* was higher than other species in the mature forest. Firstly, differences in seed size may be driving patterns of germination. Moss layers influenced the germination of small seeded species more than large seeded species (Zamfir 2000). While *Taraxacum* and *Melilotus* produce a large volume of small seeds (Turkington et al. 1978, Stewart-Wade et al. 2002), *Vicia* produces fewer, larger seeds (Aarssen et al. 1986). Seed size is known to influence the germination and success of seedlings (Eckstein

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and Donath 2005). The differences in observed germination may be a function of differences in carbohydrate reserves related to seed size, with *Vicia* having an advantage due to its greater reserve of carbohydrates to draw on for early growth.

The success of a seedling depends on whether it can achieve enough growth to break through the surface of the substrate to receive light. Vertical position in the substrate, the second reason that *Vicia* germination may be different from other species, influences the amount of growth required to reach light. The vertical position of a seed in the substrate is mediated, in part, by seed size (Bekker et al. 1998). In porous substrates such as the substrates in the mature forest, larger seeded species will reside further up in the substrate than smaller seeded species. Seed architecture may also play a role in seed position in the substrate. *Vicia* seeds are round, whereas *Melilotus* and *Taraxacum* seeds are more oblong, allowing for further penetration into the moss and fibric layers. Higher position in the substrate may have worked in synergy with larger carbohydrate reserves of *Vicia*, explaining the difference in observed germination. *Taraxacum* and *Melilotus* may not have had sufficient carbohydrate reserves to break through the moss and fibric barriers from their lower position in the substrate, while *Vicia* had less growth required to reach light, and greater reserves to draw from.

The third reason that *Vicia* germination may be different from other species relates to seedling physiology. *Melilotus* and *Taraxacum* are epigeal germinants, meaning that they rely on their photosynthetic cotyledons for early growth. *Vicia*, on the other hand, is a hypogeal germinant. The hypocotyls of hypogeal germinants are not photosynthetic, and the plants are able to draw on reserves in the hypocotyls for early growth. While long-term observation would be required to determine establishment trends, the germination differences observed here suggest that while *Melilotus* and *Taraxacum* are unlikely to colonize unburned forests, *Vicia* has the potential to colonize these sites.

The strong differences in germination across substrate types are likely due to the effects of substrate type on a seed's access to water and nutrients. The presence of bare soil is critical for the recruitment of vascular plant species (Jeschke and Kiehl 2008), and in my experiment the highest germination was always observed on the exposed mineral soil. The microtopography of a substrate influences recruitment success for surface-located seeds, through its effects on contact between seed and soil (Harper et al. 1965). Litter and moss both present barriers preventing the

seed from immediately accessing water and nutrients in the mineral soil layer. A meta-analysis of the effects of plant litter on vegetation found that litter accumulation negatively affects germination and seedling establishment in plants (Xiong and Nilsson 1999). The negative effects of litter and moss on germination and establishment, are caused not only by preventing the seed from establishing soil contact, but also by presenting a barrier preventing seedlings from reaching light (Facelli and Pickett 1991, Rotundo and Aguiar 2005). The magnitude of the negative effects of litter can be species-specific, and this is partially mediated by seed size (Kostel-Hughes et al. 2005). *Vicia* performed better than *Melilotus* and *Taraxacum* on the litter and moss substrates in the burned forest, a trend similar to the observed differences in the mature forest. Once again, this outcome is likely a function of larger carbohydrate reserves and position in the substrate.

Despite *Vicia* performing well relative to *Taraxacum* and *Melilotus* on most substrates, it did not perform better on the gravel pit substrate or the burned organic substrate. The burned organic substrate was the least favourable of all substrates, and there was no germination for any of the species on this substrate. The lack of germination is likely due to the low water content of these substrates. The porous nature and dark colour of the burned organic layer result in a dry substrate (Coyea 1988). Water retention in the burned organic layer is low due its porosity, which allows increased convection and evaporative loss of moisture. The evaporative loss of water may also be sped up by the dark colour of the substrate, which results in higher temperatures. In the gravel pit, soil compaction due to vehicular traffic may have caused lower soil moisture by reducing water infiltration (Håkansson and Medvedev 1995), although soil moisture was not measured. While large seed size may have given *Vicia* an advantage on the other substrate types, it may have been a disadvantage in the gravel pit. Larger seeds have greater water requirements for germination, and in the potentially water limited environment of the gravel pit, the higher water requirement of *Vicia* likely inhibited its germination. The poor performance of *Vicia* in the gravel pit may also explain why it is less common in roadsides than *Melilotus* and *Taraxacum* (See Chapter 1).

3.5 Conclusions

Mature forests are poor sites for invasive plant germination, and fire alters germination potential through its effects on substrate. Substrates that present a barrier between seed and contact with mineral soil appear to prevent germination of smaller seeded species. Mineral soil was the best substrate for germination, suggesting that severe fires which remove the organic layer and expose mineral soil are the most favourable for invasive plants. Both *Melilotus* and *Taraxacum* germination were enhanced on post-fire substrates, whereas this effect was less pronounced for *Vicia*. Indeed *Vicia* has the potential to colonize mature forests, although it may not persist in the inhospitable conditions of the mature forest. I suggest that severe fires that expose large amounts of mineral soil be closely monitored for invasive plant colonization, and that mature forests with adjacent populations of *Vicia* are also closely monitored. I would also recommend that further germination trials are conducted, using more invasive plant species common in roadsides of interior Alaska. I would also advise using a higher number of seeds in each plot or more individual plots to increase the power of statistical tests. As this study only looked at early germination trends, a longer observation period would be useful as it would shed light on longer term establishment trends. Such a study would be able to indicate whether competition from native plants, or the gradual return to pre-disturbance ecosystem conditions, would exclude invasive plants.

4   GENERAL CONCLUSIONS

When the results of the invasive plant surveys and seeding trials are taken together, they suggest that fire-induced change in substrate quality is a primary driver of invasibility in black spruce forests, and that mature stands are the most resistant to invasive plant colonization. In invasive plant survey models, residual organic layer depth and paper birch seedlings were good predictors of invasive plant presence. Both of these factors are indicative of substrate quality. Germination trials also showed a strong effect of substrate quality on short term invasive plant success. The secondary driver of invasibility appears to be a dispersal barrier for some species. *Melilotus* was much less common in surveys than *Taraxacum,* despite its better performance in germination trials. This finding suggests that the wind dispersed seeds of *Taraxacum* are allowing it to colonize, and that *Melilotus* would be more frequent in burned stands if sufficient dispersal vectors were available. However, any generalizations about "forest invasibility" based on this study should be made cautiously. Because of the low frequency of non-native species other than *Taraxacum*, it is difficult to make inferences with respect to other non-native species. Based on the results of the seeding trial which showed species-specific responses, I would expect that invasibility is ultimately a match between the invading species and the ecosystem. Generalizations about invasibility with respect to regional sources of non-native species may be difficult, if not impossible, to make.

It is difficult to determine natural patterns of forest colonization for *Vicia*, as it was rarely encountered adjacent to survey sites. The germination trials, however, suggest that given a seed source and dispersal vector, *Vicia* may be able to colonize both burned and mature stands. I recommend that forests adjacent to *Vicia* populations in the roadside should be heavily monitored, and that this species be given a priority status for roadside control efforts. Forests that are disturbed through fire suppression techniques should also be closely monitored for invasive plant colonization, as these treatments also facilitate invasive plant colonization.

The effects of substrate type on germination and the apparent effect of fire severity shed light on mechanisms controlling site invasibility. It appears that fire mediates site invasibility through substrate quality, with substrates characteristic of more severe fires being favourable for invasive plant colonization. Whereas Alaska has relatively low levels of plant invasion, predicted increases in fire severity and extent may put greater areas of boreal forest in Alaska at risk of

invasive plant colonization. I recommend that recent fires are closely monitored for invasive plant colonization, and that severe fires that expose mineral soil are given priority for management efforts.

This study sheds light on early colonization patterns, however long-term establishment trends remain unclear. As the forest returns to its pre-disturbance conditions, it is possible that the native vegetation will outcompete any early invasive colonizers. Long-term studies on establishment trends would shed light on this issue, however they run the risk of creating a source of invasive propagules in the forest that will allow for further spread. Future studies on long-term establishment in a highly monitored research area such as CPCRW would help to determine long-term establishment trends, while minimizing the risk that an invasion spreads deeper into a forest. If such a study were to be conducted, I would recommend that more species of invasive plants are seeded, particularly *Crepis*. The light wind-borne seeds of *Crepis* have the potential for long distance dispersal into disturbed forests. However, we lack data on its germination potential in disturbed forests. It must be reiterated that if another germination experiment were to be conducted it should be done in a highly monitored research area to ensure proper removal, and to prevent potential escape of the invasive species planted.

Further studies would also benefit from an increased sample size. Surveys indicate that invasive plant colonization of burned forests occur at relatively low frequencies, requiring many samples to detect strong patterns. A balanced sampling design targeting different types of black spruce forests, including low lying sites, upland sites, and north and south facing slopes would also enhance further studies. Because there were no restrictions on topography for my site selection, my sampling was not representative of the diversity in black spruce forest types. An expanded approach would involve randomly selecting sites, with the condition that there are an equal number of sites representing different topographies. Further study of managed areas should have a balanced sampling design with an equal number of different management types, so comparisons can be made as to how different management types influence invasive plant colonization.

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6 APPENDIX A: SITE COORDINATES AND MAP

Appendix A1: Survey coordinates for burned stands adjacent to the Dalton and Parks highways.

Site	Latitude	Longitude	Elevation(masl)
DCBU1	66.07639	150.16679	222
DCBU2	66.20036	150.22331	366
DCBU3	66.20187	150.22523	362
DCBU4	66.20366	150.22728	367
DCBU5	66.15855	150.19194	272
DCBU6	66.16156	150.19608	271
DCBU7	66.16391	150.19922	282
DCBU8	66.13938	150.17259	249
DCBU9	65.97484	149.99731	190
DCBU10	66.09384	150.15469	233
DCBU11	66.14643	150.17847	245
DCBU12	66.14991	150.18213	268
DCBU13	66.16811	150.20499	296
DCBU14	66.16586	150.20183	289
DCBU15	66.07481	150.16632	222
DCBU16	66.07317	150.16588	216
DCBU17	66.10873	150.15900	222
DCBU18	66.07986	150.16766	224
DCBU19	Missing	Missing	Missing
DCBU20	65.89957	149.76402	107
DCBU21	65.92149	149.82535	147
DCBU22	65.90988	149.78592	127
DCBU23	65.91006	149.78296	125
DCBU24	65.90690	149.77855	110
DCBU25	65.90804	149.78073	112
NEBU1	64.38049	149.02008	142
NEBU2	64.39147	149.01340	144
NEBU3	64.39700	149.01266	145
NEBU4	64.39924	149.01303	139
NEBU5	64.40218	149.01520	137
NEBU6	64.47121	149.06064	128
NEBU7	64.48678	149.07846	127
NEBU8	64.49713	149.06995	123

Note: Survey coordinates were recorded under the WGS84 Map Datum.

Appendix A2: Survey coordinates for mature stands adjacent to the Dalton and Parks highways .

Site	Latitude	Longitude	Elevation
DCBU1	66.17370	150.21123	259
DCBU2	65.95683	149.94066	178
DCBU3	66.02691	150.12350	178
DCBU4	66.06051	150.15959	249
DCBU5	66.06179	150.16135	238
DCBU6	66.18194	150.21223	308
DCBU7	66.18375	150.21219	295
DCBU8	66.09705	150.15146	230
DCBU9	66.09552	150.15303	233
DCBU10	66.09384	150.15469	233
DCBU11	66.06389	150.16145	249
DCBU12	66.06561	150.16216	228
DCBU13	66.05901	150.15883	257
DCBU14	66.07899	150.16692	215
DCBU15	66.08084	150.16667	219
DCBU16	66.09255	150.15643	239
DCBU17	66.13342	150.16785	218
DCBU18	66.05775	150.15817	260
DCBU19	66.05620	150.15791	256
DCBU20	65.93495	149.85870	180
DCBU21	65.93378	149.85597	147
DCBU22	65.93592	149.86128	186
DCBU23	65.93642	149.86366	176
DCBU24	65.93868	149.87344	171
DCBU25	65.93929	149.87682	161
NEBU1	64.08484	149.21709	321
NEBU2	64.09386	149.22726	310
NEBU3	64.10535	149.23541	311
NEBU4	64.26083	149.16292	197
NEBU5	64.26373	149.15083	170
NEBU6	64.28052	149.10594	177
NEBU7	64.29224	149.08817	176
NEBU8	64.30039	149.07938	151

Note: Survey coordinates were recorded under the WGS84 Map Datum.

Appendix A3: Survey coordinates for managed and adjacent undisturbed stands in the Fairbanks region.

General Location	Site	Latitude	Longitude	Elevation (masl)
Fort Greely	FTGC1	63.98863	-145.629	397
Fort Greely	FTGM1	63.9884	-145.63	392
Harding Lake	HDLC1	64.44281	-146.834	248
Harding Lake	HDLC2	64.44472	-146.789	251
Harding Lake	HDLC3	64.4471	-146.904	226
Harding Lake	HDLC4	64.42994	-146.809	229
Harding Lake	HDLM1	64.4426	-146.833	223
Harding Lake	HDLM2	64.44521	-146.789	230
Harding Lake	HDLM3	64.44681	-146.903	222
Harding Lake	HDLM4	64.43025	-146.808	228
Cache Creek Road	CCRC1	64.87936	-148.32	204
Cache Creek Road	CCRM1	64.87916	-148.319	185
Cache Creek Road	CCRM2	64.87897	-148.317	173
Cache Creek Road	CCRC2	64.8783	-148.318	missing
Cache Creek Road	CCRC3	64.88072	-148.31	missing
Cache Creek Road	CCRM3	64.87959	-148.31	missing
Chena Hot Springs Road	CHSRNC1	64.89977	-147.275	184
Chena Hot Springs Road	CHSRNM1	64.90075	-147.275	177
Chena Hot Springs Road	CHSRSC1	64.87956	-147.219	158
Chena Hot Springs Road	CHSRSM1	64.87978	-147.22	161
Eielson AFB	EAFBC1-2	64.69487	-146.944	234
Eielson AFB	EAFBM1	64.69473	-146.94	261
Eielson AFB	EAFBM2	64.69412	-146.937	267
Fort Greely	FTGC2	63.9726	-145.613	402
Fort Greely	FTGC3	63.9863	-145.637	407
Fort Greely	FTGM1	63.9884	-145.63	392
Fort Greely	FTGM2	63.97253	-145.614	392
Fort Greely	FTGM3	63.9862	-145.637	403
Old Murphy Dome Road	OMDEC1	64.96291	-148.045	416
Old Murphy Dome Road	OMDEM1	64.96235	-148.044	426
Old Murphy Dome Road	OMDWC1	64.95396	-148.187	513
Old Murphy Dome Road	OMDWM1	64.95328	-148.188	520

7   APPENDIX B: INVASIVE SPECIES DATA

Appendix B1: Summary of invasive species density in survey sites. Density values are an estimate of density for the whole site, based on the number of individuals encountered on the belt transect.

Site	Invasive plant presence/ absence	*Taraxacum officinale* density (individuals/m^2)	*Melilotus officinalis* density (individuals/m^2)	*Crepis tectorum* density (individuals/m^2)
DCBU1	0	0	0	0
DCBU2	0	0	0	0
DCBU3	0	0	0	0
DCBU4	0	0	0	0
DCBU5	0	0	0	0
DCBU6	0	0	0	0
DCBU7	0	0	0	0
DCBU8	0	0	0	0
DCBU9	1	0.05	0	0
DCBU10	1	0.005	0	0
DCBU11	0	0	0	0
DCBU12	1	0.1	0	0
DCBU13	0	0	0	0
DCBU14	0	0	0	0
DCBU15	1	0.1	0	0.05
DCBU16	1	1.42	0	0
DCBU17	1	0.445	0	0
DCBU18	1	0.385	0.015	0
DCBU19	1	0.275	0	0
DCBU20	0	0	0	0
DCBU21	0	0	0	0
DCBU22	0	0	0	0
DCBU23	0	0	0	0
DCBU24	0	0	0	0
DCBU25	0	0	0	0
NEBU1	1	0.015	0	0
NEBU2	0	0	0	0
NEBU3	0	0	0	0
NEBU4	0	0	0	0
NEBU5	0	0	0	0
NEBU6	1	0.015	0	0
NEBU7	0	0	0	0
NEBU8	1	0.355	0	0

1 **Appendix B2:** Summary of managed site surveys, indicating which sites had invasive plants
2 present. Control sites were undisturbed, and invasive plants were never observed in control sites.

Name	Treatment	*Crepis tectorum* density (individuals/m^2)	*Taraxacum officinale* density (individuals/m^2)
CCR-C1	Control	absent	absent
CCR-C2	Control	absent	absent
CCR-C3	Control	absent	absent
OMDW-C1	Control	absent	absent
OMDE-C1	Control	absent	absent
CHSRN-C1	Control	absent	absent
CHSRS-C1	Control	absent	absent
HDL-C1	Control	absent	absent
HDL-C2	Control	absent	absent
HDL-C3	Control	absent	absent
HDL-C4	Control	absent	absent
FTG-C1	Control	absent	absent
FTG-C2	Control	absent	absent
FTG-C3	Control	absent	absent
EAFB-C1-2	Control	absent	absent
CCR-M1	Managed	0.59	present
CCR-M2	Managed	absent	absent
CCR-M3	Managed	absent	absent
OMDW-M1	Managed	absent	absent
OMDE-M1	Managed	absent	absent
CHSRN-M1	Managed	present	absent
CHSRS-M1	Managed	present	absent
HDL-M1	Managed	absent	absent
HDL-M2	Managed	absent	absent
HDL-M3	Managed	absent	absent
HDL-M4	Managed	absent	absent
FTG-M1	Managed	0.03	absent
FTG-M2	Managed	absent	absent
FTG-M3	Managed	absent	absent
EAFB-M1	Managed	absent	absent
EAFB-M2	Managed	absent	absent

3 **Note:** "present" denotes sites where invasive plants were present at the site but do not have
4 density estimates because they were not on the transect.

8   APPENDIX C: SUPPLEMENTAL SURVEY SITE DATA

6   **Appendix C1:** Summary of functional group data for burned survey sites. Values represent the number of genera in a functional
7   group.

Site	Deciduous shrub diversity	Evergreen shrub diversity	Equisetum presence/absence	Marchantia presence/absence	Sedge presence/absence	Forb diversity	Lichen presence/absence	Functional group diversity
DCBU1	1	1	0	0	0	1	1	7
DCBU2	4	1	1	0	0	3	0	7
DCBU3	2	3	1	0	0	3	0	7
DCBU4	3	4	1	0	0	5	0	7
DCBU5	3	1	1	0	0	2	0	7
DCBU6	2	3	1	0	0	1	1	8
DCBU7	1	2	1	0	0	1	1	8
DCBU8	4	3	1	0	0	1	0	7
DCBU9	0	2	1	1	0	3	0	7
DCBU10	1	3	1	0	0	2	1	8
DCBU11	2	3	1	0	0	5	0	7
DCBU12	2	1	1	0	0	2	0	7
DCBU13	1	1	1	0	0	1	0	7
DCBU14	4	3	0	0	0	2	0	6
DCBU15	3	1	0	0	0	2	0	6
DCBU16	1	1	1	0	0	2	0	7
DCBU17	1	2	0	0	0	2	0	6
DCBU18	2	2	0	0	0	5	1	7
DCBU19	3	2	1	1	1	3	1	10
DCBU20	3	1	1	1	1	4	1	10
DCBU21	3	4	1	0	1	4	1	9
DCBU22	3	3	0	0	0	5	1	7

Site	Deciduous shrub diversity	Evergreen shrub diversity	Equisetum presence/absence	Marchantia presence/absence	Sedge presence/absence	Forb diversity	Lichen presence/absence	Functional group diversity
DCBU23	1	0	1	1	0	1	0	7
DCBU24	4	3	1	1	1	5	0	9
DCBU25	2	2	1	0	1	5	1	9
NEBU1	1	4	1	0	1	4	0	8
NEBU2	1	4	1	0	1	8	1	9
NEBU3	2	3	1	0	1	3	1	9
NEBU4	2	3	1	0	1	2	0	8
NEBU5	3	3	1	0	1	2	0	8
NEBU6	2	3	1	0	1	2	0	8
NEBU7	3	4	1	0	0	5	0	7
NEBU8	4	3	0	0	0	3	0	6

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11   **Appendix C2:** Summary of environmental data from burned survey sites.

SITE	Mineral soil pH	Hydrosense % Volumetric Moisture	Moisture class	Residual organic layer depth (cm)	Active layer depth (cm)
DCBU1	5.10	3.5	1	0.75	73.3
DCBU2	6.21	47	4	13.5	111.67
DCBU3	7.10	42	4	13.3	116.67
DCBU4	5.40	60	6	22.4	120
DCBU5	6.40	43	3	11.3	120
DCBU6	6.56	32	3	6.21	120
DCBU7	6.80	32	3	9.31	120
DCBU8	6.74	34	4	9	120
DCBU9	6.16	9	1	7.21	120
DCBU10	5.96	43	4	15	100
DCBU11	6.43	46	5	12.1	120
DCBU12	6.82	41	4	4.4	120
DCBU13	5.64	26	4	7.67	120
DCBU14	5.7	25	3	6	120
DCBU15	5.09	13	1	3	100
DCBU16	5.37	17	1	2.67	90
DCBU17	5.35	10	1	2.67	46.67
DCBU18	6.68	36	3	13	106.67
DCBU19	6.96	45	4	8	120
DCBU20	6.9	53	6	26	103.33
DCBU21	6.38	55	5	22	110
DCBU22	7.04	57	6	24.3	110
DCBU23	7.22	31	3	12	120
DCBU24	6.92	51	5	21.3	120
DCBU25	6.69	50	4	23.67	120
NEBU1	6.52	36.33	3	15.33	106.67
NEBU2	6.25	82	6	15.67	100
NEBU3	6.11	38	3	21.67	110
NEBU4	5.49	64.67	6	27	98.33
NEBU5	5.53	48.67	4	15	120
NEBU6	5.47	19.67	2	1.7	120
NEBU7	5.73	7.33	4	0	105
NEBU8	7.02	48	3	12.67	120

12   **Note**: All columns represent the average from three measurements per site. For moisture class: 1= xeric,
13   2= subxeric, 3=subxeric to mesic, 4=mesic, 5=mesic to subhygric, 6=subhygric.

14 **Appendix C3:** Summary of ground cover types at burned survey sites. Values represent percent cover averaged from ten points.

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Site	Mineral soil	Moss	Marchantia	Leaf litter	Lichens	Grass	Dead wood	Residual organic layer	Rock	Sedge
DCBU1	69.4	23.5	0	3.2	0.1	2	0.6	2	0	0
DCBU2	0	39.5	0	34.1	0	5.3	4.1	15.5	0	0
DCBU3	0	18.7	0	72.5	0	0.2	7.5	2.5	0	0
DCBU4	0	47	0	51.5	0	1	4.1	0	0	0
DCBU5	0	53	0	32.5	0	0.3	2.2	13	0	0
DCBU6	0	18.1	0	48	0.3	1.2	3.7	27.5	0	0
DCBU7	0	22.5	0	19.5	0.1	1.5	8.2	51	0	0
DCBU8	0	41	0	49	0	7.7	1.1	0.5	0	0
DCBU9	3.5	30	9.2	40.1	0	0.1	9.5	7.6	0	0
DCBU10	10	19	0	61.5	0.1	3.1	1.6	3	0	0
DCBU11	0	28.1	0	61	0	5.5	0	5	0	0
DCBU12	0	37	0	56	0	0.1	7.5	0	0	0
DCBU13	0	56.5	0	24.5	0	8.5	2	8	0	0
DCBU14	0	50.5	0	16	0	22	10.5	1	0	0
DCBU15	0	66	0	5	0	0	6	22.5	0.5	0
DCBU16	0.5	71	0	11	0	1.5	6.5	9.5	0	0
DCBU17	0.5	81	0	5	0	0	2	11.5	0	0
DCBU18	0	56	0	6.5	2.5	25	0	10	0	0
DCBU19	0	57	7	6.5	1.5	17	1	0	0	10
DCBU20	0	21	0.5	37.5	11.5	29	0	0.5	0	1
DCBU21	0	32	0	46	0.5	10	0	10	0	1.5
DCBU22	0	84	0	4.5	8.5	2.5	0	0.5	0	0
DCBU23	0	3	0.5	96.5	0	0	0	0	0	0
DCBU24	0	29	3	8	0	0	0	14	0	46
DCBU25	0	39	0	38	1.5	10	0	10.5	0	1

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Site	Mineral soil	Moss	Marchantia	Leaf litter	Lichens	Grass	Dead wood	Residual organic layer	Rock	Sedge
NEBU1	0	37.5	0	5.5	0	57	0	0	0	0
NEBU2	0	72	0	10	0.5	17.5	0	0	0	0
NEBU3	0	48	0	0.5	2.5	46.5	0	2.5	0	0
NEBU4	0	69	0	12	0	9	0	10	0	0
NEBU5	0	35	0	0	0	36	0	29	0	0
NEBU6	0	33.5	0	8.5	0	9	0	39	0	10
NEBU7	20	5	0	43	0	16	0	16	0	0
NEBU8	0	12.5	0	14	0	17.5	0	56	0	0

16   **Note:** Percent cover values represent averages from ten points in each site.

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18 **Appendix C4:** Understory lant community data for mature and burned sites along the Parks and Dalton highways, and managed sites
19 near Fairbanks,Alaska.

Family	Genus	Mature sites (%)	Burned sites (%)	Managed sites (%)	Dalton highway sites (%)	Parks highway sites (%)
Non-flowering plants						
Equisetaceae	*Equisetum*	27	79	83	54	5
Lycopodiaceae	*Lycopodium*	3	0	8	2	0
Graminoids						
Cyperaceae	Sedge	6	18	16	8	25
	Eriophorum	3	18	17	4	31
Poaceae	Grass	36	82	5	62	5
Angiosperms (non-graminoid)						
Asteraceae	*Achillea*	6	21	17	12	19
	Erigeron	0	3	0	0	6
	Petasites	42	39	42	36	56
Betulaceae	*Alnus*	21	24	8	28	6
	Betula	3	11	8	4	16
Boraginaceae	*Mertensia*	45	33	8	44	25
Caprifoliaceae	*Linnaea*	6	3	0	4	6
Cornaceae	*Cornus*	30	21	42	8	81
Droseraceae	*Drosera*	0	3	0	0	6
Eleagnaceae	*Shepherdia*	9	12	8	1	13
Ericaceae	*Arctostaphylos*	24	17	8	21	19
	Empetrum	45	0	16	28	6
	Ledum	9	70	58	74	1
	Oxycoccus	3	3	17	4	0
	Vaccinium uliginosum	70	67	67	6	94
	Vaccinium vitis-idaea	97	70	42	8	94

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Family	Genus	Mature sites (%)	Burned sites (%)	Managed sites (%)	Dalton highway sites (%)	Parks highway sites (%)
Fumariaceae	*Corydalis*	0	3	16	2	0
Iridaceae	*Iris*	0	3	0	0	6
Onagraceae	*Chamerion*	18	89	58	52	56
Orchidaceae	Orchid	6	0	8	4	0
Polygonaceae	*Polygonum*	6	0	8	4	0
Pyrolaceae	*Pyrola*	33	15	0	32	0
Rosaceae	*Fragraria*	0	9	0	0	19
	Potentilla	15	21	8	22	6
	Ribes	12	15	3	16	6
	Rosa	94	45	58	7	69
	Rubus	12	21	33	18	13
	Spiraea	9	12	17	14	0
Salicaceae	*Salix*	48	85	41	7	56
Santalaceae	*Geocaulon*	58	3	8	26	44
Saxifragaceae	*Parnassia*	12	21	8	22	0
Unknown	Unknown forb	3	9	0	8	0

Note: Values represent the percentage of sites in which the genera were encountered. Only vascular plants are included in this table. Only *Vaccinium* genera were identified to species. *Betula* represents dwarf shrub birches, which were not identified to species. Grasses, sedges, and orchids were not identified to genus (with the exception of the sedge *Eriophorum*). Unknown forbs were plants which I was unable to identify to genus.