

**Effects of fire and harvesting on tree regeneration and ground-layer vegetation in
forested peatland communities in northern Minnesota**

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Abstract

Large-scale, catastrophic fires have historically been rare in peatland ecosystems in the Great Lakes region with surface fires, windthrow, and insects being the main disturbance agents. With climate change, these disturbances are predicted to become more common due to increases in the frequency and severity of drought. Boreal peatlands at their southern range margin, such as those in northern Minnesota, are expected to be particularly vulnerable to these impacts.

In 2012, a wildfire burned over 10,000 ha of a large forested peatland complex in north-central Minnesota providing a rare opportunity to document the early regeneration response of vascular and nonvascular plant species in black spruce (*Picea mariana*) and tamarack (*Larix laricina*) dominated communities. Post-fire vegetation data were also used to compare with data collected from clearcuts, the most commonly used management approach for these systems. Selected clearcut sites were harvested the same year as the fire and within the same community types.

Distinct differences in tree regeneration and vegetation composition were observed between burned and harvested sites. Community response to disturbance was also varied, largely reflecting the amount of disturbance to the peat layer. Burned areas had a greater abundance of tree seedlings in black spruce-dominated stands relative to harvests, however, the reverse was true for tamarack-dominated communities due to a complete removal of suitable seed beds and seed sources by the fire. In these tamarack communities, fire disturbance shifted plant community composition towards marsh-like conditions with cattails (*Typha* spp.) now the dominant species creating challenging conditions for future tree regeneration in these areas. In contrast, fire increased the

availability of favorable seedbed conditions in black spruce by reducing the depth of peat and the abundance of Labrador tea (*Rhododendron groenlandicum* (Oeder) Kron & Judd), an ericaceous shrub known to compete with conifer seedling regeneration and growth. These divergent responses indicate that tamarack-dominated systems may be more vulnerable to increases in the frequency and severity of fire due to the potential for phase shifts towards non-forested conditions. The increased levels of black spruce regeneration following fire relative to harvests suggest that application of prescribed fire should be considered for enhancing regeneration efforts in these important communities.

Tables of Contents

Acknowledgements	i
Abstract	iii
List of Tables	vii
List of Figures	viii
Chapter 1: Introduction	1
Chapter 2 : Effects of fire severity on short-term tree regeneration and ground layer vegetation response in two forested peatland communities	5
Introduction.....	5
Methods.....	9
Study Area	9
Study Sites	10
Plot Selection	13
Sampling design and severity assessment.....	15
Statistical Analyses	17
Results.....	19
Fire severity effects on Seedling Regeneration	19
Bryophytes and microtopography	19
Species richness and diversity	22
Ericaceous shrubs.....	23
Discussion.....	23
Conclusions and Management Implications.....	30
Chapter 3: Early response of ground layer plant communities to fire and harvesting disturbance in lowland conifer systems in northern Minnesota, USA	41
Introduction.....	41
Methods.....	45
Study Area.....	45
Study Sites.....	46
Plot Selection	47
Sampling design	49
Statistical Analysis	50
Results.....	54
Seedling Regeneration.....	54
Bryophytes and microtopography	55

Ericaceous shrubs.....	57
Species richness and diversity	57
Species functional group cover	59
Understory community composition.....	60
Discussion.....	63
Disturbance effects on seedling regeneration	64
Disturbance effects on bryophyte communities	66
Disturbance effects on ericaceous shrub abundance	69
Response of understory community composition to disturbance	70
Conclusions and management implications	71
Chapter 4 : Conclusions	84
Management implications	87
Study limitations and research recommendations	90
References.....	94
Appendix A.....	104
Appendix B.....	106

List of Tables

Table 2.1. Plot stratification for fire severity for black spruce bogs and rich tamarack swamps.....	38
Table 2.2. Mean cover for the main response variables across different levels of fire severity for black spruce bog sites.	39
Table 2.3. Mean cover for the main response variables across different levels of disturbance severity for rich tamarack swamp.....	40
Table 3.1. Plot stratification for fire severity and harvest plots for Spruce Bogs and Rich Tamarack Swamps	79
Table 3.2. Mean cover for main response variables across fire and harvest disturbance for black spruce bog sites.....	80
Table 3.3. Mean cover for main response variables across fire and harvest disturbance for rich tamarack swamp sites.....	81
Table 3.4. Indicator species analyses for disturbance categories	82

List of Figures

Fig. 2.1. Location of study area for fire and control plots in northern Minnesota	34
Fig.2.2. Bivariate relationships between post-fire vegetation conditions and fire severity for black spruce plots.	35
Fig.2.3. Bivariate relationships between post-fire vegetation conditions and fire severity for rich tamarack plots.....	36
Fig. 2.4. High severity study site in rich tamarack swamp.....	37
Fig.2.5. Example of concentrated burning surrounding black spruce boles.....	37
Fig. 3.1. Location of study area showing harvest, fire, and control plots in Minnesota...	75
Fig.3.2. Boxplots of mean seedling densities for <i>Picea mariana</i> and <i>Larix laricina</i> across disturbance categories	76
Fig.3.3. Mean percent cover of understory vegetation by functional group for black spruce bogs and rich tamarack swamps across disturbance groups.....	77
Fig. 3.4. Non-metric multidimensional scaling (NMS) ordination of ground layer vegetation across disturbance categories	78
Fig. 4.1. Stringers of unburned tamarack in the North Minnie fire	93

Chapter 1: Introduction

The boreal forest region of North America is defined by a cool, moist climate that sustains rates of production that exceed decomposition (Wright 1992). This delicate balance between temperature and precipitation, in a region where flat topography and poorly drained soils predominate, has led to the development and maintenance of large peatland systems throughout the boreal ecozone (Wright 1992). With warmer temperatures and increases in drought frequency and severity predicted for north temperate and boreal regions as a result of climate change (Turetsky et al. 2004; Dale et al. 2001; IPCC 2007; Frelich and Reich 2010; Clark et al. in press), the species and plant communities dependent on cool, moist climatic conditions will be increasingly put at risk. Decreased moisture levels for Minnesota wetlands will likely mean a shift in these plant communities, either as a direct response to water level changes or indirectly through altered soil and water chemistry, decomposition, or disturbance regimes with the boreal peatlands experiencing the most dramatic changes of the state's wetland ecosystems (Galatowitsch et al. 2009).

Climate-mediated disturbances such as wildfire are of particular concern for peatlands already at their southern range margin, such as those in the northern Lake States region, USA, given the elevated susceptibility of range-margin populations to shifts in prevailing disturbance regime. Large-scale fires have historically been rare in lowland ecosystems in the upper Great Lakes region (Curtis 1959; Dale et al. 2001), although vulnerability to fire often increases substantially during dry seasons when hot weather, high winds, and drought conditions combine to dry out the vegetation and surface peat (Wein 1983; Zoltai et al. 1998; Turetsky 2004). Despite future predictions

for increasing fire events as a result of drought, the role of this type of disturbance in poorly drained landscapes still remains poorly understood (e.g., Turetsky and St. Louis 2006), with much of our knowledge regarding fire and the interaction between disturbance factors based on upland ecosystems in boreal regions.

Lowland conifer forests are commonly managed for wood products through much of the upper Great Lakes region, with clear cutting-based systems being the primary management approach. These management methods are largely incongruous with the historically low frequencies of stand-replacing natural disturbances in these forests. Although regeneration can be successful following clearcutting in lowland conifer systems, there is still little known about the potential effects of clearcutting as a replacement for fire, and its impact on the future resilience of these forest ecosystems to climate change (Fenton et al. 2005; Fenton et al. 2013).

During the summer of 2012, severe drought conditions developed in northern Minnesota, helping to facilitate the spread of a wildfire that burned over 10,000 ha of a large peatland complex. The fire provided an opportunity to document black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) and tamarack (*Larix laricina* (Du Roi) K. Koch) seedling establishment, composition of vascular and nonvascular plant regeneration, as well as disturbance related changes to the acrotelm—the upper peat surface above the water table—in a black spruce ombrotrophic bog and a nutrient rich tamarack-dominated swamp. Data were also collected from clearcuts that were harvested in the same year as the fire to allow for comparisons of post-disturbance patterns of vegetation development between fire and harvest disturbance. These findings demonstrate that important differences exist between forested peatland types, where

changes in hydrology and vegetation can be influential in determining the spatial spread and severity of fire. In addition, this work points to several differences between the impacts of disturbance type on vegetation response due to varying levels of disturbance to the acrotelm peat layer.

The second chapter of this thesis examines how fire severity affected important biotic conditions typical of a black spruce bog and rich tamarack swamp. Fire severity is widely recognized as an important driver of post-fire regeneration (Rowe 1983; Wang and Kembell 2005). The results from this chapter indicate that moderate and high severity fire in the tamarack swamps induced significant changes with the combustion of the peat surface, resulting in retrogression of this community to marsh-like conditions. As a result, vegetation shifted towards cattails (*Typha* spp.) and graminoid dominance, with post-fire colonizing moss and liverwort species replacing *Sphagnum*. These changes were not reflected in species richness or diversity measures given the wholesale shifts in species composition for this community. The near complete removal of the upper peat surface resulted in little to no measurable tamarack seedling germination.

Low and moderate levels of fire severity in the black spruce bog community resulted in a high degree of spatial variation across the well-developed peat surface where a large proportion of *Sphagnum* hummocks were only partially consumed with hollows and low areas more completely combusted. This variation led to a slight, but significant increase in vascular plant species richness and diversity and helped facilitate the re-growth of ericaceous shrubs, in particular *Rhododendron groenlandicum*. The variable levels of peat consumption also enhanced black spruce regeneration with higher seedling densities occurring on peat that was more effectively consumed by fire, particularly for

lower severity burned plots.

The third chapter explores how seedling regeneration and vascular and nonvascular vegetation differed between the above-mentioned plant communities across a range of fire severities and clearcut disturbance. Significant differences in seedbed conditions, regeneration densities, and plant community composition were detected between the harvest and fire disturbance. For black spruce bogs, seedling regeneration was significantly higher on burned sites than on harvested ones; however, the reverse was true for tamarack swamps, because fire removed a large majority of the seedbed. Other distinct differences relating to species richness and diversity, as well as moss species abundance were observed between disturbance types and between communities. These changes largely corresponded to the degree of peat disturbance and removal. The low levels of black spruce regeneration observed in harvested areas relative to burned sites suggests that current clearcutting-based methods, which do not include aerial seeding, are not emulating natural disturbance processes associated with stand-replacing disturbance in these systems.

The final chapter of this thesis offers conclusions based on this research as it relates to the impacts of fire severity and clearcut disturbance for the two forested communities, particularly in light of climate change. Management implications, with respect to the findings of this work, are presented for developing silvicultural methods that further emulate the natural disturbance processes in these systems, which aim to sustain understory species diversity and conifer regeneration. Lastly, the potential limitations of this study are outlined and recommendations for future research are presented.

Chapter 2. Effects of fire severity on short-term tree regeneration and ground layer vegetation response in two forested peatland communities

Introduction

The influence of fire on short-term vegetation dynamics and forest succession has long been a central area of ecological research (e.g., Ahlgren 1960; Rowe and Scotter 1973; Johnson 1992; Heinselman 1963, 1981). This work has predominantly focused on upland forest ecosystems given the notion wetland forests, including forested peatlands on deep peat substrates, typically burn less readily than upland systems (Kuhry 1994 ; Zoltai et al. 1998; Lavoie and Pellerin 2007; Magnan et al. 2011). Nevertheless, forested wetlands are vulnerable to fires, particularly during dry seasons when hot weather, high winds and drought conditions combine to dry out vegetation and surface peat (Wein 1983; Zoltai et al. 1998). With an increase in drought frequency and severity predicted for north temperate and boreal regions as a result of climate change (Clark et al. in press), sub-boreal peatlands are likely to be impacted significantly not only by increased temperatures, but also indirectly through more frequent fire events (Dale et al. 2001; Galatowitsch et al. 2009).

The sub-boreal forested peatlands of Minnesota are dominated by black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) and tamarack (*Larix laricina* (Du Roi) K. Koch), which require on-site seed sources for post-disturbance recovery. Consequently, an increase in fire frequency and severity, as well as fire extent, could all greatly impact seed availability and seedbed quality (Knowles et al. 1992; Wang and Kembell 2005; Brown and Johnstone 2012), which is of particular concern for peatlands already at their southern range margin in the northern Lake States region, USA.

For forested peatlands, fire severity is the most important element of the fire regime that affects not only tree regeneration but also ecology recovery (Wang and Kemball 2005), where severity is often defined as the amount of organic matter, or peat, consumed (Rowe 1983; Wein 1983; Kasischke et al. 2008). A complex gradient of biotic and abiotic conditions largely associated with groundwater hydrology is attributed to an equally complex gradient of peatland community successional development (Glaser 1987, 1992; Rydin and Jeglum 2006). Response to variations in fire severity between community types might also be expected to vary, with some communities more or less resilient to fire disturbance depending on depth of the water table and the amount of peat development.

For example, low severity fire in black spruce bogs can result in a high degree of spatial heterogeneity in peat consumption as a result of fire behavior and differences in moisture gradients between highly developed hummock and hollow microtopography (Vitt and Slack 1984; Benscoter et al. 2011). Particular *Sphagnum* species occur at different positions along the microtopographic gradient where densely packed individuals occupying the upper hummocks (e.g., *Sphagnum fuscum* (Schimper) Klinggräff), are able to transport and retain water more efficiently than those of hollows (Rydin 1986; Benscoter et al. 2005; Thompson and Waddington 2012). *Sphagnum* species characteristic of hollows and lawns (e.g., *S. angustifolium* (Warnstorff) Jensen and *S. magellanicum* Bridel, respectively) are more loosely arranged and thus prone to desiccation. Consequently, combustion can be greatest during wildfire in these lower hollows—particularly during drought when the water table is well below the peat surface—while hummocks remain largely unburned (Benscoter et al. 2005; Thompson

and Waddington 2012). As a result, this burn irregularity in black spruce bogs has been shown to strongly influence post-fire seedbed conditions, where favorable microsite conditions for seedling establishment are created in areas of reduced or consumed *Sphagnum* peat, which have lowered vascular plant competition (Chrosciewicz 1974; Zasada et al. 1983; Aksamit and Irving 1984; Charron and Greene 2002; Greene et al. 2004; Johnstone and Chapin 2005).

The relative success of different plant regeneration strategies is also determined by spatial variation in peat consumption, where remaining hummocks provide protection to belowground reproductive structures (Rowe 1983; Schimmel and Granström 1996; Veilleux-Nolin and Payette 2012). Ericaceous and dwarf shrub species typical of forested peatlands, such as Labrador tea (*Rhododendron groenlandicum*) and bog birch (*Betula pumila* L.), often resprout after fire and thus have a competitive advantage over other plants that establish from seed (Flinn and Wein 1977; Rowe 1983). Ericaceous shrubs in particular have been implicated in conifer regeneration failure due to allelochemical inhibition of conifer seed germination and nutrient competition (Inderjit and Mallik 1996; Mallik 2003). Without sufficient fire intensity or combustion to remove plant propagules (roots, rhizomes, and plant stems), post-fire shrub abundance is unlikely to decrease (Johnstone and Kasischke 2005).

In contrast, minerotrophic tamarack swamps can be highly vulnerable to increasing fire severity, where relatively shallow peat by comparison is readily consumed by fire down to the water table, leaving little if any seedbed for germination (Duncan 1959; Heinselman 1981; Uchytel 1991; Busque and Arseneault 2005). Microtopography –as well as ericaceous shrub dominance– in these tamarack peatlands is less pronounced,

where dominant *Sphagnum* species are less differentiated by hummock and hollow vertical gradients and more characteristic of shady, moist hollows (e.g., *Sphagnum warnstorffii*). As a result, during drought conditions *Sphagnum* peat is potentially more susceptible to desiccation community-wide. Although at present there is inadequate knowledge with respect to drought and disturbance from fire and in these communities and further study is needed to understand how these factors interrelate. Furthermore, the responses of *Sphagnum* to rare but extreme drought conditions may be of importance but are poorly documented (Clymo and Hayward 1982).

To examine the effects of fire severity on seedling regeneration and ground layer vegetation in lowland conifer communities, this study takes advantage of a rare fire event that occurred during a severe drought in September of 2012 in northern Minnesota, USA. The North Minnie fire burned over 10,000 ha and resulted in a range of fire severities across a mosaic of peatland communities, providing an opportunity to increase our understanding of wildfire effects on boreal peatlands at the southern-most extent of their range. These ecosystems are projected to be highly vulnerable to climatic warming and increased wildfire. Insights from this work will provide a greater understanding of the capacity of these forests to recover from large-scale fire events under contemporary environmental conditions. The study sites for this research included a portion of a large black spruce-dominated ombrotrophic bog, as well as minerotrophic, tamarack-dominated swamps.

Given the importance of suitable seedbed conditions for germination and seedling survival, the objectives of this study were to 1) contrast fire severity between an ombrotrophic black spruce bog and a minerotrophic tamarack swamp, 2) relate tree

seedling densities to fire severity, and 3) document differences in ericaceous shrub density and bryophyte community abundance with respect to patterns of tree establishment in these systems.

Methods

Study Area

The study area is located in the Red Lake Wildlife Management Area (WMA) and Beltrami Island State Forest, in Beltrami and Lake of the Woods counties, Minnesota, USA. This area is known as the Agassiz Lowlands, an area formerly occupied by Glacial Lake Agassiz. The region is characterized by flat (topographic relief is less than 15 m), poorly drained soils of lacustrine origin, which have helped facilitate the development of extensive peatlands through paludification (Glaser 1987).

Climate is mid-continental and dominated by cool, humid air masses from the north; however, the western and southern edge of this region coincides closely with a change from a climate of slight moisture excess to one of substantial deficits (Heinselman 1961). This steep climatic gradient marks what is known as the prairie-forest border, where moisture quickly becomes insufficient to support forest growth to the west as a result of dry, western air masses that result in frequent summer droughts (Glaser 1992).

Mean annual precipitation for the region is 66 cm, with approximately 70% occurring during the growing season. In 2012, the year of the North Minnie Fire, precipitation for the region prior to the fire (Oct. 2011-Sept. 2012) was approximately 41 cm below average (Minnesota Climatology Working Group; <http://climate.umn.edu>). The growing season is short, generally 98 to 111 days. The normal mean temperatures for

summer months (June-August) range from 15 to 20° C with winter months averaging -20 to -7° C (NOAA Climate Monitoring for 1971-2015; <http://ncdc.noaa.gov/cag/time-series>).

Study Sites

This study was replicated across several sites in two forested peatland communities—[nutrient poor] Northern Spruce Bog (hereafter referred to as “black spruce bogs” or BSB) and Northern [nutrient] Rich Tamarack Swamp (hereafter referred to as “rich tamarack swamps” or RTS). These communities were selected for the study as they represented the two plant communities most affected by the North Minnie wildfire as well as the larger forested Agassiz Lowlands landscape. Plant community classification followed the Minnesota Department of Natural Resources Laurentian Mixed Forest Field Guide to Native Plant Communities (MN DNR 2003). Four disturbance severity levels were recognized within these communities (low, moderate, and high fire severity, and undisturbed; Table 2.1; see below for details on disturbance severity classification). The fire study sites consisted of two BSB sites within Malcolm Bog and three nearby RTS sites within accessible areas of the fire’s extent (Fig. 2.1).

Black spruce bogs within the study area are dominated by black spruce with occasional tamarack. Peat is often very deep (> 1m) resulting in a raised topographic profile that isolates the plant rooting zone from the underlying mineral-rich groundwater with nutrient inputs supplied primarily by atmospheric precipitation (Glaser 1992). As a result, surface pH is typically acidic (<4.2) and tree growth rates are often very low. Species diversity is also quite low, where the ground layer is often dominated by a dense

cover of ericaceous shrubs such as Labrador tea (*Rhododendron groenlandicum*), leatherleaf (*Chamaedaphne calyculata* (L.) Moench), and bog laurel (*Kalmia polifolia* Wangenh.). Graminoids such as few-flowered sedge (*Carex pauciflora* Light.) and tussock cottongrass (*Eriophorum vaginatum* L.), and herbaceous species such as pitcher plant (*Sarracenia purpurea* L.) and round-leaved sundew (*Drosera rotundifolia* L.) are also common. The well-developed *Sphagnum* peat microtopography in these communities is dominated species typical of hummocks such as *Sphagnum rubellum* Wilson, *S. russowii* Warnstorf, *S. capillifolium* (Ehrhart) Hedwig, and *S. fuscum*, while the lower hummocks and hollows are dominated by *S. angustifolium* and *S. magellanicum*.

Historically, the return interval of catastrophic fires in black spruce bogs has been estimated to be in excess of 1,000 years (MN DNR 2003) and possibly even longer in larger peatland systems in northern Minnesota (P. Glaser, personal communication, May 22, 2014). Smaller disturbances that include light surface fires are more common and have been estimated to occur roughly every 120 years (MN DNR 2003); however, these superficial fires can still result in significant mortality of black spruce trees. New recruitment of black spruce in these communities, in the absence of fire, is typically through layering.

Rich tamarack swamps also occur on well-developed peat; however, much less (typically over 40 cm) than that of bogs. These communities are influenced by mineral-rich groundwater with pH ranging from 5.5-7 and as a result, species diversity is much higher than in black spruce bogs. The canopy is dominated by a continuous cover of tamarack (50-75% cover) with occasional black spruce and northern white cedar (*Thuja*

occidentalis L.) in the understory. Hummock and hollow microtopography is less pronounced with a diverse assemblage of shade-tolerant mosses such as *Sphagnum warnstorffii* Russow and *S. angustifolium*, *Plagiomnium ellipticum* (Bridel) Koponen and *Drepanocladus aduncus* (Hedwig) Warnstorff. Sedges and ericaceous shrubs are also present, as are several minerotrophic species such as bog birch (*Betula pumila* L.), alder (*Alnus incana* (L.) Moench), tufted loosestrife (*Lysimachia thyrsiflora* L.), and three-leaved false Solomon's seal (*Maianthemum trifolia* (L.) Sloboda).

Stand-replacing fires in these rich tamarack swamps are infrequent, with estimates of this type of disturbance occurring approximately every 390 years (MN DNR 2003). Extensive rich tamarack-dominated swamps, like those within the study area, likely have persisted because the rate of recurrence of large, stand-replacing fires has been relatively infrequent, allowing these areas to act as fire-free refugia for the fire-intolerant tamarack (Busque and Arseneault 2005). Smaller disturbances resulting in partial mortality of the canopy are somewhat more common, with a rotation of about 80 years.

Plot Selection

Initial selection of sites representing different fire severity categories was aided using a differenced Normalized Burn Ratio map of the study area (dNBR; Banskota and Falkowski, unpublished data 2013). The dNBR map was generated based on Landsat-derived estimates of burn severity for the extent of the fire using bands 4 and 7 from two LANDSAT Thematic Mapper images (pre-fire and 1 year post-fire), which was transformed to relate it to four burn categories: 1) unchanged (minimal or no visible effect of fire), 2) low-severity, 3) moderate-severity, and 4) high-severity (Key and

Benson 2006; Soverel et al. 2010). Given the limitations of remotely-sensed fire severity assessments for quantifying belowground impacts of fire in peatland communities, fire-severity classifications were verified in the field and adjusted where necessary (see *Sampling design and severity assessment* below). Based on these field observations we determined that only two classes of fire severity were present for BSB plots: low and moderate.

A potential limitation of using a dNBR scaled index map for the initial selection of fire severity site locations for this study was that this approach has primarily been used to remotely sense fire severity for upland coniferous forests. The effectiveness of this approach to assess forested peatlands and the degree of peat consumption has been more limited (Allen and Sorbel 2008; Kasischke et al. 2008; Keeley 2009). Discrepancies between remotely-sensed and field-based severity assessments typically occurred when imagery showed low severity fire in areas that did not burn, which is consistent with what Cocks et al. (2005) found for upland sites.

Given the lack of consistent criteria for classifying fire severity in the field (Ryan 2002), particularly for lowland systems (Kasischke et al. 2008), two measures of fire severity were assessed for each plot, one characterizing tree canopy consumption and another characterizing the consumption of the peat surface. These measures were combined with satellite-derived data as a means to quantify fire severity categories *a posteriori*, along a continuous gradient. This gradient was represented using a numerical measure of fire severity, referred to as fire severity index (FSI). FSI values were calculated for all plots by combining the resulting 30-m resolution dNBR pixel number values ($\Delta\text{NBR} = \text{NBR}_{\text{prefire}} - \text{NBR}_{\text{postfire}}$) from the burn severity map that expressed the

degree of vegetation change (Cocke et al. 2005; Soverel et al. 2010) with two field measures of fire severity (average canopy consumption and peat layer consumption score; see *Sampling design and severity assessment*). Because these variables were not expressed in the same units, data were first standardized for each measure by generating z-scores at the community level (i.e., BSB and RTS) and then combined. The summation of these scores was then used to generate a numeric value of fire severity for each plot relative to other plots within a given community type where controls had the value of zero for no mortality. Initial field categorization of plots according to low, moderate, and high severity was also retained to examine differences between *a priori* groups.

It is recognized that pre-disturbance information on vegetation abundance and composition is necessary for making direct inferences on changes in community structure and composition resulting from disturbance. This information was not available for the areas affected by the North Minnie fire and therefore an attempt was made to select undisturbed forests similar to the sampled fire areas in terms of pre-disturbance stand age, overstory tree stocking, peat depth, microtopography and canopy composition. Unburned control plots for both the BSB and RTS communities were identified from neighboring areas of the fire within Beltrami Island State Forest and Red Lake WMA based on previous field knowledge and remotely sensed data. After representative plant communities were identified, ArcGIS was used to randomly select plot locations within digitized stand boundaries. Stand ages for BSB sites ranged from 100-150; RTS sites ranged from 100-140 years old.

Sampling design and severity assessment

Sampling took place June 07 through August 28, 2014 during the second growing season following the North Minnie Fire. Sites were sampled using an 11.3 m (400 m²) fixed-radius plot, initially located with a random point generator in ArcGIS. Individual plots were required to be at least 90 m from the impacts of roads or ditches and at least 60 m away from another plot. Each plot was marked permanently with a 1.5 m length of PVC pipe marking the center, inserted approximately 1 m into the peat substrate.

All trees species within the plot with ≥ 10 cm dbh (diameter at breast height) were recorded according to diameter. Standing dead trees for both RTS and BSB burned plots (>10 cm DBH) were also assigned a value of canopy and crown consumption following the methods of Kasischke et al. (2008). Values ranged from 0 (alive) to 6 (tree deceased, bole charring present) and were then averaged to the plot level (Appendix A).

A qualitative assessment of peat consumption was also assigned based on a rating of observable fire effects for the entire plot on a scale of 0 (unburned) to 6 (majority of surface peat consumed by fire (Appendix A). The exact amount of peat consumption could not be quantified because of a lack of pre-fire measurements; therefore, severity classes reflected the extent of burning on the forest floor. The methods for assessing canopy consumption were based on Kasischke et al. (2008) who demonstrated that the Composite Burn Index (CBI), a field-based assessment of fire severity typically used for uplands (Key and Benson 2006), had limited application for black spruce forests beyond quantifying aboveground impacts and did not adequately address variations in peat or crown biomass consumption.

In an attempt to ensure sampled stands were approximately of similar origin dates, stand ages were determined from tree ring counts obtained from prepared increment cores. Cores were collected from 10–15 canopy trees at all BSB sites and approximately half of the RTS sites. Logistical constraints prevented a more thorough sampling of stand ages from all RTS sites, due to a later sampling date and inaccessibility. In cases where stand ages for RTS stands were not obtained, Forest Inventory data from the Minnesota DNR coupled with an examination of the earliest aerial photographs (ca. 1940; used to identify major disturbance events) were used to estimate stand age. In dating increment cores, trees were assumed to have grown for a minimum of 10 years before reaching the height of the tree-ring sample (20 cm above the substrate), because the root collar for both tamarack and black spruce is well below the peat surface beneath an extensive adventitious root system (DesRochers and Gagnon 1997). Minimum stand age was estimated from the ages of the oldest trees in the stand.

To evaluate tree regeneration, ericaceous shrub abundance, and seedbed condition (remaining microtopography), six-1 m² quadrats were placed along one of three transects at 4 and 10 meters, emanating from plot center at azimuths of 0, 120, and 240°. Conifer seedlings and dominant, upright ericaceous shrubs (i.e., not prostrate as in *Vaccinium oxycoccos* L.) were identified to species and tallied by height class (0-15 cm; 15-100 cm; 100-137 cm). Spruce seedlings and saplings were noted as either regenerated through layering or germination via seed. Total projected foliage cover was also visually estimated for all individual herbaceous plant species to the nearest 1% on a scale of 1-100%. Additional measurements characterizing the substrate and microtopography of each quadrat were made to the nearest 5%, where the proportion occupied by hummock,

hollow, or lawn was estimated. Hummocks were defined as being raised peat mounds that were 20-50 cm above the lowest surface level, with lawns being distinct, flatter areas 5-20 cm above the water table, and hollows distinguishable as depressions forming below the latter (see Rydin and Jeglum 2013).

Each quadrat also included a nested 0.5 m² plot, where bryophyte species were identified and their percent cover was visually estimated. A smaller nested plot was chosen to measure lichens and bryophytes, due to the fact that different vegetation types require different quadrat sizes and a smaller size has been shown to be appropriate for these smaller, non-vascular species (Daubenmire 1968; Grieg-Smith 1983; McCune and Lesica 1992). Measures of cover in each of the six quadrats and nested plots were averaged to the plot level.

Statistical Analyses

The impact of fire severity on tree regeneration was examined using generalized linear models (GLMs) with a negative binomial distribution and a logarithmic link function. A GLM was used for analyzing seedling data, as they have been shown to adequately handle count data, which often have several zero observations recorded and typically do not conform to a normal distribution (Zuur et al. 2009; O'Hara and Kotze 2010).

Mixed model analysis of variance (ANOVA) was used to examine the impact of disturbance severity on total ericaceous shrub abundance, vascular plant species richness (number of species per plot) and diversity (Shannon–Wiener index, H'), cover of specific bryophyte species or groups, and microtopographical conditions. The impact of

disturbance severity on *Rhododendron* abundance was analyzed in addition to examining total ericaceous cover for BSB sites given that this species has been suggested as the cause for reduced black spruce regeneration due to growth inhibition through competition and allelopathy. For RTS sites, the decision was made to analyze all ericaceous species together due to the fact that while *Rhododendron* makes up the vast majority of this total cover, this species does not occur at same level of abundance typical of BSB sites.

All species in the *Sphagnum* sect. *Acutifolia* were grouped together for ANOVAs for the BSB site as the species encountered largely consisted of hummock-forming *Sphagna*, several of which are notoriously difficult to tell apart without further microscopic cellular differentiation. For the RTS sites, where diversity of *Sphagnum* species was much higher and the abundance of any one species was fairly low, all *Sphagnum* species were grouped together.

Disturbance severity was treated as a fixed effect (using initial, field-verified fire severity categorizations) and site was treated as a random variable. In cases where significant effects were detected, post-hoc Tukey's honest significant difference tests were used for pairwise comparisons among disturbance levels with $p < 0.10$ considered significant. This significance level was used for all analyses given the study was largely observational and had a relatively small number of replications in each disturbance condition. When assumptions of normality and constant variance were not met, data were transformed using a square root transformation (this excludes the seedling count data, because non-normality was addressed using a GLM model – see above discussion). In addition to ANOVAs, Spearman's rank correlation coefficient was used to examine the bivariate relationships between fire severity index (FSI) and seedling densities and

associated seedbed conditions and potential competitive vegetation. All analyses were performed in R version 3.1.2 (R Core Development Team 2014).

Beta diversity (β) was assessed for vascular plants using a multiple-site dissimilarity measure. This measure partitions β into its spatial turnover and nestedness components following Baselga (2010), where spatial turnover or species replacement is the loss of a species followed by the gain of another and nestedness being a pattern where the species present at species-poor sites form subsets of the species in species-rich sites (Baselga 2010; Ulrich and Almeida-Neto 2012). In short, this method relies on the fact that Sørensen (β_{SOR}) and Simpson (β_{SIM}) dissimilarities are equal in the absence of nestedness (β_{NES}), so their difference is a measure of the nestedness component, which is derived from pairwise dissimilarity matrices of beta diversity (Baselga 2010). Thus, overall beta diversity (Sørensen dissimilarity) is equal to the sum of Simpson dissimilarity (turnover component of Sørensen dissimilarity) and nestedness measures ($\beta_{\text{SOR}} = \beta_{\text{NES}} + \beta_{\text{SIM}}$; Baselga and Orme 2012). The function ‘betadiver’ in the R package ‘vegan’ (Oksanen et al. 2015; R Development Core Team 2014) was used to compute mean beta diversity indices from pairwise Sørensen dissimilarity matrices, as well as the R package ‘betapart’ (Baselga et al. 2013), which includes the functions to compute the partitioned, multiple-site Sørensen dissimilarity index.

Results

Fire severity effects on Seedling Regeneration

Fire significantly affected black spruce seedling densities in BSB communities with plots experiencing low and moderate severity fire having significantly higher

densities than control plots; however, lower severity plots had significantly higher seedling densities than moderate severity plots (Table 2.2). This was also reflected in the generally curvilinear relationship between black spruce seedling densities and fire severity index (FSI; Fig. 2.2a).

Disturbance severity did not significantly increase tamarack seedling densities in RTS sites, because densities were quite low at all levels of fire severity (low, moderate and high) as well as for controls (Table 2.3). Similarly, there was no relationship between FSI and tamarack seedling densities (Fig. 2.3b).

Bryophytes and microtopography

Total cover of *Sphagnum* was significantly reduced for BSB plots at both low and moderate fire severity levels compared with controls, where control plots had a mean cover of 67% (0.5 m²) as opposed to moderate fire severity with 3% (0.5 m²) cover. In examining individual species cover, *S. angustifolium*, a species characteristic of hollows, had the most significant reduction for any one species (or group) in response to fire disturbance with significantly lower cover in low and moderate severity plots compared with controls (Table 2.2). The other two main species (or groups) for the BSB sites, *S. magellanicum* and the hummock- forming group *S. sect. Acutifolium*, did not have significant reductions at the low severity level compared with unburned controls, but did have significant reductions at moderate levels of fire severity (Table 2.2). The total cover of *Sphagnum* (where all species were combined) was both significantly and negatively correlated with FSI, as were all individual species, with *S. angustifolium* being most strongly correlated with increasing fire severity (Fig. 2.2c-d).

Polytrichum strictum Bridel, a common post-fire colonizing moss, increased significantly on exposed bare peat in both low and moderate levels of fire severity compared with unburned plots in black spruce bog sites (Table 2.2), where mean cover increased from 2% for the controls to 21% cover for moderate fire severity plots.

Polytrichum was also well correlated with FSI (Fig. 2.2b). While *Polytrichum* was the dominant species present after fire, other species were also present, with minor cover of *Aulacomnium palustre* (Hedwig) Schwägrichen, *Ceratodon purpurea* (Hedwig) Bridel, and *Ptychostomum pseudotriquetrum* (Hedwig) Spence. Parallel with the increase in *Polytrichum* cover, the amount of exposed peat lawns (a reduction in microtopographic hummocks and hollows resulting from fire) significantly increased at both low and moderate levels of fire severity compared to control plots in BSB sites; however, mean cover of hummock and hollow microtopography was not significantly affected by fire due to the high variability in cover across the plots. Only the increase in the cover of lawns (Fig. 2.2g; Table 2.2) was positively correlated with FSI.

For RTS sites, there was also a significant reduction in total mean *Sphagnum* cover at all levels of fire severity, compared with undisturbed control plots (Table 2.3). As a result, total cover of *Sphagnum* had a significant, negative relationship with FSI (Fig. 2.3b). While *Sphagnum* cover declined significantly, post-fire colonizing mosses and the liverwort *Marchantia polymorpha* L. that is often associated with fire, increased significantly in cover at all levels of fire severity compared with controls in RTS sites (Table 2.3). Much of the cover of mosses post-fire was restricted to recolonizing exposed root surfaces. These post-fire colonizing species primarily included *Ceratodon purpureus*, *Funaria hygrometrica* Hedwig, *Pohlia nutans* (Hedwig) Lindberg,

Polytrichum strictum, and *Ptychostomum pseudotriquetrum*. Peat surfaces, which scarcely rose above the water table (i.e., lawns), were often dominated by the liverwort *Marchantia polymorpha*, particularly at higher levels of fire severity. This group of post-fire colonizers was significantly correlated with increased FSI (Fig. 2.3c).

Hummocks, lawns and hollows were also significantly different than control plots for RTS sites, where cover of hummocks decreased and hollows and lawns increased with fire at moderate and high levels of fire severity (Table 2.3). FSI correspondingly was significantly and negatively correlated with mean cover in hummock microtopography, with a positive correlation in hollows. Lawn cover was only moderately correlated with an increase in FSI.

Species richness and diversity

For BSB sites, fire significantly affected richness, where both low and moderate sites showed increases, relative to controls. Species diversity (H') had a significant increase with disturbance as well, but only with low severity fire. The mean pairwise Sørensen dissimilarity index for fire and control sites was $\beta=0.80$ and $\beta=0.73$, respectively. In assessing multiple-site dissimilarity for all pooled sites together, species turnover ($\beta_{SIM}=0.50$) contributed approximately 75% to total beta diversity ($\beta_{SOR}=0.67$), with species nestedness contributing a lesser amount ($\beta_{NES}=0.18$) across fire and controls. Only mean species richness had a significant correlation with FSI (Fig. 2.2h; Table 2.2).

While species richness for RTS sites was highly variable, ranging from 19 to 42 species, there was no clear relation to fire disturbance for mean species richness, nor was there a significant effect on species diversity (H'; Table 2.3). The mean pairwise Sørensen

dissimilarity index for fire and control sites was $\beta=0.61$ and $\beta=0.55$, respectively. However, in assessing multiple-site dissimilarity for all pooled sites together, it is possible to see that species turnover or replacement ($\beta_{SIM}=0.77$) contributed considerably to total beta diversity ($\beta_{SOR}=0.82$), with species nestedness only contributing a minor amount ($\beta_{NES}=0.04$) across fire and controls.

Ericaceous shrubs

For BSB plots, total ericaceous cover decreased at low and moderate levels of fire severity relative to controls; however, the main effect of disturbance severity was not found to be statistically significant (Table 2.2). There was also a weakly significant, negative correlation with FSI (Fig. 2.2f). Separate examinations of *Rhododendron* cover indicated this species had significantly lower cover for low severity plots compared to controls, whereas there was no difference between moderate severity plots and controls (Table 2.2). Given this divergence in cover as it relates to fire severity, *Rhododendron* cover was poorly correlated with FSI (Fig. 2.2e).

Post-fire ericaceous shrub cover was significantly lower than controls for both moderate and high levels of fire severity for RTS plots (Table 2.3) and had a strong negative correlation with FSI (Fig. 2.3d).

Discussion

Although the first requirement for natural conifer regeneration is a seed source, the results of this study underscore the importance of accounting for the impacts of fire severity as it affects seedbed conditions for sustaining lowland tree species.

The effect of fire was more acute for rich tamarack swamps (RTS) where there was little to no regeneration of conifer seedlings after the fire. Tamarack, a fire-sensitive species, can survive only the lowest severity fires (Duncan 1954; Busque and Arseneault 2005), which was evident in the extensive and almost complete mortality of tamarack observed at all levels of fire severity. The lack of mature, surviving tamarack was just one limiting factor in post-fire recruitment of this species, as it solely relies on seed from surviving trees to regenerate burned stands (Duncan 1959; Busque and Arseneault 2005; Johnson 1990; Uchytíl 1991). Given the limited dispersal distances associated with tamarack (\leq two mature tree heights; Duncan 1959; Johnson 1990), tamarack is not well adapted to rapidly reseeding large burns. The lack of seed sources in the areas examined in this study likely were exacerbated by the effects of unprecedented outbreaks of eastern larch beetle (McKee and Aukema 2015), which has caused extensive mortality of mature tamarack in areas adjacent to the fire boundaries.

Beyond the lack of mature tamarack seed sources, the influence of fire on seedbed conditions also likely contributed to the lack of tamarack recruitment across the communities examined. Burned organic surfaces have been cited as suitable for tamarack seedling establishment in other works (Uchytíl 1991); however, a large majority of the upper peat surface, or acrotelm, examined in this study was consumed or severely reduced by fire with only small areas of peat lawns rising above the water table. The negative impacts of these post-fire seedbed conditions on tamarack establishment may have been exacerbated by above-average levels of precipitation during the summer of data collection with water levels in hollows often >10 cm deep. This increase in the water table presumably limited the survival of tamarack seedlings, which cannot tolerate more

than a week of complete submergence (Duncan 1959). The loss of evapotranspiration and interception due to the mortality of overstory trees may have also enhanced the levels of standing water in these areas after the fire.

The dramatic shifts in vegetation conditions observed in these tamarack-dominated areas are consistent with general successional patterns reconstructed via palynological work in this region and across Canada (Janssen 1967; Griffen 1977; Kuhry et al. 1993). Earlier pollen analyses have shown that large-scale fire events have historically resulted in complete stand-level mortality in these minerotrophic systems generating concomitant ecosystem-level shifts in vascular plant and bryophytes species composition with a substantial amount of the upper peat layer removed (Griffen 1977; Heinselman 1963). With fire disturbance –including early peatland developmental succession, these communities have followed fairly predictable patterns according to pollen analyses. Tamarack-dominated peatland systems often shift back to open *Typha-Cyperaceae*-dominated wetlands with fire, where brown moss assemblages (e.g., *Drepanocladus aduncus*) as opposed to *Sphagnum* peat, regain dominance (Griffen 1977; Heinselman 1963; Kuhry 1994). The shift in vegetation observed –though not captured by differences in species richness or diversity (H') measures– for the tamarack swamps in the extent of the North Minnie fire appeared to follow this historical pattern. In all but the lowest levels of fire severity, the ground layer vegetation shifted to a *Typha* and graminoid-dominated wetland (Fig. 2.4), much like what previous studies have shown through pollen analyses. Additionally, with the removal of the upper *Sphagnum* peat surface and an increase in the water table, herbaceous species typical of marshes and wet meadows now dominate these sites.

Based on past paleoecological studies, these areas often proceed again towards a mesotrophic, treed environment primarily as a result of internal processes related to peat accumulation; however, these successional processes are dependent upon local hydrology and other allogenic factors such as landscape position (Janssens 1967; Kuhry et al. 1993; Bauer et al. 2003; Magnan et al. 2012). These developmental pathways have taken centuries, thus rapid stand regeneration in the North Minnie fire area is unlikely in the near term without direct seeding, once water levels recede. Additional research is needed to understand if these historical patterns of post-fire vegetation development will be realized in the face of current and future climate patterns and the recent, unprecedented outbreaks of the eastern larch beetle.

In contrast to the minerotrophic tamarack swamps, ombrotrophic bog communities are generally thought to be fairly resilient to fire. Changes in vegetation and microtopography are relatively short-lived, particularly following low severity fires where combustion does not entirely consume the peat horizon down to the water table (Wein 1983; Kuhry 1994; Magnan et al. 2012). Hummocks have been shown to have fairly quick returns to *S. fuscum* dominance post-fire, whereas hollows require more time to reach a community composition capable of significant peat accumulation (Benscoter et al. 2005). Disturbances such as wildfires also provide a mechanism for perpetuating microtopography where differential combustion during wildfire can reinforce or reinstate hollow elevations and microhabitat conditions (Benscoter et al. 2015).

The establishment of small-seeded species, such as black spruce, are dependent on these reduced hollows or fire-exposed seedbeds (Johnstone et al. 2004; Brown and Johnstone 2012) with numerous studies indicating that a considerable reduction in the

organic layer is essential for optimal recruitment (Chrosiewicz 1976; Zasada et al. 1983; Charron and Greene 2002; Jayen 2006; Johnstone and Chapin 2006; Greene et al. 2007). The results of this study were consistent with these previous findings, where black spruce seedling densities increased significantly in fire-affected portions of the study area compared with unburned forests (where regeneration through layering was the primary means of recruitment). Examination of the range of disturbance severity effects revealed that a threshold might exist in the degree to which increasing fire disturbance promotes post-fire recruitment success. In particular, while black spruce seedling recruitment generally increased with fire, densities peaked with lower levels of fire severity and then declined with increasing severity. This observed pattern was unexpected and the reasons are not entirely clear; however, the following sections outline several hypotheses to explain these observed relationships.

First, the observed patterns in post-fire black spruce densities may be related to the amount of available seed. Regeneration of this species after fire disturbance strongly depends on the size of the aerial seed bank and stand age and basal area at the time of fire have been positively correlated to the amount of seed released (Greene et al. 2004; Johnstone and Kasischke 2005; Johnstone et al. 2009; Viglas et al. 2013). While the typical growth form of black spruce, which has low-lying branches that connect the ground and canopy fuels can lead to fires that readily spread to crowns and cause high levels of stand mortality (Viereck 1983; Johnson 1992), there were only slight variations (none significantly different) in canopy burn severity across the sites. This canopy consumption was reflected in the fire severity index. Therefore, it is unlikely that higher canopy consumption for the moderate level fire areas affected the amount of aerial seed

available for post-fire regeneration and it is more likely that the relationship observed for spruce seedling densities was related to differences in seedbed conditions between low and moderate severity areas.

The majority of seedlings were observed germinating on exposed peat “lawns” that were approximately 10 cm or less above the water table (i.e., recently reduced peat layers as a result of fire). An increase in the percent cover of lawns was also significantly correlated with increasing fire severity; however, localized, deeper smoldering adjacent to black spruce tree boles and roots relative to other portions of the stand may have led to a higher frequency of unsuitable seedbeds for seedling germination, at least in the short-term (cf. Greene et al. 2007). These areas were largely under water due to high precipitation during the summer sampling period (Fig. 2.5), but are not likely the primary cause for the observed decline in seedlings.

Peat lawns also showed increases in the cover of the *Polytrichum strictum*. This colonizing moss species was significantly correlated, at least indirectly, with black spruce seedling increases, which is consistent with several other studies that found higher black spruce seedling regeneration associated with *Polytrichum* spp. (Aksamit and Irving 1983; Charron and Greene 2002; Greene et al. 2004; Jayen et al. 2004; Johnstone and Chapin 2006; Veilleux-Nolin and Payette 2012). The positive relationship between *P. strictum* and black spruce seedling recruitment could solely reflect that this moss species is coincident on more severely burned substrates where it is often a post-fire colonizing species. Past work, however, has found that *Polytrichum*, along with *Ceratodon purpureus* turfs, were associated with improved black spruce seedbed conditions, where they may provide partial insulation to new seedling roots and intercept rainfall and

moisture (Moul and Buell 1955; Ahlgren and Ahlgren 1960). Regardless, *Polytrichum* spp. may serve as a proxy for identifying microsites that have been reduced by fire where seedlings would have a greater level of germination success.

The negative response of black spruce seedlings to higher fire severity in the study area may largely be the result of an indirect effect caused by interactions between the ericaceous shrub *Rhododendron groenlandicum* and fire effects. *Rhododendron* has been frequently cited as an inhibiting factor in conifer seedling establishment across a wide range of forested peatland communities, either through allelopathic interactions or direct competition for nutrients (Inderjit and Mallik 1996; 1997; Mallik 2003; Hebert et al. 2010). In the black spruce bog sites, mean cover of *Rhododendron* was significantly lower with low severity fire plots relative to controls, whereas moderate fire severity plots had higher levels of *Rhododendron* dominance relative to unburned areas. The positive correlation with moderate fire severity for this species relative to other ericads is likely due to the greater rooting depths (mean depth was ca. 45cm) of *Rhododendron*, where deeper rhizomes are protected from damaging fire impacts (Flinn and Wein 1977). Regenerating stems of this ericad were mainly found resprouting on remnant, charred hummocks with black spruce seedlings more commonly occurring on the severely reduced lawns. *Rhododendron* was the only ericaceous species that exhibited this distinct pattern of increasing cover at greater levels of fire severity, while other species decreased. Thus, without further reduction in the organic layer, or surface peat, underground vegetative propagules of *Rhododendron* will continue to have a competitive advantage.

The threshold detected between increasing fire severity and black spruce densities is contrary to what has been described by several other studies, which have documented black spruce seedling densities generally increasing with higher fire severity (Chrosiewicz 1974; Charron and Greene 2002; Greene et al. 2004; Jayen 2006; Johnstone and Chapin 2006; Greene et al. 2007). The differences between the findings of this and other studies may be attributable to the dissimilarities between the sites examined. Previous work has largely focused on comparatively nutrient rich, southern boreal mixedwood forests, or sites with shallower pre-fire organic layers averaging 10 to 30 cm depths. The ombrotrophic bogs included in this study have estimated peat depths between 100-200 cm.

Conclusions and Management Implications

Early seedling regeneration is not always indicative of long-term patterns in forest succession; however, the patterns observed following the North Minnie fire suggest that the impacts of fire on conifer regeneration in these system is highly dependent on the community affected and level of fire severity. In tamarack-dominated systems, fire impacts were particularly pronounced with no detectable post-fire regeneration of tamarack seedlings and retrogression towards marsh-like conditions; an expected pattern based on paleoecological work in the region. Aerial seeding is frequently employed for reforesting lowland conifer communities and the lack of living, mature tamarack trees in the areas examined suggests that seeding may be an option to minimize how long these areas remain open, herbaceous communities. Although, the distribution of poor seedbed

conditions observed in these communities may limit how effective seeding will be for reforestation.

Maintaining viable populations of native species in light of climate change will continue to be ever more important, where managers will need to consider not only whether regenerating forests are meeting stocking level guidelines, but whether communities are maintaining resilient ecological processes. Thus, management goals for these regenerating tamarack communities should represent a longer timeframe that takes into consideration the evolutionary potential of species and ecosystem processes, which may or may not include aerial seeding.

If no management action is taken, these areas may remain open, wet meadow-marsh communities for extended periods based both on our understanding of the long-term ontogeny of vegetation patterns following disturbance in these ecosystems, as well as the prevalence of seedbed conditions unsuitable for tamarack establishment in the short-term. While this might be the preferred approach from an ecological process standpoint, given the understanding that successional trajectories will eventually lead to predictable reforestation of these areas over time, long range predications suggest that tamarack is expected to do very poorly under high emissions scenarios, to the point of declining significantly by the year 2100 due to a loss of suitable habitat in the state (Iverson et al. 2008). Climate change has been predicted to threaten biodiversity in a number of ways (IPCC 2007; Parmesan 2006), many of which are associated with the expected low adjustment rates of species to rapidly shifting habitat conditions, especially at range margins (Davis and Shaw 2001; Hulme 2005). Therefore, if the goal is to

attempt to circumvent short-term climate-driven extinction as a conservation priority, aerial seedling should be considered a management option.

The results of this work have implications for future conservation and management of these ecologically important forested peatland communities, particularly if the short-term patterns in seedling establishment continues to persist over time. With eastern larch beetle already causing extensive mortality across tamarack-dominated stands in the region, the added effects from increased fire frequency and severity could put the future of this community at risk, particularly if future drought conditions, such as those documented in the fall of the North Minnie fire, become more common.

Fire impacts on the black spruce communities were more nuanced with low burn severities promoting black spruce regeneration, whereas higher severity areas had lower seedling densities of this species. Increasing fire severity in the black spruce bog in the present study may have led to seedbed conditions that were too saturated for successful recruitment in hollows and too dry and competitive on more elevated hummocks dominated by *Rhododendron*.

The potential connection between seedling densities and the abundance of *Rhododendron* suggest that if fire is not of adequate intensity to set back competition (Mallik 2003), seedling density will continue to be lower than pre-fire stem densities, with some areas likely remaining open, ericaceous-dominated stands into the future (Viereck 1983; Girard and Payette et al. 2009). Thus, aerial seeding may be an option to improve black spruce tree densities due to the fact that there may be a high degree of spatial variability in regeneration establishment across these sites corresponding to the matrix of suitable seedbed conditions that were documented. Although, despite lower

regeneration for the moderate fire severity sites ($14,164 \text{ seedlings} \cdot \text{acre}^{-1}$), relative to low severity ($55,038 \text{ seedlings} \cdot \text{acre}^{-1}$), seedling densities currently meet stocking level guidelines in Minnesota provided there isn't significant mortality throughout the next four years. Current guidelines are 600 trees per acre at the seventh growing season (MN DNR 2008).

Environmental conditions are important drivers of stable successional cycles and fire impacts on successional trajectories are likely to be contingent on a number of landscape factors including abiotic conditions and prefire vegetation (Johnstone et al. 2010). Changing climate conditions and increases in drought severity and frequency may result in future fire events that could generate compound disturbance effects, disrupting autogenic successional processes in these lowland systems.

Given the short timeframe of this study and variability across the expansive peatlands that were sampled, the results of this work need to be interpreted with caution in terms of projecting long-term patterns in post-fire development to other northern conifer-dominated peatlands. In addition, seed dispersal can be highly variable over space and time (Johnstone et al. 2009); therefore an expanded network of sites is needed to adequately capture regeneration patterns in conjunction with spatial variation in peat consumption. Future monitoring of these areas will be critical for understanding the long-term impacts of fire disturbance to these communities, particularly because both tamarack and black spruce occur near the edge of their range in the Glacial Lake Agassiz lowlands and have little functional redundancy or opportunity for replacement from more southerly species, should climate change shift species suitable habitat conditions further north.

Figures

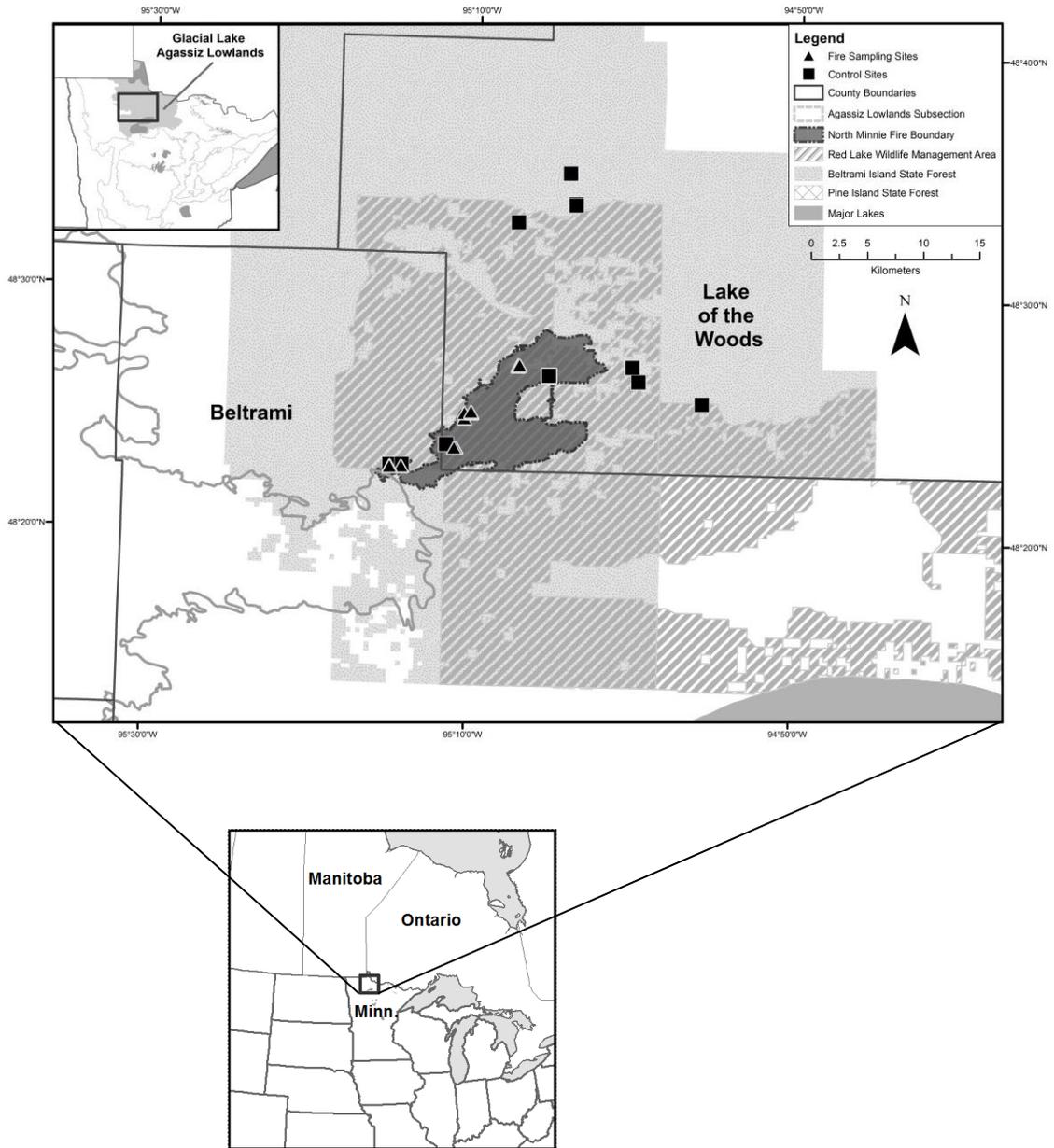


Fig. 2.1. Location of study area for fire and control plots in northern Minnesota, U.S.A. with the North Minnie fire area in dark grey.

Fig.2.2. Bivariate relationships between post-fire vegetation conditions and fire severity for BSB plots. Values in each panel represent the linear Spearman correlation coefficients where dashed lines are approximate general trend.

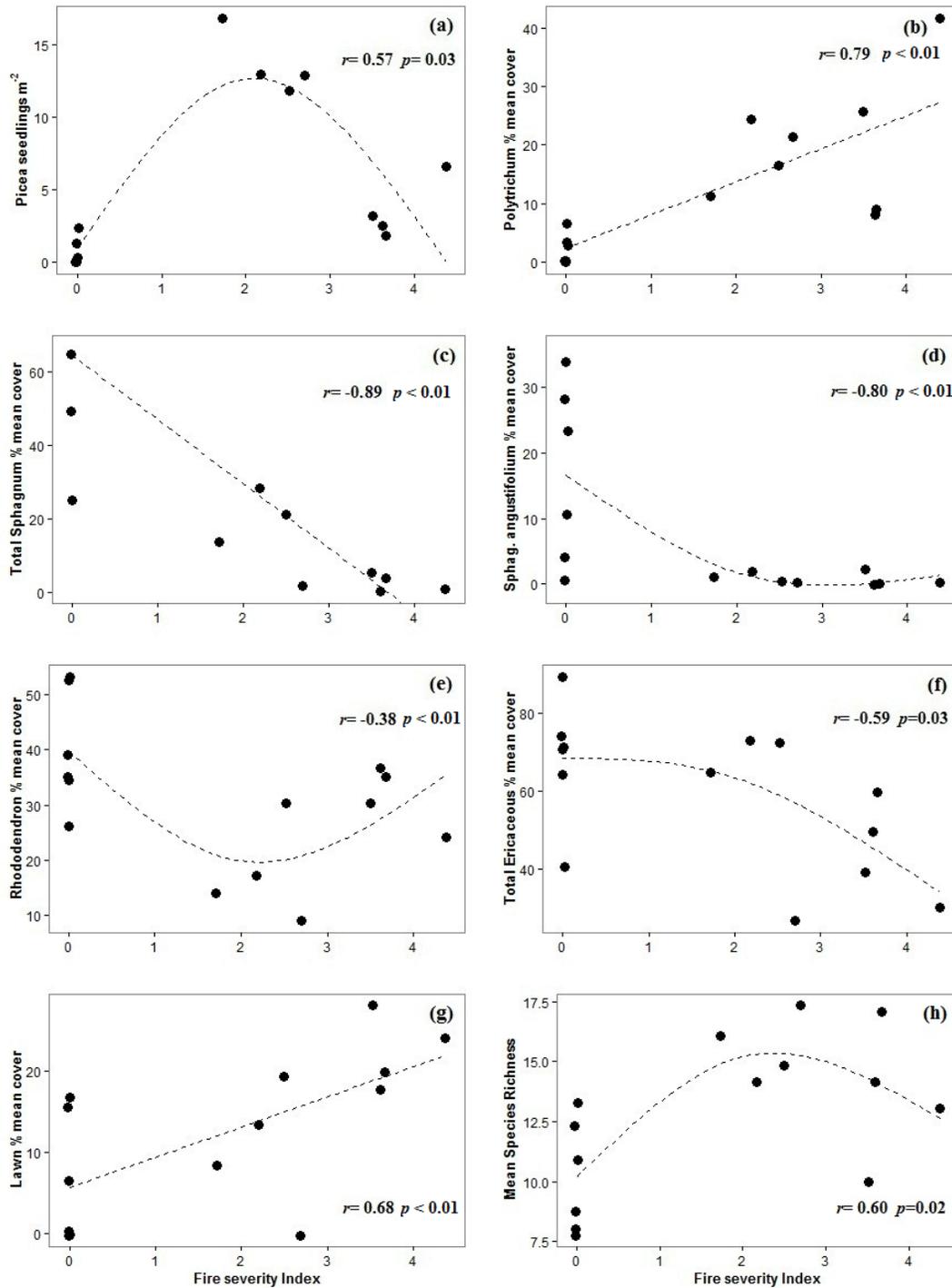


Fig.2.3. Bivariate relationships between post-fire vegetation conditions and fire severity for RTS plots. Values in each panel represent linear Spearman correlation coefficients where dashed lines are approximate general trend.

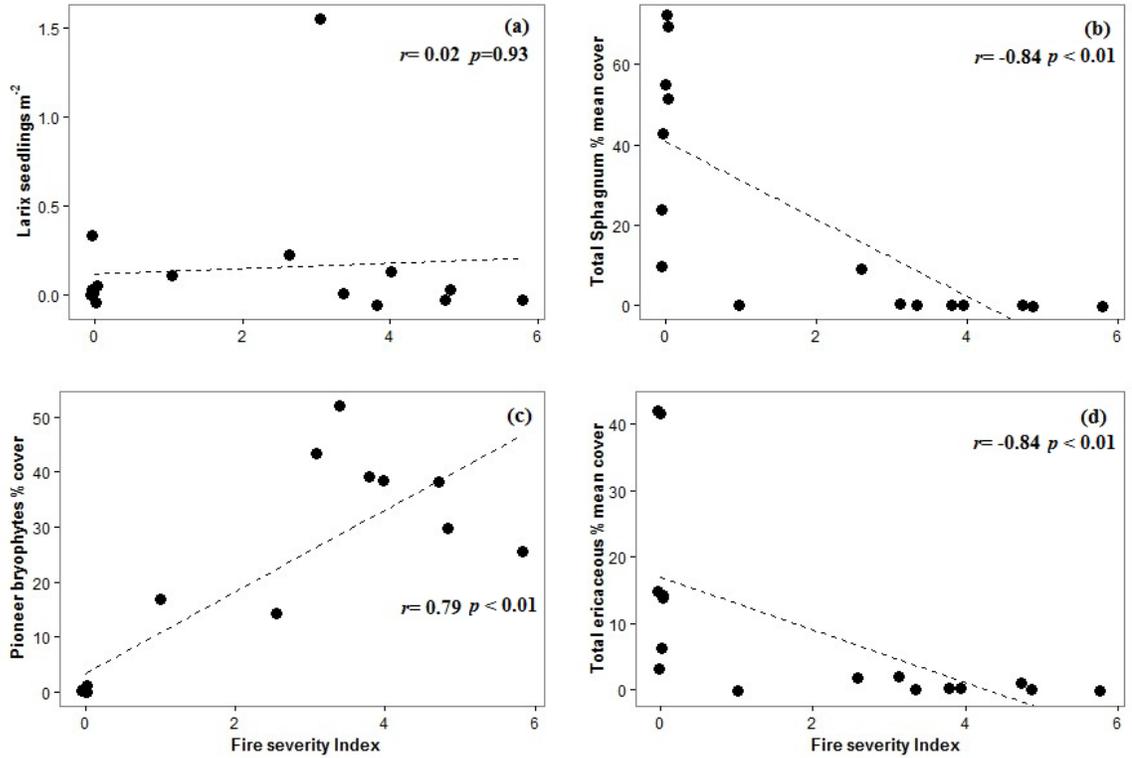


Fig. 2.4. High severity study site in rich tamarack swamp in North Minnie fire area, showing conversion to graminoid dominated vegetation.



Fig.2.5. Example of concentrated burning surrounding black spruce boles and main lateral roots in black spruce bog site.



Tables

Table 2.1. Number of plots across differing levels of burn severity in Northern Spruce Bogs (BSB) and Northern Rich Tamarack Swamps (RTS) in the Agassiz Lowlands Subsection, Minnesota.

NPC	Treatment Groups				Total
	Undisturbed (control)	Low severity	Mod Severity	High Severity	
BSB	6	4	4	-	14
RTS	7	2	3	4	16
Total Plots	13	6	7	4	30

Table 2.2. Mean cover (\pm S.E.) for the main response variables across different levels of disturbance severity for black spruce bog sites (BSB). F-statistic and p-values correspond to one-way ANOVA testing effect of disturbance severity on a given response variable. C=unburned control, L=low severity and M=moderate severity fire. Different letters indicate significant differences between disturbance treatments at $p < 0.1$ using Tukey's HSD. Bold p-values indicate a significant disturbance severity effect.

Response variable	C	L	M	F	p-value
<i>Picea mariana</i> seedling densities (stems \cdot m ⁻²)	0.7(0.4) ^a	13.6(1.1) ^b	3.5(1.1) ^c	12.57	<0.01
<i>Sphagnum magellanicum</i> cover (%)	28.0(8.5) ^a	10.1(3.0) ^{ab}	2.0(0.9) ^b	3.9	0.05
<i>Sphagnum angustifolium</i> cover (%)	16.8(5.6) ^a	0.88(0.4) ^b	0.6(0.6) ^b	7.7	0.01
<i>Sphagnum</i> sect. <i>acutifolium</i> cover (%)	22.4(8.1) ^a	5.4(3.1) ^{ab}	0.1(0.1) ^b	3.7	0.06
<i>Sphagnum</i> total cover (%)	67.2(10.7) ^a	16.5(5.7) ^b	2.7(1.3) ^b	22.8	<0.01
<i>Polytrichum</i> cover (%)	2.1(1.1) ^a	18.4(2.9) ^b	21.1(8.0) ^b	11.8	<0.01
Lawn cover (%)	6.5(3.3) ^a	10(4.1) ^a	22.5(2.4) ^b	5.9	0.02
Hummock cover (%)	80.0(5.0) ^a	78.3(6.5) ^a	69.6(6.2) ^a	0.9	0.40
Hollow cover (%)	10.7(4.7) ^a	11.5(4.1) ^a	8.3(3.8) ^a	1.4	0.30
Species richness	10.2(0.9) ^a	15.5(0.7) ^b	13.5(1.5) ^b	7.5	0.01
Shannon's diversity (H')	1.7(0.1) ^a	2.1(0.1) ^b	1.7(0.1) ^a	6.8	0.01
Total ericaceous species cover (%)	68.2(6.5) ^a	59.0(11.0) ^a	44.5(3.2) ^a	2.3	0.15
<i>Rhododendron</i> cover (%)	40.0(4.4) ^a	17.7(4.5) ^b	31.5(2.8) ^a	7.1	0.01

Table 2.3. Mean cover (\pm S.E.) for the main response variables across different levels of disturbance severity for rich tamarack swamp (RTS) communities. F-statistic and p-values correspond to one-way ANOVA testing effect of disturbance severity on a given response variable. C=unburned control, L=low severity, M=moderate severity, and H=high severity fire. Different letters indicate significant differences between disturbance treatments at $p < 0.1$ using Tukey's HSD. Bold p-values indicate a significant disturbance severity effect.

Response variable	C	L	M	H	F	p-value
<i>Larix laricina</i> seedlings (stems \cdot m ⁻²)	0.0(0) ^a	0.2(0) ^a	0.5(0.5) ^a	0.04(0.1) ^a	1.2	0.35
Total <i>Sphagnum</i> cover (%)	46.4(8.7) ^a	4.6(4.6) ^b	0.1(0.1) ^b	0.0(0) ^b	10.1	<0.01
Hummock cover (%)	73.2(4.8) ^a	39.2(14.1) ^b	21.9(13.1) ^b	18.3(3.6) ^b	15.7	<0.01
Hollow cover (%)	22.0(3.0) ^a	57.1(12.1) ^b	53.6(10.0) ^b	65.0(4.4) ^b	15.2	<0.01
Lawn cover (%)	0.5(0.5) ^a	2.9(2.9) ^{ab}	24.4(11.3) ^b	17.1(6.2) ^b	5.0	0.02
Colonizing bryophyte cover (%)	0.3(0.2) ^a	15.6(1.3) ^b	44.8(3.8) ^c	33.0(3.2) ^d	167.2	<0.01
Species Richness	26.7(2.7) ^a	25.0(4.0) ^a	27.3(4.2) ^a	27.2(1.5) ^a	0.3	0.80
Species Diversity (H')	2.5(0.2) ^a	2.5(0.0) ^a	2.6(0.2) ^a	2.8(0.1) ^a	0.1	0.95
Total ericaceous species cover (%)	19.4(6.0) ^a	0.9(0.9) ^{ab}	0.8(0.6) ^{ab}	0.3(0.3) ^b	3.7	0.04

Note: Post-fire colonizing bryophyte cover consisted of species that were present primarily post-fire including *Ceratodon purpureus*, *Funaria hygrometrica*, *Pohlia nutans*, *Polytrichum strictum*, and *Ptychostomum pseudotriquetrum* and the liverwort *Marchantia polymorpha*.

Chapter 3: Early response of ground layer plant communities to fire and harvesting disturbance in lowland conifer systems in northern Minnesota, USA

Introduction

Clearcutting-based silvicultural systems are widely applied in fire-dependent ecosystems around the globe (Gustafsson et al. 2012). In many cases, this management approach has been suggested as a surrogate for stand-replacing fire events and used as a general strategy for encouraging the regeneration of shade-intolerant tree species (Nyland 2007). Despite the similarities in levels of overstory mortality that may exist between stand-replacing fires and clear-cut harvests, there are key differences between these disturbances in terms of patterns in ground-layer disturbance and the distribution of live and dead-tree legacies that may generate diverging ecosystem responses (McRae 2001; Franklin et al. 2007; Fenton et al. 2013). As management approaches increasingly integrate an understanding of natural disturbance processes to satisfy ecologically-based objectives, a greater understanding of how stand-replacing harvests and natural disturbances affect ecosystem structure and composition is needed (Nguyen-Xuan 2000; Perera and Cui 2010).

The impacts of forest harvesting disturbance on ground-layer plant communities have been extensively studied, particularly in upland forest systems, given the disproportionate contribution of these communities to ecosystem-level diversity and their importance in affecting forest successional dynamics (Gilliam 2007). In most studies, patterns of post-harvest vegetation have highlighted a range of differences in post-logging communities when compared with undisturbed mature forest communities, which include a higher abundance of ruderal species and lower levels of vernal herbs and other

dispersal limited taxa relative to unharvested areas (Duguid and Ashton 2013). Yet, there is still little known about how post-disturbance patterns in ground-layer plant communities differ between clearcutting and stand-replacing fire in peatland forest systems. Given the projected increases in the frequency of fire with climate change and continued reliance on clear-cutting-based harvesting regimes in many ecosystems, there is a need for evaluations of the long-term impacts of these disturbances on the resilience and biodiversity of the wide array of forest ecosystem types managed for wood products (Brumelis and Carleton 1988; Dussart and Payette 2002; Bouchard and Pothier 2011; Fenton et al. 2013), including the extensive forested peatlands in North America.

Black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) and tamarack (*Larix laricina* (Du Roi) K. Koch)-dominated peatlands of the upper Great Lakes region, USA are relatively unique in regards to the differences in the nature of the prevailing natural disturbance regime for these systems and the silvicultural approaches used for their management. Return intervals for catastrophic, stand replacing fires range from 400 years for tamarack swamps up to 1000 years or more for black spruce bogs (MN DNR 2003); however, clearcutting-based management, the typical method used for harvesting these systems, is on a much shorter rotation of 80-120 years for these lowland systems in Minnesota, and elsewhere throughout the Midwest (Johnston 1977; MNDNR 1997, 2008; WDNR 2006). Both fire and harvest have been shown to have clear differences in the level soil disturbance (cf. Roberts 2004), and as such, there is the potential for divergent responses in regards to post-disturbance patterns of vegetation recovery. In particular, during wildfire there may be considerable spatial differences in fire behavior as a result

of moisture gradients in hummocks and hollows, but also the degree and depth of burning can be variable where fire can readily smolder for days in organic peat soils (Rein et al. 2008). These fire-induced effects in peatlands can increase pH and mineralization rates in areas more severely burned (Dyrness and Norum 1983; McRae 2001). In contrast, while harvesting disturbance can also be varied with respect to the upper peat surface, impact to the cover and abundance of moss species through compaction or removal, can affect soil temperature and seedling survival rates differently than disturbance from fire (Jeglum 1981; LaFleur et al. 2011). Harvesting also typically has less impact on nutrient cycling than wildfire, where logging largely removes macronutrients contained in the tree biomass (Brumelis and Carleton 1989; McRae et al. 2001; Roberts 2004; Kemball et al. 2005).

An important additional consideration in examining disturbance impacts on lowland conifer communities is the influence of disturbance processes on the presence of ericaceous shrubs that may impact tree regeneration through allelochemical reactions and nutrient competition (Mallik 1995; Inderjit and Mallik 1996; Mallik 2003). Ericaceous shrubs, particularly Labrador tea (*Rhododendron groenlandicum* [Oeder] Kron & Judd; hereafter referred to as *Rhododendron*), can regenerate vigorously by vegetative methods from belowground root rhizomes that survive harvest (Viereck 1983; Mallik 2003). Current harvest methods that minimize soil disturbance can also encourage similar vigorous vegetative regrowth of ericaceous plants (Mallik 2003; Hebert 2010; Lafleur et al. 2011) with several works documenting increases in ericaceous cover following harvesting in black spruce communities (Groot 1996; Dussart and Payette 2002). Given

the comparatively low levels of soil disturbance associated with winter harvesting relative to stand-replacing fire, these post-harvest areas generally lack the suitable seedbeds for conifer regeneration that fire creates, i.e., reduced peat microtopography and ericaceous competition (Malik 2003). A continued examination of the impacts of harvesting on ground-layer communities and regeneration dynamics is critical to verify that these activities maintain the disturbance-related processes and dynamics that are central to securing adequate tree regeneration following harvests (Nguyen-Xuan 2000; Perera and Cui 2010).

To compare post-disturbance plant community and regeneration patterns between fire and harvest, this study takes advantage of a rare fire event that occurred following severe drought conditions in September of 2012 in northern Minnesota, USA. The North Minnie fire burned over 10,000 ha and resulted in a range of fire severities across a mosaic of peatland communities providing a unique opportunity to increase our understanding of wildfire in lowland conifer peatlands. This region also represents the southern-most extent for boreal peatlands in North America and is uniquely situated to examine the impacts of fire and forest harvesting due to the fact that these ecosystems are projected to be highly vulnerable to changes in future climate and disturbance regimes (Brown and Johnstone 2012).

The objectives of this study were to quantify differences in seedling regeneration and seedbed quality, as well as understory plant community composition, one and half years after fire and clearcut harvesting disturbance in two forested peatland types in northern Minnesota, USA. It is hypothesized that many of the compositional differences

following these two disturbance types are related to differences in ground layer disturbance and resultant microsite conditions. By relating the early vegetation development observed following wildfires and clearcut harvesting to the level of disturbance, we sought to address the following questions: 1) does disturbance severity, as well as type, affect early regeneration success of conifer seedlings in minerotrophic tamarack swamps and ombrotrophic black spruce bogs; 2) does disturbance type affect composition of ground layer vascular and nonvascular plant species in these systems, and 3) how does vegetation response to disturbance vary between tamarack swamps and black spruce bogs?

Methods

Study Area

The study area was located primarily in the Red Lake Wildlife Management Area (WMA), with additional sites in Pine Island and Beltrami Island State Forests in northern, Minnesota, USA (Fig. 3.1). This region was formerly occupied by Glacial Lake Agassiz and as such is characterized by flat (topographic relief is less than 15 m), poorly drained soils of lacustrine origin that have developed through paludification into some of the most extensive peatlands in the lower United States. Climate is mid-continental and dominated by cool, humid air masses from the north; however, the western and southern edge of this region coincides closely with a change from a climate of slight moisture excess to one of substantial deficits (Heinselman 1961). This steep climatic gradient marks what is known as the prairie-forest border, with moisture quickly becoming

insufficient to support forest growth to the west as a result of dry, western air masses that result in frequent summer droughts (Glaser 1992).

Mean annual precipitation for the region is 66 cm, with approximately 70% occurring during the growing season. In 2012, the year of the North Minnie Fire, precipitation for the region prior to the fire (Oct. 2011-Sept. 2012) was approximately 41 cm below average (Minnesota Climatology Working Group; <http://climate.umn.edu>). The growing season is short, generally 98 to 111 days. The normal mean temperatures for summer months (June-August) range from 15 to 20° C with winter months averaging -20 to -7° C (NOAA Climate Monitoring for 1971-2015; <http://ncdc.noaa.gov/cag/time-series>).

Study Sites

This study was replicated across several sites in two forested peatland communities—[nutrient poor] Northern Spruce Bog (hereafter referred to as “black spruce bogs” or BSB) and Northern [nutrient] Rich Tamarack Swamp (hereafter referred to as “rich tamarack swamps” or RTS). These communities were selected for the study as they represented the two plant communities most affected by the North Minnie wildfire as well as the larger forested Agassiz Lowlands landscape and are commonly managed for forest products. Plant community classification followed the Minnesota Department of Natural Resources Laurentian Mixed Forest Field Guide to Native Plant Communities (MN DNR 2003). Five disturbance conditions were sampled across these communities (low, moderate, and high fire severity, harvested and undisturbed; Table 3.1).

Plot Selection

Initial selection of sites representing different fire severity categories was aided using a differenced Normalized Burn Ratio map of the study area (dNBR; Banskota and Falkowski, unpublished data 2013). The dNBR map was generated based on Landsat-derived estimates of burn severity for the extent of the fire using bands 4 and 7 from two LANDSAT Thematic Mapper images (pre-fire and 1 year post-fire), which was transformed to relate it to four burn categories: 1) unchanged (minimal or no visible effect of fire), 2) low-severity, 3) moderate-severity, and 4) high-severity (Key and Benson 2006; Soverel et al. 2010). For further discussion of how categories of fire severity were identified and verified in the field for both BSB and RTS sites, see Ch. 2.

Harvested study sites consisted of three black spruce clearcuts and four tamarack swamp clearcuts in the Beltrami Island and Pine Island State Forests. The BSB harvest sites ranged in size from 8.5 to 22 ha and had a mean stand age of 131 years prior to harvest. RTS harvest sites ranged from 8 to 29 ha with a mean stand age of 80 years prior to harvest. These management regimes are characteristic of the general approach in terms of rotation age for lowland conifer communities in northern Minnesota. Average harvest size is suggested to be less than 40 ha for both black spruce and tamarack stands MN DNR (2013a); however, where eastern dwarf mistletoe (*Arceuthobium pusillum*) is present, clearcuts can be greater than 120 ha, which is more the case given increases in this serious patristic disease of black spruce in northern Minnesota. Stand ages were determined from forest inventory data from the Minnesota DNR.

Harvested sites were initially selected based on the following criteria: year of harvest concurrent with the North Minnie Fire (or at least the winter preceding or following the fire), no aerial seeding applied (to allow for evaluation of natural regeneration dynamics), and accessibility. These requirements resulted in a fairly small list of harvests to choose from, particularly for BSB, as most lowland conifer clearcuts in the region are aerially seeded after harvest. In view of the fact that the harvested sites were not experimentally designed treatments, but rather actual operations carried out by contract loggers for the MN DNR, they represent a range of logging operations under a variety of conditions; however, all were clearcut operations harvested during winter months. Pre-harvest stand age, basal area, and site conditions were determined from forest inventory data and aerial photo interpretation. Community classification was confirmed in the field by assessing adjacent uncut stands.

Undisturbed control plots for both the BSB and RTS communities were identified from neighboring areas of the North Minnie fire within Beltrami Island State Forest and Red Lake WMA based on previous field knowledge and remotely sensed data. After plant communities representative of burned and harvested areas were identified, GIS was used to randomly select plot locations within an identified stand. Randomly selected sites were followed by field verification to confirm that community type, age, and basal area were similar to stand characteristics within the fire and harvest areas prior to data collection.

It is recognized that the lack of information on vegetation abundance and composition prior to disturbance precludes making any direct inferences on change as a

result of disturbance, and it is necessary to support the assumption that differences observed after disturbance are a direct result of the effects of fire. An attempt was made to account for this by selecting undisturbed forests found on sites with similar stand ages, overstory tree stocking, peat depth, microtopography and canopy composition to the sampled burned and harvested sites.

Sampling design

Sampling took place June 07 through August 28, 2014 during the second growing season following the North Minnie Fire. Each site was sampled using a series of 11.3 m (400 m²) fixed-radius plots, initially located with a random point generator in ArcGIS. Individual plots were located at least 90 m from the impacts of roads or ditches and were required to be at least 60 m away from another plot. Each plot was marked permanently with a 1.5 m length of PVC pipe in the center, inserted approximately 1 m into the peat substrate. Each burn severity had 2 plots per site. Undisturbed controls and harvested sites had 1-3 plots per site depending on size of the sampling site.

To evaluate tree regeneration, ericaceous shrub abundance and seedbed condition (remaining microtopography), six-1m² quadrats were placed along one of three transects at 4 and 10 meters, emanating from plot center at azimuths of 0, 120, and 240°. Conifer seedlings and dominant, upright ericaceous shrubs (i.e., not prostrate as in *Vaccinium oxycoccos* L.) were identified to species and tallied by height class (0-15cm; 15-100cm; 100-137cm). Spruce seedlings and saplings were noted as either regenerated through layering or germination via seed. Total projected foliage cover was also visually estimated for all individual herbaceous plant species to the nearest 1% on a scale of 1-

100%. Additional measurements characterizing the substrate and microtopography of each quadrat were made to the nearest 5%, where the proportion occupied by hummock, hollow, or lawn was estimated. Hummocks were defined as being raised peat mounds that were 20-50 cm above the lowest surface level, with lawns being distinct, flatter areas 5-20 cm above the water table, and hollows distinguishable as depressions forming below the latter (see Rydin and Jeglum 2013).

Each quadrat also included a nested 0.5 m² plot, where bryophyte species were identified and their percent cover was visually estimated. A smaller nested plot was chosen to measure lichens and bryophytes, due to the fact that different vegetation types require different quadrat sizes and a smaller size has been shown to be appropriate for these smaller, non-vascular species (Daubenmire 1968; Grieg-Smith 1983; McCune and Lesica 1992). Measures of cover in each of the six quadrats and nested plots were averaged to the plot level.

Statistical Analysis

Mixed model analysis of variance (ANOVA) was used to examine the impact of disturbance type on total ericaceous shrub abundance, vascular plant species richness (number of species per plot) and diversity (Shannon–Wiener index, H'), cover of specific bryophyte species or groups, and microtopographical conditions. The impact of disturbance type on *Rhododendron* abundance was analyzed in addition to examining total ericaceous cover for BSB sites given that this species has been suggested as the cause for reduced black spruce regeneration due to growth inhibition through competition and allelopathy. For RTS sites, the decision was made to analyze all ericaceous species

together due to the fact that while *Rhododendron* makes up the vast majority of this total cover, this species does not occur at same level of abundance typical of BSB sites.

All species in the *Sphagnum* sect. *Acutifolia* were grouped together for ANOVAs for the BSB site as the species encountered largely consisted of hummock-forming *Sphagna*, several of which are notoriously difficult to tell apart without further microscopic cellular differentiation. For the RTS sites, where diversity of *Sphagnum* species was much higher and the abundance of any one species was fairly low, all *Sphagnum* species were grouped together.

ANOVA was also used to examine the impact of general disturbance categories (i.e., control, fire, harvest) on the percent cover of different functional groups in the BSB and RTS communities. The six groups used for these analyses were ericaceous evergreen shrubs, deciduous trees and shrubs, coniferous trees, graminoids, forbs, and bryophytes. Ferns were also included as a separate group, but only for the RTS analysis due to the fact that fern cover was notable only for this community and not for BSB.

Analyses of conifer seedling count data were conducted with generalized linear models (GLMs) with a negative binomial distribution and a logarithmic link function to determine the effect of disturbance on seedling density. A GLM was used for analyzing seedling data separately from the above response variables because these models have been shown to adequately handle count data, which often have several zero observations recorded and typically do not conform to a normal distribution (Zuur et al. 2009; O'Hara and Kotze 2010).

Disturbance type was treated as a fixed variable and site was treated as a random variable for all models. In cases where significant effects were detected, post-hoc Tukey's honest significant difference tests were used for pairwise comparisons among disturbance levels with $p < 0.10$ considered significant. This significance level was used for all analyses given the study was largely observational and had a relatively small number of replications in each disturbance condition. When assumptions of normality and constant variance were not met, data were transformed using a square root transformation (this excludes the seedling count data, because non-normality was addressed using a GLM model – see above discussion). All analyses were performed in R version 3.1.2 (R Core Team 2014).

Beta diversity (β) was assessed for vascular plants using a multiple-site dissimilarity measure. This measure partitions β into its spatial turnover and nestedness components following Baselga (2010), where spatial turnover or species replacement is the loss of a species followed by the gain of another and nestedness being a pattern where the species present at species-poor sites form subsets of the species in species-rich sites (Baselga 2010; Ulrich and Almeida-Neto 2012). In short, this method relies on the fact that Sørensen (β_{SOR}) and Simpson (β_{SIM}) dissimilarities are equal in the absence of nestedness (β_{NES}), so their difference is a measure of the nestedness component, which is derived from pairwise dissimilarity matrices of beta diversity (Baselga 2010). Thus, overall beta diversity (Sørensen dissimilarity) is equal to the sum of Simpson dissimilarity (turnover component of Sørensen dissimilarity) and nestedness measures ($\beta_{\text{SOR}} = \beta_{\text{NES}} + \beta_{\text{SIM}}$; Baselga and Orme 2012). The function 'betadiver' in the R package

'vegan' (Oksanen et al. 2015; R Development Core Team 2014) was used to compute mean beta diversity indices from pairwise Sørensen dissimilarity matrices, as well as the R package 'betapart' (Baselga et al. 2013), which includes the functions to compute the partitioned, multiple-site Sørensen dissimilarity index.

Non-metric multidimensional scaling (NMS) was used to examine the variation in community composition within and among the main disturbance categories (undisturbed, fire, harvest) for all ground layer species (including bryophytes) for both forest community types (i.e., black spruce bogs and rich tamarack swamps). NMS was performed using PC-ORD version 6.0 (McCune and Mefford 2006), and optimal dimensionality for the ordination was based on the number of dimensions with the lowest stress (i.e., smallest departure from monotonicity in the relationship between distance in original ordination space and distance in reduced ordination space (McCune and Grace 2002). Dissimilarity was assessed using Sørensen's distance index. For this study, the minimum stress configuration included three axes for the BSB plots (final stress = 11.9, instability <0.00001) and three axes for the RTS plots (final stress = 9.2, instability <0.00).

Multi-response permutation procedures (MRPP) in PC-ORD were used to test whether there was a significant difference between disturbance categories based on species composition. This test provides a P-value, which is a probability measure of significant differences between groups, and an A-value for within-group agreement ranging from 1 (total within-group agreement) to 0 (heterogeneity within groups equals expectations from chance; McCune and Grace 2002). Sørensen's distance metrics were

also used for MRPP, which was followed by indicator species analysis (ISA; Dufrêne and Legendre 1997) to determine which species were significantly associated with a particular disturbance category. This test compares the relative frequency of occurrence and abundance of species in different disturbance categories and identifies species that vary more between categories than would be expected by chance (Dufrêne and Legendre 1997). ISA indicator values (IV) range from 0% (complete absence) to 100% (perfect fidelity; McCune and Grace 2002). All species with significant indicator values ($p < 0.10$) were determined by using a Monte Carlo test with 1000 randomizations. In all of the analyses (NMS, MMRP and ISA), species present in less than 5% of plots were not included and data for percent cover was relativized by species total.

Results

Seedling Regeneration

For black spruce bog (BSB) communities, the abundance of spruce seedlings (stems·m⁻²) was significantly impacted by disturbance type, with seedling densities generally higher in low severity fire plots compared to moderate levels of fire as well as harvest and undisturbed control plots (Fig. 3.2a; Table 3.2). Harvested plots were no different than controls for seedling regeneration. Additionally, both low and moderate fire severity categories had significantly greater densities of trembling aspen (*Populus tremuloides*) seedlings in the 0-15 cm height class, relative to harvest and undisturbed controls, which both had mean densities close to zero (Table 3.3).

For the rich tamarack swamp sites (RTS), only harvest disturbance had a significant increase in seedling densities (stems·m⁻²), with densities in this disturbance type significantly greater than all other disturbance categories (2 stems·m⁻² in contrast to zero for all other categories). All remaining disturbance categories were not significantly different from each other and had mean seedling counts closer to zero (Fig. 3.2b; Table 3.3). Similar to the BSB sites, aspen seedlings also increased significantly for RTS sites compared to undisturbed and harvested plots; however, significant increases were only found for the moderate and high severity levels of fire (Table 3.3).

Bryophytes and microtopography

Total *Sphagnum* cover in the BSB sites was significantly reduced by fire at both low and moderate fire severities relative to undisturbed controls and harvested plots. This overall reduction in cover was considerably greater for moderate fire severity plots (Table 3.2). In examining individual species or group cover, *Sphagnum angustifolium*, a species primarily of hollows, had the most significant differences across categories with reductions in cover at both the low and moderate fire severity level. Undisturbed controls and harvested plots had no detectable differences in *S. angustifolium* cover. The hummock-forming group *Sphagnum* sect. *Acutifolium* had reductions in cover with fire, primarily with moderate fire severity, but also with harvest which was found to not be statistically different (Table 3.2). Cover for *Sphagnum magellanicum*, a species characteristic of lower hummocks and lawns, had significantly lower cover primarily at the moderate fire severity as well, compared to undisturbed controls and harvests (Table

3.2). In contrast to *Sphagnum* cover, *Polytrichum strictum*, a post-fire colonizing moss species, had significantly increased cover relative to controls and harvested plots for the BSB sites (Table 3.2). There was no difference in cover of *P. strictum* between harvested and control areas.

Disturbance also influenced moss community structure at RTS sites, with significant reductions in total mean cover of *Sphagnum* at moderate and high levels of fire severity. Low fire and harvest plots were not statistically different from one another, however, they were both lower than undisturbed controls (Table 3.3). Post-fire bryophyte cover increased significantly in moderate and high fire severity plots compared with controls or harvested plots (Table 3.3). These post-fire mosses consisted of *Ceratodon purpureus*, *Funaria hygrometrica* Hedwig, *Pohlia nutans* (Hedwig) Lindberg, *Polytrichum strictum*, and *Ptychostomum pseudotriquetrum* that were mostly colonizing exposed root surfaces. Additionally, the liverwort *Marchantia polymorpha* L., which was also included in this group of post-fire bryophytes, was largely restricted to low peat substrates that scarcely rose above the water table.

Microtopography was not significantly different across disturbance categories for BSB sites, due in large part to substantial variation in documented cover of hummocks, hollows and lawns (Table 3.2).

Conversely, microtopographic features for the RTS sites were significantly impacted by disturbance with fire reducing total cover of hummocks significantly, relative to controls and harvests. There was no difference in cover of hummocks between fire severity categories or between harvest and control plots. Hollows were significantly

expanded by fire (or rather, more were created) with the loss of hummocks relative to controls and harvests. All fire severity categories were similar in mean cover of hollows, as were controls and harvested plots. Lastly, the creation of lawns as a result of fire was most pronounced at moderate and high levels of fire severity and significantly higher than all other disturbance categories (Table 3.3).

Ericaceous shrubs

Total combined ericaceous cover for the BSB sites was not significantly affected by disturbance; however, in examining the cover of *Rhododendron* separately, cover for this species was significantly lower with fire, but only with the low fire severity category. This reduction was not statistically different from harvested plots (Table 3.2). For RTS sites, fire and harvest significantly reduced the total mean ericaceous cover at all levels of fire severity, relative to controls. There were no differences between fire categories and harvest plots in terms of ericaceous cover (Table 3.3).

Species richness and diversity

The effect of disturbance on vascular and nonvascular species richness and diversity (Shannon–Wiener index, H') exhibited opposing responses, for both forest types. Significant differences were found for BSB sites for both vascular plant species richness and diversity (H'), where low severity fire showed slight increases over undisturbed controls, and in the case of species richness, harvest also had a slight increase over controls (Table 3.2). The mean pairwise Sørensen dissimilarity index for fire,

harvest and control sites was $\beta=0.80$, $\beta=0.65$, and $\beta=0.73$, respectively. Moreover, species turnover ($\beta_{SIM}=0.74$) contributed approximately 94% of total beta diversity ($\beta_{SOR}=0.79$) for multiple-site dissimilarity when fire, harvest and control sites were pooled together, with species nestedness contributing a lesser amount ($\beta_{NES}=0.05$). The greater turnover in species replacement occurred between controls and fire sites where species turnover accounted for 94% ($\beta_{SOR}=0.79$, $\beta_{SIM}=0.74$), as opposed to controls and harvest sites which had 90% turnover ($\beta_{SOR}=0.72$, $\beta_{SIM}=0.65$).

Bryophyte species richness and diversity (H') for BSB sites, on the other hand, did not appear to be affected by disturbance, as no significant differences were found (Table 3.2).

A similar, but reverse trend was found for the RTS sites, where no differences were detected between vascular plant species for both richness and diversity (H') between disturbance groups (Table 3.3). While species richness for RTS sites was highly variable, ranging from 19 to 42 species, there was no clear relation to disturbance for mean species richness. The mean pairwise Sørensen dissimilarity index for fire, harvest and control sites was $\beta=0.61$, $\beta=0.59$, and $\beta=0.55$, respectively.

However, in assessing multiple-site dissimilarity for all pooled sites together, it was possible to see that species turnover ($\beta_{SIM}=0.81$) contributed considerably to total beta diversity ($\beta_{SOR}=0.85$), with species nestedness only contributing a minor amount ($\beta_{NES}=0.04$) for fire, harvest, and control sites. Moreover, if considering only control and fire sites, turnover ($\beta_{SIM}=0.77$) contributed to 95% of the overall beta diversity ($\beta_{SOR}=0.82$), with species nestedness again only contributing a minor amount

($\beta_{\text{NES}}=0.04$). Similarly, in considering turnover across controls and harvest sites, 91% of the overall beta diversity ($\beta_{\text{SOR}}=0.78$) is from species turnover ($\beta_{\text{SIM}}=0.71$).

In contrast, significant differences were detected for bryophytes species richness and diversity (H'), with fire and harvest disturbance having the most notable reductions in mean cover for species richness (Table 3.3).

Species functional group cover

For BSB sites, significant differences were found across the main disturbance categories (undisturbed, fire and harvest) for total cover of graminoids (ANOVA, $F=3.7$, $p\text{-value}=0.05$) and bryophytes (ANOVA, $F=36.7$, $p\text{-value} < 0.01$; Fig. 3.3a). For graminoids, harvested sites had significantly higher cover relative to fire sites with bryophyte cover significantly higher for undisturbed controls. Bryophyte cover was lowest for fire sites. The main effect of disturbance was not found to be significant for ericaceous and deciduous shrubs, conifer or forb cover.

RTS sites had significant differences across disturbance categories for several functional groups (Fig. 3.3b). Total mean cover of ericaceous cover was lowest for fire disturbance, where mean cover was near zero compared to approximately 20% cover for controls ($F=21.3$, $p\text{-value} < 0.01$). Mean graminoid cover was also significantly affected by disturbance with mean cover for harvested plots significantly higher than fire and controls ($F=12.7$, $p\text{-value} < 0.01$). For the harvested plots, graminoids were largely dominated by *Carex disperma*, *C. stricta* and *Calamagrostis canadensis*, whereas fire plots were dominated by *Carex lacustris* and *Carex chordorrhiza*. Mean cover for deciduous shrubs and seedlings were significantly higher for harvested plots relative to

controls and fire disturbance ($F=8.9$, $p\text{-value}=0.01$). Deciduous species for harvested plots were dominated primarily by speckled alder (*Alnus incana*) and a diverse array of willow species (*Salix* spp.), as well as raspberries (*Rubus idaeus*). The cover of forbs was significantly higher for harvest and fire plots relative to controls ($F=8.4$, $p\text{-value}=0.01$), the latter reflecting the high abundance of cattails (*Typha* spp.). Bryophyte cover was also significantly different across disturbance groups, with undisturbed controls having the highest mean cover ($F=7.7$, $p\text{-value}=0.01$), which was largely dominated by *Sphagnum*. Harvest and fire were not different from one another. The main effect of disturbance was not found to be significant for either fern or conifer cover.

Understory community composition

The composition of post-disturbance understory species communities varied significantly among disturbance categories for BSB (MRPP A = 0.12, $P<0.01$). These differences were also reflected in the distribution of sample plots in ordination space within the NMS analysis for BSB. These disturbance gradients were captured by axis one and two of the ordination, which accounted for 42% and 27% of the total variance (77%), respectively, in the understory community explained by the three-dimensional NMS solution (Fig. 3.4a).

Plots on the positive end of axis one for BSB sites, were strongly associated with harvested plots and had slight, but significant, increases in species richness. This area of the ordination was correlated with vascular plant species such as willow-herbs (*Epilobium* spp.), diamond-leaved willow (*Salix planifolia*) and the cottongrass

Eriophorum angustifolium. The negative end of axis one (i.e., undisturbed controls) was correlated with a higher abundance of advance regeneration of *Picea mariana*, ericaceous species such as blueberry (*Vaccinium angustifolium*) and *Rhododendron* as well as the moss *Dicranum polysetum* and the feathermoss *Ptilidium crista-castrensis* (Fig. 3.4a, also see Appendix B).

A discrete cluster of fire plots was associated with the negative end of axis two, which was correlated with increased fire severity, whereas harvest and control plots defined the positive end of the axis. A higher abundance of non-hummock forming species such as *Sphagnum angustifolium* and *S. magellanicum* were more associated with portions of the ordination defined by harvested and control plots. Where harvest plots overlapped with controls, an increased frequency and abundance of *Rhododendron* was observed. Species that differentiated either end of axis two were primarily bryophytes with *Polytrichum strictum* and other post-fire mosses such as *Ceratodon purpureus* associated with the negative portion of the axis (i.e., fire disturbance) and the feathermoss *Pleurozium schreberi* more strongly associated with the positive end (i.e., harvests and controls; Fig. 3.4a). See Appendix B for species correlations with NMS axes 1 and 2.

Several species were identified as significant indicators of a given disturbance category for BSB (per Indicator Species Analysis, $p < 0.1$; Table 3.4a). Graminoid species, including the sedges *Carex trisperma*, *C. chordorrhiza* and the cottongrass *Eriophorum angustifolium*, and the bryophyte *Sphagnum angustifolium* were more associated with harvest disturbance. Species associated with fire disturbance, including the bryophyte *Polytrichum strictum*, were strong indicators for the fire disturbance group. Vascular

plant species associated with fire disturbance were trembling aspen and bog rosemary (*Andromeda polifolia*). Undisturbed plots were more associated with hummock-forming *Sphagnum* species (*S. sect. Acutifolium*) as well as ericaceous species such as *Rhododendron* and lingonberry (*Vaccinium vitis-idaeus*).

For the RTS sites, the post-disturbance understory species composition was even more discrete clustered than BSB disturbance groups (MRPP A = 0.22, $P < 0.01$), a result which was evident in the NMS ordination of community composition for disturbance groups (Fig. 3.4b). A distinct disturbance gradient was also exhibited primarily along axis one, which accounted for 40% of the total variance (77%) explained by the three-dimensional NMS solution. The distribution of plots along axis one represented a distinct disturbance gradient ranging from fire plots in the positive end of the axis to control plots in the negative end of the axis. This axis was strongly and negatively correlated with increased disturbance severity and an increase in hollows and exposed, or combusted peat. Species associated with the positive end of axis one consisted of trembling aspen seedlings, post-fire colonizing bryophytes, and cattails. The negative portion of axis one was significantly correlated with higher covers of hummock microtopography and *Sphagnum* spp., as well as higher cover of ericaceous shrubs, particularly *Rhododendron*. Other species associated with this portion of the first axis were the herbaceous species one-sided pyrola (*Orthilia secunda*) and the feathermoss *Pleurozium schreberi*.

The second axis explained 22% of the variation in understory species composition and ranged from harvested plots with greater levels of tamarack seedlings associated with the positive portion of this axis to control plots at the negative portion of the axis, which

was characterized by a higher abundance of speckled alder and three-seeded bog sedge (*Carex trisperma*). See Appendix B for all species correlations with NMS axes 1 and 2.

Several species were identified as significant indicators of a given disturbance category for the RTS sites (per Indicator Species Analysis, $p < 0.1$; Table 3.4b). Harvest disturbance had several significant indicators associated with this category, including dwarf raspberry (*Rubus pubescens*), pussy willow (*Salix discolor*), red-stemmed aster (*Symphyotrichum puniceum*) and tamarack seedlings. No mosses were significantly associated with harvest disturbance. Indicator species related to fire disturbance were largely the collection of post-fire bryophytes, particularly the liverwort *Marchantia aquatica*, followed by other post-fire colonizing species such as *Ceratodon purpureus*, *Funaria hygrometrica*, and *Ptychostomum pseudotriquetrum*. Other vascular plants were cattails, wide-leaved willow-herbs (*Epilobium coloratum* or *E. glandulosum*), and seedlings of trembling aspen. Indicator species for undisturbed plots ranged across several functional groups that included the forbs one-sided pyrola and marsh willow-herb (*Epilobium palustre*), to graminoids such as *Carex magellanicum*. Mosses identified as significant indicators included *Sphagnum warnstorffii*, and the feathermoss *Pleurozium schreberi*.

Discussion

Differences in the severity of disturbance as well as the disturbance type were both strongly reflected in the two plant communities' distinct ground-layer vegetation responses following the second growing season after disturbance. In addition, there were

striking differences in disturbance impacts between the two forested communities examined with fire disturbance impacts most pronounced in tamarack-dominated forests, where the significant reduction, and in some cases removal, of upper peat surface for RTS sites resulted in homogenization of community composition and retrogression towards marsh-like conditions. A greater heterogeneity in ground-layer disturbance from fire across the BSB sites reflected fire behavior and smoldering effects resulting in a variety of seedbed and peat substrate conditions that retained many of the pre-disturbance species, albeit with a shift in abundance. In contrast, harvest disturbance had less impact on important seedbed characteristics such as ericaceous and *Sphagnum* moss cover and generally were more similar to undisturbed controls, especially for BSB sites. Given the disproportionate importance of peat disturbance in structuring post-fire patterns in plant community composition and regeneration, this aspect of the disturbance regime requires more formal integration into management systems aimed at emulating stand-replacing disturbances in peatland communities.

Disturbance effects on seedling regeneration

Fire generally had a positive influence on black spruce regeneration within BSB sites, particularly areas experiencing lower levels of fire severity, with seedling densities significantly higher than harvest and control areas. The greater abundance of black spruce in burned areas relative to harvests showed that there was both a significant release of seed from semi-serotinous cones in burned areas, but also generated favorable seedbed conditions through alterations, or reduction, of surface microtopography relative to the

water table and the abundance of competing ericaceous shrubs (Chrosiewicz 1976; Zasada et al. 1983; Charron and Greene 2002; Jayen 2006; Johnstone and Chapin 2006; Greene et al. 2007). Regeneration limitations due to reduced seed supply and lack of suitable microsites following harvesting has been demonstrated in other work and shown to become more problematic with increasing clearcut size (Pothier 2000).

In contrast to BSB sites, harvest disturbance in RTS sites had a positive effect on tamarack seedling densities, where seedling densities were statically higher than all other disturbance categories, despite the seemingly low 2 seedlings \cdot m⁻² averages for clearcut areas. Seedling densities documented in the study area (8,094 seedlings per acre) exceed current stocking-level guidelines, however, which are 600 trees per acre at the fifth growing season (MN DNR 2008). Given the fact that tamarack is a shade-intolerant species, removal of the canopy would have been beneficial for seedling establishment (Duncan 1954), so is not a surprising result. Although harvests were statistically higher than other disturbance types, the somewhat low seedling densities could have merely reflected that while substrate conditions were suitable in the harvested sites, a limited amount of seed from nearby stands was able to disperse throughout clearcuts given that distance of dispersal is only about equal to twice the height of the seed tree (Duncan 1954); The significantly higher cover of graminoids in harvested plots could have also limited early survival rates due to competition.

The lack of regeneration in burned plots is also indicative of limited seed dispersal from adjacent living trees; however, unlike harvested areas that were fairly small (8-29 ha) on average, fire affected areas were significantly larger making dispersal

more difficult. The lack of seedling establishment in burned plots was also likely restricted by the complete or near removal of suitable tamarack seedbed conditions due to significant reductions in *Sphagnum* cover and increased expansion of deep water-filled hollows following fire. The complete absence of overstory disturbance in control plots limited the ability of tamarack to establish given its high light requirements.

Fire increased the abundance of trembling aspen seedlings across both forest types, despite the fact that mature trembling aspen was not present in the sampled stands prior to disturbance. Aspen disperses its seeds over great distances (Burns & Honkala 1990), up to 15 km (Turner et al. 2003), and long-distance seed dispersal and establishment following large, severe fires has been documented by other studies across the boreal forest (Greene et al. 2004; Johnstone et al., 2004; Jayen 2006). The general lack of aspen seedlings in harvested sites relative to burned sites is likely indicative of the influence that fire disturbance has in creating favorable germination conditions for aspen, including suitable moisture conditions and an absence of competition (Burns & Honkala 1990). Despite the increase in aspen seedlings following fire, this response is likely to be ephemeral given the perennially high water tables in both communities and aspen's low tolerance to prolonged inundation and nutrient-poor conditions.

Disturbance effects on bryophyte communities

Bryophyte community response to disturbance was largely reflective of the degree of ground-layer disturbance associated with a given disturbance type. Disturbance effects were most acute on RTS sites where fire shifted composition from a diverse array of *Sphagnum* species to a somewhat homogeneous community dominated by a limited

number of post-disturbance species such as *Polytrichum strictum*, *Ceratodon purpureus*, and the liverwort *Marchantia aquatica*. Total *Sphagnum* cover was also significantly reduced following harvest in this community; however, this reduction was far less than on burned sites. The remaining *Sphagnum* cover for harvest sites was heavily dominated by *S. angustifolium* post-harvest, compared to control sites, which were dominated largely by *S. warnstorffii*. The shift in dominance to *S. angustifolium* is likely due to the removal of the canopy through harvest, which promoted the expansion of species more tolerant of sun and open conditions and negatively affected the shade-tolerant *S. warnstorffii* typical of the undisturbed controls.

For the BSB sites, fire significantly reduced total cover of all living *Sphagnum*, regardless of severity, whereas clearcut harvest appeared to have no effect on total cover, relative to controls. These results are similar to those found in other post-fire, paludified black spruce forests where total cover of *Sphagnum* was significantly reduced compared with clearcut areas (Renard et al. 2016). Although there were no significant differences in microtopographic features (i.e., hummocks, hollows, and lawns) for the different disturbance types (Table 3.2) –likely due to the fact there was a high amount of variability in cover across plots, differences in the individual species responses were instead more notable.

Individual species (or group) responses for *S. magellanicum*, *S. angustifolium* and the hummock forming group *S. sect. Acutifolium* showed slightly differing patterns. While cover for *S. magellanicum* and *S. angustifolium* were significantly reduced by fire, cover of *S. angustifolium* increased with harvest relative to all other disturbance

categories. These responses are likely related to changes in microtopographic and hydrologic conditions as well as resource and light availability resulting from both fire and harvest (Vitt and Slack 1984; Benschoter and Weider 2003; Benschoter et al. 2005). Densely-packed species characteristic of hummocks make these features more resistant to combustion due to increased water transport and retention capacity, whereas hollow species such as *Sphagnum angustifolium*, are more effectively consumed by fire (Benschoter et al. 2005). In contrast, mechanical disturbance (i.e., compaction) from harvesting (despite winter harvest), coupled with the removal of the canopy, may have affected the peat microtopography allowing for species characteristic of lower hummocks and hollows to thrive, such as *S. magellanicum* and *S. angustifolium*. Relative to other *Sphagnum* species, *S. angustifolium* is also better able to adapt to environmental changes and can increase growth in the lower, wetter conditions often found following harvest disturbance (Vitt and Slack 1984; Benschoter et al. 2005; Robroek 2006; Fenton and Bergeron 2007).

The increased abundance observed for *Polytrichum strictum* in BSB sites often coincided with black spruce and trembling aspen seedling recruitment on fire-reduced peat. Based on these findings and those of other work in lowland black spruce communities, *Polytrichum* species may serve as a proxy for identifying suitable post-fire microsites for black spruce regeneration (Aksamit and Irving 1983; Charron and Greene 2002; Greene et al. 2004; Jayen et al. 2004; Johnstone and Chapin 2006; Lavoie et al. 2007; Veilleux-Nolin and Payette 2012). Similar increases in this species were not observed following harvest disturbance with *Sphagnum* species largely dominating the

moss layer in these areas. This indicates that harvest did not create similar disturbance for *Polytrichum* to colonize these areas in any great degree. These disturbance responses highlight a key difference between the effects of fire and harvest on seedbed conditions and may partially explain the challenges with black spruce regeneration often associated with clearcut areas.

Debate regarding which type of substrate is best for black spruce germination and growth on paludified soils is ongoing (Lafluer et al. 2011; Lavoie 2007); however, several studies have now documented that *Sphagnum* carpets are not ideal as a substrate for new growth due in large part to lower nutrient availability (Jeglum 1981; Groot and Adams 1994; Lavoie et al. 2007; Lafluer et al. 2011). Fast growing species, such as *S. angustifolium*, can also quickly outpace new seedling growth (Jeglum 1981; Groot and Adams 1994). This *Sphagnum* species was significantly reduced with fire in the present study.

Disturbance effects on ericaceous shrub abundance

There was no significant difference between disturbance types in the combined cover of ericaceous shrubs in BSB sites; a finding consistent with other work examining black spruce-dominated peatlands (Renard et al. 2016). In contrast, the cover of *Rhododendron* was significantly lower following fire and harvest disturbance relative to controls suggesting that disturbance generates at least an initial reduction in cover of this species, despite its documented ability to recover after disturbance from belowground rhizomes (Flinn and Wein 1977). The lack of black spruce regeneration in undisturbed

areas has been previously linked, in part, to interactions with *Rhododendron* through resource competition and the production of allelochemicals (Inderjit and Mallik 1996; Mallik 2003; Fenton et al. 2005).

The significant reduction, or in some cases near complete removal, of the upper peat layer in burned RTS sites led to a significant reduction in total ericaceous species cover. Given that peat depth (<1m) and well-developed microtopography in these communities is generally much lower than for BSB communities, the upper peat surface is more susceptible to higher consumption of plant reproductive tissues by fire. In contrast, harvest disturbance retained much of the ericaceous component where no differences were found between harvest and controls. *Rhododendron* is also a common species in these communities; however, cover is much lower than black spruce communities and its negative impacts on conifer regeneration are expected to be much lower, although there is little published data to confirm this.

Response of understory community composition to disturbance

The disturbance from harvesting and fire generated plant community assemblages that were distinctly different for both peatland communities. These differences in ground layer species responses for both communities underscore the importance of disturbance type and the degree to which it impacts the forest floor, signifying a further need to evaluate whether forest harvesting regimes are approximating natural disturbance processes. This is particularly important in peatland ecosystems where fire impacts can vary significantly for peat consumption, generating important feedbacks between post-

fire seedbed conditions and patterns of vegetation recovery. This was also demonstrated by the fact that in ordinations analyses for both communities, bryophytes played a large roll in differentiating the disturbance groups, where BSB plots were associated strongly by post-fire colonizers, whereas harvests (and controls) were more characterized by *Sphagnum* species. In RTS sites, fire plots were again associated strongly by post-fire colonizing bryophytes, whereas harvests were not associated with any bryophyte indicators.

Conclusions and management implications

The results of this study lend further support to the prevailing notion that forest floor disturbance is an important element in driving the dynamics of lowland conifer forest regeneration. The forest floor conditions generated by forestry practices in the black spruce communities examined in this study have not led to similar patterns of regeneration as those observed following fire, despite similar levels of overstory disturbance. Differences in ground-layer community composition and structure may be driving these trends, as less favorable *Sphagnum* substrates for seedling establishment were maintained during harvests, whereas reduced peat microsites dominated by *Polytrichum* were generated by fire. The low abundance of many colonizing moss species after harvest and the promotion species such as ericaceous shrubs may have implications for the conservation of diversity as well as future stand development.

Wildfire, though rare, has been an important, historical disturbance influencing forest dynamics in the upper Great Lakes region for millennia; however, most fire-origin,

peatland black spruce stands have not burned for over 200 years with logging the primary contemporary disturbance. Despite the challenges and costs of prescribed fire, earlier studies have shown that even low severity fire is highly effective at increasing the success of black spruce regeneration on peat or organic soils while reducing cover of *Sphagnum* (Johnson 1971; Chrosiewicz 1976; Aksamit and Irving 1984; McRae et al., 2001; Renard et al. 2016).

In addition to the benefits of prescribed fire regarding improved seedbed conditions, prescribed fire has also been used as an effective method for controlling the spread of eastern dwarf mistletoe, a serious parasitic disease of black spruce in northern Minnesota (Johnson 1971; Geils et al. 2002; Baker and Knowles 2004). As such, the application of prescribed fire following clearcut harvesting should be considered in those areas where mistletoe is present prior to harvest in an attempt to return natural processes, such as the chemical and biological effects of fire (Dyrness and Norum 1983) to these managed ecosystems.

In contrast, the environment created by fire in the tamarack swamps examined in this study is likely not a desirable condition to emulate through management, despite the fact that fires such as those observed in this study historically occurred with more regularity (Heinselman 1970, 1981). The differences in community composition for RTS sites suggest that changes in the cover and frequency of particular species after fire and harvest are offset by increases in other species, leading to little net change in richness or cover in the understory as a whole following disturbance. Nevertheless, the reductions in bryophyte abundance as a result of fire disturbance generated post-disturbance seedbed

conditions that were inhospitable for tamarack recruitment. In contrast, harvesting retained a significant amount of the *Sphagnum* cover, relative to fire, where removal of the canopy increased light availability, which promoted tamarack recruitment, albeit at low levels.

Silvicultural practices that create disturbance to the forest floor, particularly where peat depth is significant as a result of paludification, such as in the black spruce bog systems, facilitates favorable conditions for the establishment of disturbance-adapted lowland conifers (Nguyen-Xuan et al. 2000). However, tamarack swamps are more susceptible to disturbance of the organic layer, as observed in this study, where fire consumed a considerable amount of the peat. While the depth of peat is great enough to isolate the plant rooting zone from nutrient sources in the underlying mineral soil, they are structurally weak and much more susceptible to disturbance (MN DNR 2003) than black spruce bogs. In light of the results of this study, which shows that ground layer responses to harvesting varied between the two forest types, forest managers will need to tailor harvesting methods to the ecological conditions prevalent in different stand types in order to promote ground layer and conifer tree regeneration.

The stark differences in early understory and seedling responses between fire and harvesting in BSB sites suggest that clearcutting-based practices in lowland conifer systems are not approximating historic patterns of stand-replacement. Reintroducing prescribed fire on a limited basis, a management practice historically more common for these communities, in order to enhance regeneration success and restore critical ecosystem processes, may be an option for managers. Although this practice of

prescribed fire should only be considered for areas only where *Sphagnum* peat and associated microtopography is of considerable depth as to improve seedling success. Moreover, harvesting is currently practiced on a 80 to 100 year rotation in Minnesota's black spruce communities –a rotation much shorter than from natural disturbance such as stand-replacing fire. Introducing prescribed fire on such a frequent basis, even where feasible, would not be a sustainable practice. Additionally, the importance of peatlands in sequestering substantial amounts of carbon is increasingly understood (Gorham 1991; Clymo 1998; Parish 2008), so long as the formation of new peat exceeds the losses of decay (Belyea and Malmer 2004). Thus, burning away several hundreds years of peat for the benefit of increased seedling densities might not prove to be advantageous practice in the future. Because fires remove vegetation and stimulate decay, peatlands can also function as net sources of atmospheric carbon post-fire due to diminished primary production and enhanced mineralization rates (Turetsky et al. 2002). Shorter recovery times are more likely, however, for smaller fires in moist, lower latitude boreal peatlands (Turetsky et al. 2002) if prescribed fires are of low severity and limited to the upper peat surface.

Figures

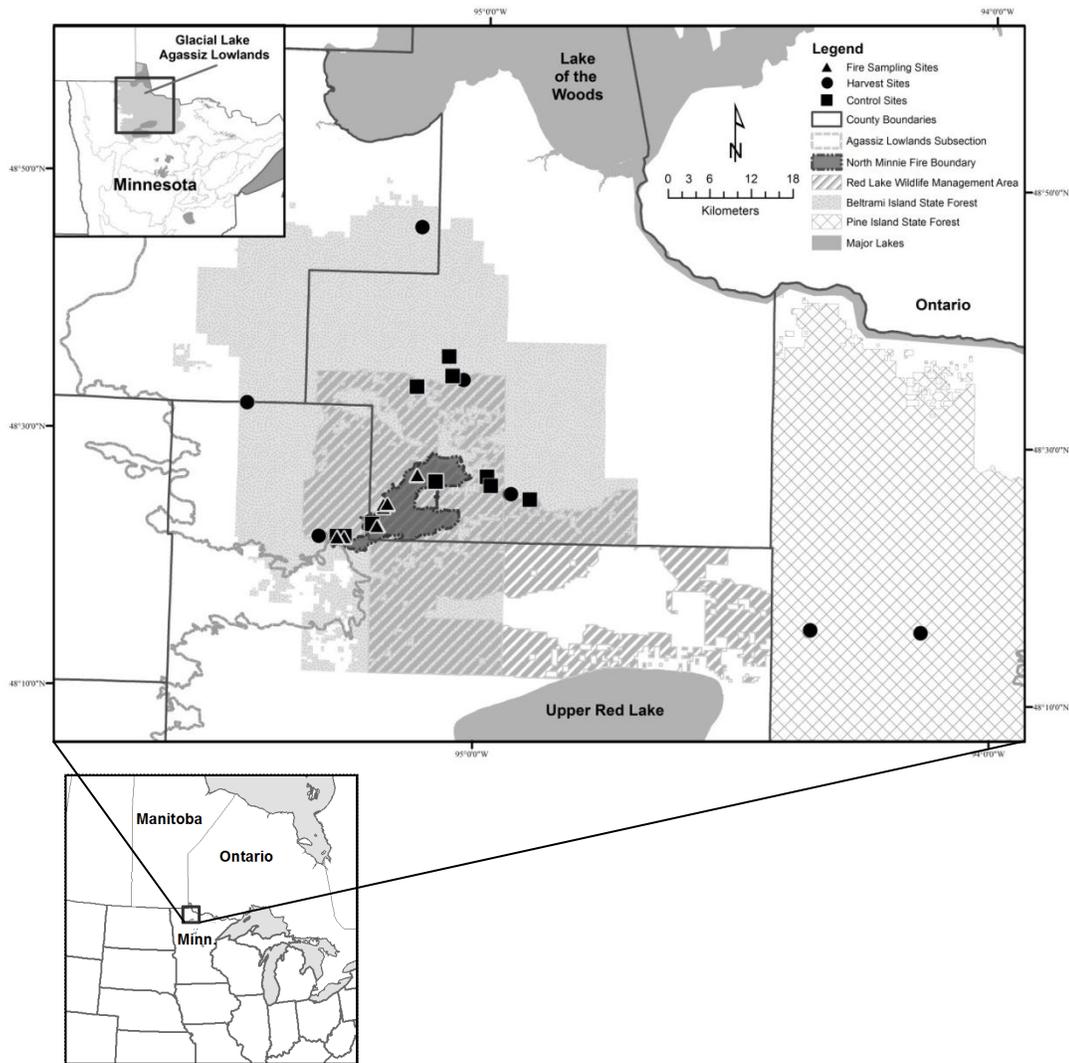


Fig. 3.1. Location of harvest, fire, and control plots in northern Minnesota, U.S.A. with the North Minnie fire area in dark grey.

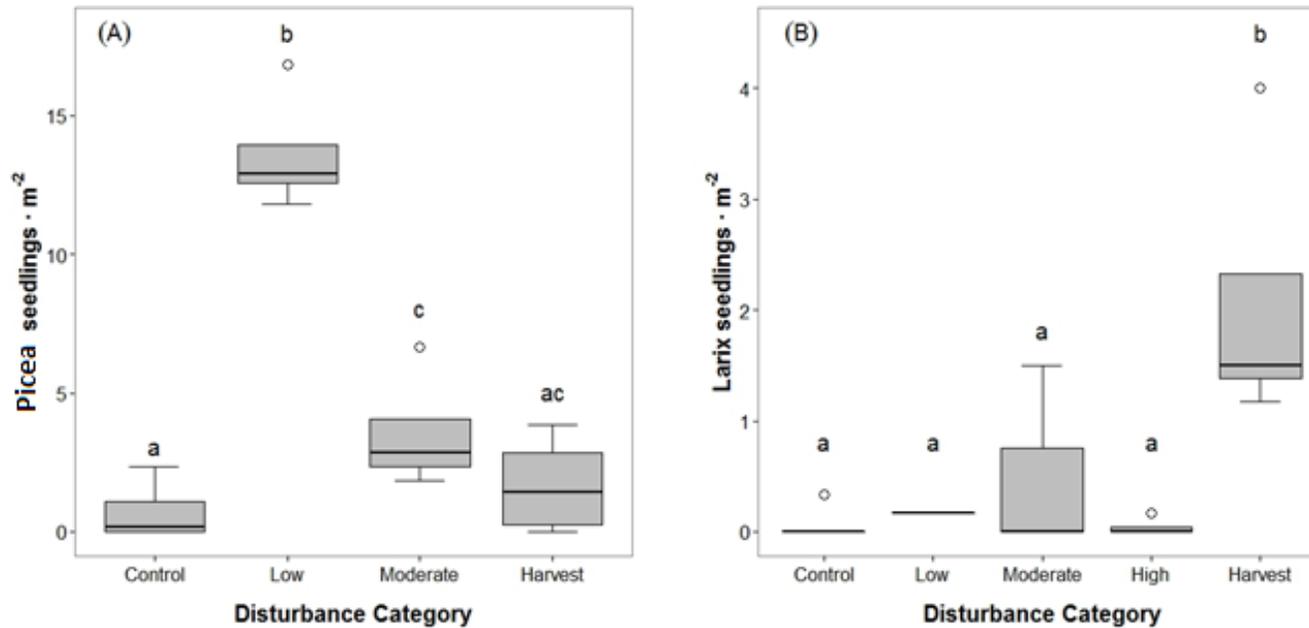


Fig.3.2. Boxplots of mean seedling densities for a) *Picea mariana* for black spruce bogs and b) *Larix laricina* for rich tamarack swamps across disturbance categories. The horizontal line in each box is the median. Boxes enclose the 75th and 25th percentiles and error bars enclose the 90th and 10th percentiles. Significant differences ($p < 0.1$ with ANOVA and Tukey's HSD) between disturbance categories are indicated by different letters above the boxes.

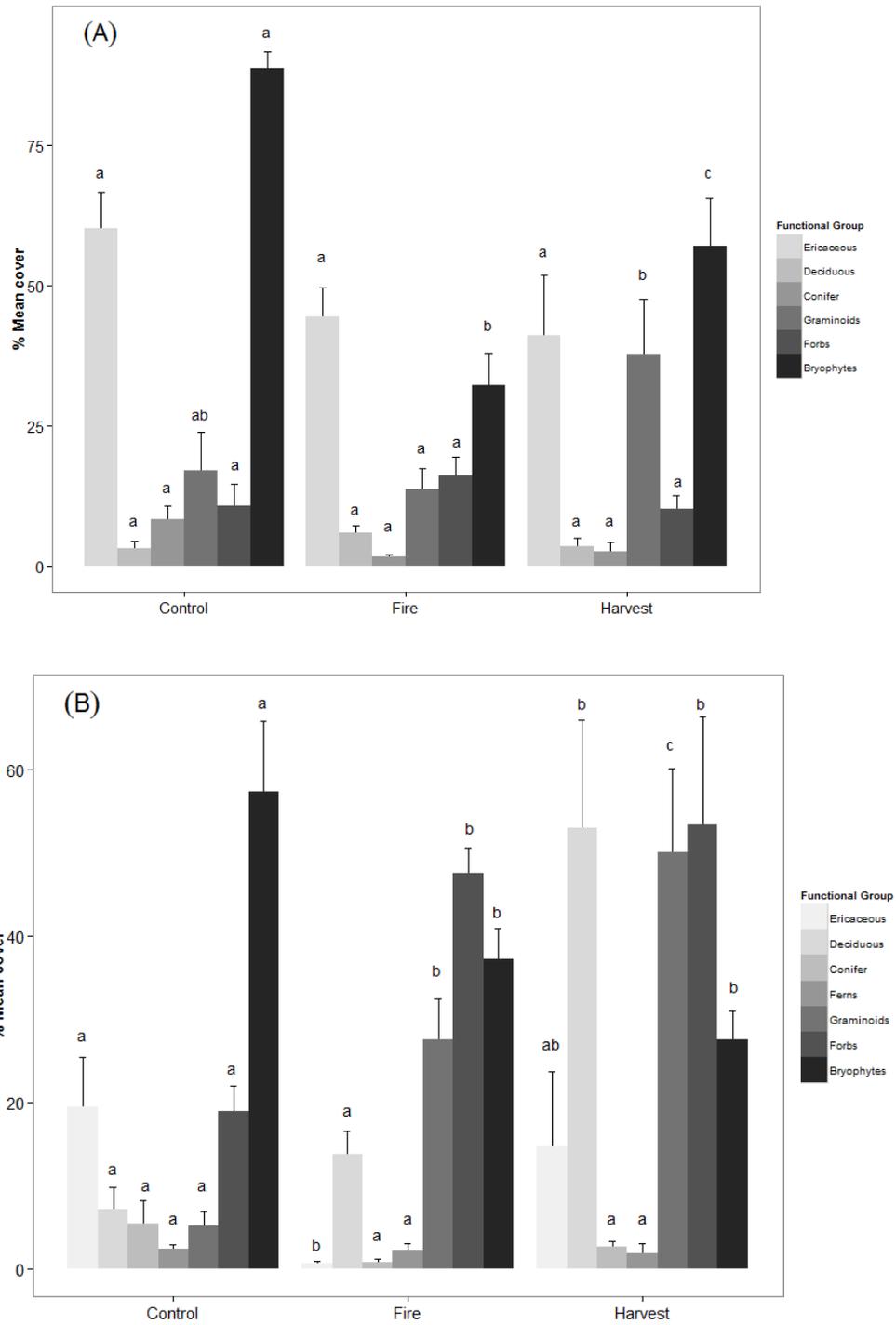


Fig.3.3. Mean percent cover of plot averaged understory vegetation by functional group for a) black spruce bog (BSB) and b) rich tamarack swamp (RTS) across disturbance categories. Error bars represent ± 1 standard error. Values with different letters are significantly different within functional groups at $P < 0.1$ using Tukey's HSD.

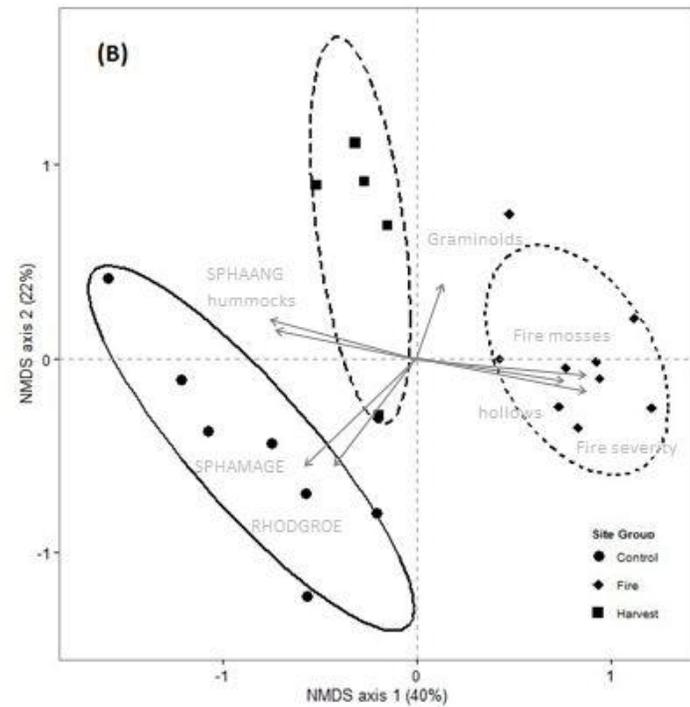
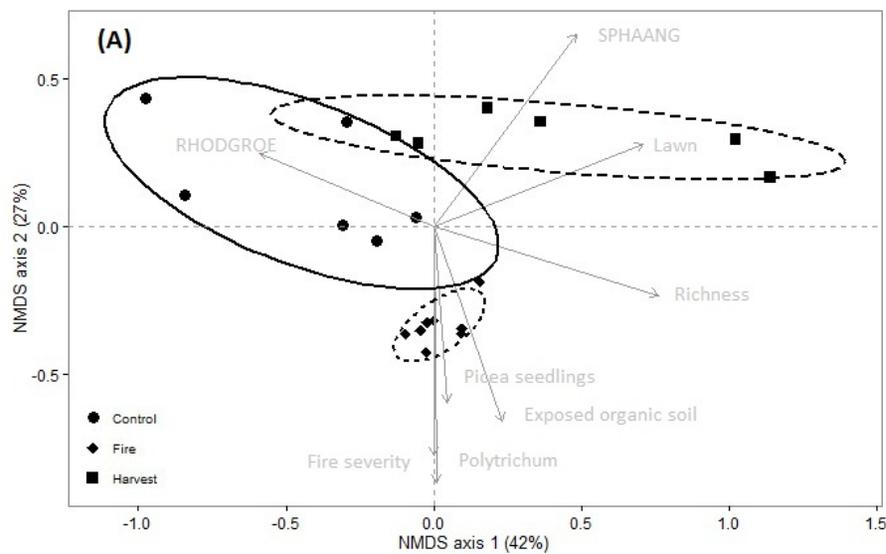


Fig.3.4. Non-metric multidimensional scaling (NMS) ordination of groundlayer species composition across disturbance treatments for a) black spruce bog and b) rich tamarack swamp. Arrows indicate the nature and strength of significant correlations of variables with the ordination axes with 80% confidence ellipses around plots from each disturbance group. See Appendix B for species correlations with NMS axes 1 and 2.

Tables

Table 3.1. Number of plots across differing levels of disturbance categories in Northern Spruce Bogs (BSB) and Northern Rich Tamarack Swamps (RTS) in the Agassiz Lowlands Subsection, Minnesota.

NPC	Treatment Groups				Harvested	Total
	Undisturbed (control)	Low severity	Mod Severity	High Severity		
APn80	6	4	4	-	6	20
FPn81	7	2	3	4	5	21
Total Plots	13	6	7	4	11	41

Table 3.2. Mean cover (± 1 S.E.) for the main response variables across different levels of disturbance severity for black spruce bog sites (BSB). F-statistic and p-values correspond to one-way ANOVA testing effect of disturbance severity on a given response variable. C=unburned control, L=low severity fire, M=moderate severity fire, HR=harvest. Different letters indicate significant differences between disturbance treatments at $p < 0.1$ using Tukey's HSD. Bold p-values indicate a significant disturbance severity effect.

Response variable	C	L	M	HR	F	P
<i>Picea mariana</i> seedling densities (stems \cdot m ⁻²)	0.7(0.4) ^a	13.6(1.1) ^b	3.5(1.1) ^c	1.64(0.7) ^{ac}	22.7	<0.01
<i>Populus tremuloides</i> seedling densities (stems \cdot m ⁻²)	0(0) ^a	10.6(1.9) ^b	23.6(16.5) ^b	1.1(0.4) ^a	9.7	0.01
<i>Sphagnum magellanicum</i> cover (%)	28.0(8.5) ^{ac}	10.1(3.0) ^{bc}	2.0(0.9) ^b	22.5(4.2) ^c	8.3	0.01
<i>Sphagnum angustifolium</i> cover (%)	16.8(5.6) ^a	0.88(0.4) ^b	0.6(1.1) ^b	29.0(8.7) ^a	14.3	<0.01
<i>Sphagnum</i> sect. <i>Acutifolium</i> cover (%)	22.4(8.1) ^a	5.4(3.2) ^{ab}	0.1(0.6) ^b	0.7(0.4) ^b	4.9	0.03
<i>Sphagnum</i> total cover (%)	67.2(10.7) ^a	16.5(6.0) ^b	2.7(1.3) ^c	50.3(9.7) ^a	26.2	<0.01
<i>Polytrichum</i> cover (%)	2.1(1.1) ^a	18.4(2.9) ^b	21.1(8.0) ^b	0.6(0.2) ^a	16.2	<0.01
Lawn cover (%)	6.5(3.3) ^a	10.2(4.1) ^a	22.5(2.4) ^a	33.9(13.0) ^a	2.1	0.18
Hummock cover (%)	80.0(5.0) ^a	78.3(6.5) ^a	69.6(6.2) ^a	57.2(9.0) ^a	1.9	0.21
Hollow cover (%)	10.7(4.7) ^a	11.5(4.1) ^a	8.3(3.8) ^a	6.1(3.9) ^a	1.6	0.25
Vascular Species richness	10.2(0.9) ^a	15.5(0.7) ^b	13.5(1.5) ^{ab}	16.2(1.7) ^b	5.1	0.03
Bryophyte Species richness	7.7(1.0) ^a	6.3(1.1) ^a	5.0(0.8) ^a	5.7(0.6) ^a	1.6	0.3
Vascular Species diversity (H')	1.7(0.1) ^{ab}	2.1(0.1) ^a	1.7(0.1) ^b	1.9(0.2) ^{ab}	3.6	0.06
Bryophyte Species diversity (H')	1.3(0.1) ^a	1.1(0.2) ^a	0.7(0.2) ^a	0.9(0.1) ^a	2.5	0.13
Total ericaceous species cover (%)	68.2(6.5) ^a	59.0(11.0) ^a	44.5(6.4) ^a	44.6(11.6) ^a	2.3	0.15
<i>Rhododendron</i> cover (%)	40.0(4.4) ^a	17.7(4.5) ^b	31.5(2.8) ^a	25.7(9.1) ^{ab}	4.7	0.04

Table 3.3. Mean cover (± 1 S.E.) for the main response variables across different levels of disturbance severity for rich tamarack swamp (RTS) communities. F-statistic and p-values correspond to one-way ANOVA testing effect of disturbance severity on a given response variable. C=unburned control, L=low severity, M=moderate severity, and H=high severity fire, HR=harvest. Different letters indicate significant differences between disturbance treatments at $p < 0.1$ using Tukey's HSD. Bold p-values indicate a significant disturbance severity effect.

Response variable	C	L	M	H	HR	F	P
<i>Larix laricina</i> seedlings densities (stems \cdot m ⁻²)	0.0(0.03) ^a	0.2(0.0) ^a	0.5(0.5) ^a	0.0(0.1) ^a	2.1(0.8) ^b	5.6	0.03
<i>Populus tremuloides</i> s.d. densities (stems \cdot m ⁻²)	0(0) ^a	0.1(0.1) ^{ac}	6.6(4.2) ^b	9.2(2.3) ^b	0.9(0.3) ^c	43.1	<0.00
Total <i>Sphagnum</i> cover (%)	46.4(8.7) ^a	4.6(4.6) ^{bc}	0.1(2.4) ^b	0.0(0) ^b	21.1(6.1) ^c	15.1	<0.00
Hummock cover (%)	73.2(4.8) ^a	39.2(14.1) ^b	21.9(13.1) ^b	18.3(3.6) ^b	73.4(5.7) ^a	15.6	<0.00
Hollow cover (%)	22.0(3.0) ^a	57.1(12.1) ^b	53.6(10.0) ^b	65.0(4.3) ^b	26.6(5.8) ^a	11.9	0.01
Lawn cover (%)	0.5(0.5) ^a	2.9(2.9) ^{ac}	24.4(11.3) ^b	17.1(6.1) ^{bc}	0(0) ^a	8.4	0.01
Post-fire colonizing bryophyte cover (%)	0.3(0.2) ^a	15.6(1.3) ^b	44.8(3.8) ^c	33.0(3.2) ^d	0.4(0.4) ^a	129.0	<0.00
Vascular Species Richness	26.7(7.1) ^a	25.0(4.0) ^a	27.3(4.2) ^a	27.3(1.5) ^a	36.0(2.6) ^a	1.1	0.11
Bryophyte Species Richness	12.3(1.1) ^a	7.0(0) ^b	4.3(0.2) ^b	4.0(0.3) ^b	8.2(0.7) ^b	17.0	<0.00
Species Diversity (H')	2.5(2.7) ^a	2.5(0.0) ^a	2.6(0.2) ^a	2.8(0.1) ^a	2.6(0.1) ^a	0.2	1.00
Bryophyte Species Diversity (H')	1.3(0.1) ^{ac}	1.4(0.1) ^{ac}	0.9(0.1) ^{ab}	0.9(0.1) ^{ab}	1.5(0.1) ^c	3.1	0.10
Total ericaceous species cover (%)	19.4(6.0) ^a	0.9(0.9) ^{bc}	0.8(0.6) ^{bc}	0.3(0.3) ^{bc}	14.3(9.1) ^{ac}	5.9	0.03

Note: Post-fire colonizing bryophyte cover consisted of species that were present primarily post-fire including *Ceratodon purpureus*, *Funaria hygrometrica*, *Pohlia nutans*, *Polytrichum strictum*, and *Ptychostomum pseudotriquetrum* and the liverwort *Marchantia polymorpha*.

Table 3.4. Indicator species analyses for a) black spruce bog (BSB) and b) rich tamarack swamp (RTS) disturbance categories. IV=indicator value; all species with $p < 0.1$ are reported.

NPC	Disturbance Category	Species	IV	p-value	
a) BSB	Undisturbed	<i>Vaccinium vitis-idaeus</i>	73.7	0.0008	
		<i>Picea mariana</i> (adv. regen)	70.1	0.0086	
		<i>Sphagnum</i> sect. <i>Acutifolium</i>	76.4	0.0088	
		<i>Rhododendron groenlandicum</i>	44.3	0.0700	
		<i>Pleurozium schreberi</i>	55.7	0.0762	
	Fire	<i>Polytrichum strictum</i>	88.1	0.0002	
		<i>Populus tremuloides</i>	80	0.0004	
		<i>Marchantia aquatica</i>	75	0.0014	
		Post-fire bryophytes (e.g. <i>Ceratodon</i>)	75	0.0028	
		<i>Andromeda polifolia</i>	61.3	0.0168	
	Harvest	<i>Carex trisperma</i>	84.3	0.0030	
		<i>Eriophorum angustifolium</i>	82.3	0.0038	
		<i>Carex chordorrhiza</i>	66.7	0.0068	
		<i>Salix planifolia</i>	50	0.0374	
		<i>Epilobium</i> spp. (wide-leaved)	45.7	0.0386	
		<i>Sphagnum angustifolium</i>	62.3	0.0438	
	NPC	Disturbance Category	Species	IV	p-value
	b) RTS	Undisturbed	<i>Orthilia secunda</i>	93.2	0.0002
<i>Epilobium palustre</i>			71.4	0.0020	
<i>Pleurozium schreberi</i>			74.7	0.0020	
<i>Carex magellanicum</i>			80	0.0022	
<i>Sphagnum warnstorffii</i>			65.3	0.0080	
<i>Aulacomnium palustre</i>			61.9	0.0142	
<i>Plagiomnium ellipticum</i>			61.4	0.0268	
<i>Campylium stellatum</i>			42.9	0.0320	
<i>Lonicera oblongifolia</i>			42.9	0.0334	
<i>Rhododendron groenlandicum</i>			58.3	0.0500	
<i>Pyrola asarifolia</i>			42	0.0610	
<i>Sphagnum magellanicum</i>			52	0.0610	
<i>Dryopteris cristata</i>			37.6	0.0754	
<i>Salix pedicellaris</i>		35.6	0.0854		
Fire		<i>Typha</i> spp.	99	0.0002	
		Post-fire bryophytes	100	0.0002	
		<i>Marchantia aquatica</i>	100	0.0002	
		<i>Populus tremuloides</i>	75.7	0.0018	
		<i>Epilobium</i> spp.(wide-leaved group)	82.4	0.0018	
		<i>Cicuta bulbifera</i>	59.9	0.0116	

	<i>Polytrichum strictum</i>	72.5	0.0196
	<i>Salix serissima</i>	44.4	0.0466
	<i>Carex diandra</i>	44.4	0.0484
	<i>Agrostis scabra</i>	44.4	0.0492
	<i>Carex chordorrhiza</i>	57.4	0.0504
	<i>Campanula aparinoides</i>	55.2	0.0830
	<i>Impatiens capensis</i>	43.3	0.0966
Harvest	<i>Salix discolor</i>	83.6	0.0010
	<i>Rubus pubescens</i>	86.3	0.0012
	<i>Symphyotrichum puniceus</i>	79.5	0.0016
	<i>Epilobium leptophyllum</i>	76.6	0.0022
	<i>Larix laricina</i>	76.3	0.0032
	<i>Galium triflorum</i>	74.7	0.0044
	<i>Fragaria virginiana</i>	60	0.0062
	<i>Scutellaria galericulata</i>	60	0.0072
	<i>Trientalis borealis</i>	66	0.0072
	<i>Carex disperma</i>	59	0.0076
	<i>Alnus incana</i>	62.2	0.0140
	<i>Glyceria striata</i>	56.5	0.0152
	<i>Maianthemum canadensis</i>	64.6	0.0172
	<i>Symphyotrichum borealis</i>	56.3	0.0194
	<i>Carex leptalea</i>	69	0.0210
	<i>Rhamnus alnifolia</i>	45.1	0.0260
	<i>Cornus canadensis</i>	50.5	0.0310
	<i>Rubus idaeus</i>	63.4	0.0326
	<i>Carex trisperma</i>	45.5	0.0386
	<i>Cornus sericea</i>	51.3	0.0672

Chapter 4: Conclusions

Forested peatland communities dominated by black spruce and tamarack cover over 1.1 million hectares of northern Minnesota, providing habitat for an array of animal species as well as critical ecological functions including carbon sequestration (Gorham 1991) and maintenance of important ecohydrologic feedbacks related to the water table depth such as methane emissions, organic matter decomposition and run-off (Waddington et al. 2015). Boreal forested peatlands also serve as a primary source of raw materials for forest industries in the continent. Since the presettlement period, the area covered by these forests has declined significantly due to historic land-use patterns, including alterations of peatlands through extensive ditching and road construction (Bradof 1992), as well as through recent outbreaks of larch sawfly and eastern larch beetle (MN DNR 2013b). Projected future increases in temperature, as well as the frequency and severity of drought events may serve to further threaten black spruce and tamarack, as well as the communities they inhabit, given their southern range margin in Minnesota (Iverson et al. 2008; Galatowitsch et al. 2009). Beyond direct physiological stress from these changing climatic patterns, increases in the severity, areal extent and frequency of climate-mediated events, such as drought and fire, have the potential for triggering large-scale shifts in vegetation conditions. Given this potential threat and recent concerns regarding the sustainability of forest harvesting in lowland conifer systems (MN DNR 2013b), the overall objective of this thesis was to characterize patterns in vegetation regeneration following natural and anthropogenic disturbance in black spruce and tamarack-dominated forested peatland communities.

A central finding of this work was the importance of accounting for impacts of disturbance to the peat layer when examining post-disturbance patterns of tree regeneration in these forests with optimal seedbed conditions varying appreciably between the two communities of focus. For tamarack communities, the highest seedling densities were observed following harvesting disturbance, which largely preserved pre-harvest seedbed conditions despite the removal of all overstory trees. In contrast, very few seedlings were encountered in burned tamarack swamps due in large part to the complete removal of suitable tamarack seedbed conditions through significant reductions in *Sphagnum* peat and increased expansion of deep water-filled hollows. These burned areas have largely shifted towards marsh-like conditions and may remain in a non-treed state for extended periods based on the timescales of peatland ontogeny documented in the paleoecological record (Heinselman 1970). These findings are particularly concerning given recent documented declines in the extent of tamarack-dominated communities and suggest these systems are highly vulnerable to future increases in fire frequency.

The impacts of fire on black spruce bogs was remarkably different than for tamarack communities and resulted in greater levels of black spruce regeneration compared to harvested and undisturbed plots, particularly in areas experiencing lower levels of fire severity. Unlike tamarack, which does not maintain a bank of viable seeds, black spruce releases large quantities of seed from semiserotinous cones soon after fire providing a mechanism for post-disturbance regeneration even when overstory mortality is extensive (Johnstone et al. 2009; Viglas 2013). In addition, overall peat depth and pre-fire microtopography was greater in black spruce bogs which resulted in a mosaic of

moisture conditions that led to a greater range of spatial heterogeneity in ground layer combustion, compared to tamarack swamps where peat was effectively consumed to the water table. As a result, post-fire black spruce seedbed conditions were more conducive to seedling establishment; especially in areas of lower peat lawns dominated by post-fire colonizing mosses and reduced cover of *Rhododendron*. These contrasting results suggest black spruce communities is be more resilient to increases in fire frequency than tamarack systems given the feedbacks between seed dispersal and levels of peat consumption.

The North Minnie Fire was a relatively rare fire event; however, fire has historically been an important, albeit infrequent driver of black spruce forest dynamics in northern Minnesota while also reducing the presence and spread of insects and disease in these communities (e.g., Baker and Knowles 2004; McRae et al. 2001). Despite these historic dynamics, logging is presently the main disturbance of lowland black spruce bogs with even-aged, silvicultural systems in the form of block clearcuts the general management approach. The results from this work indicate that seedbed conditions created as a result of clearcut harvests did not lead to the development of regeneration patterns similar to those observed following fire. Harvesting had less impact on important seedbed characteristics such as ericaceous and *Sphagnum* moss cover and generally were more similar to undisturbed controls in terms of plant community composition and tree regeneration. In addition, the removal of a large proportion of the aerial seedbank during harvesting likely limited the amount of seed available for regenerating these areas. Similar regeneration limitations due to reduced seed supply and

lack of suitable microsites following harvesting have been demonstrated in other work and shown to become more problematic with increasing clearcut size (Pothier 2000).

These findings argue for a reexamination of the importance of creating appropriate seedbed conditions when managing in black spruce systems in the state. Additional methods of harvesting should also be considered, such as careful logging around advance growth (CLAAG), where merchantable stems of black spruce are cut and smaller individuals are protected to various degrees as future crop trees (Groot 1995; Pothier 2000). This method of harvest, which has been more widespread throughout Canada, has been well studied for black spruce-dominated forests on peatland sites where black spruce advance regeneration, predominantly of layer origin, is often abundant, particularly in older stands with low stand basal areas (Groot 1995; Pothier 2000; Harvey and Brais 2002). These studies have also shown it to be an effective natural regeneration method and low cost alternative (Groot 1995; Chen and Wang 2006); however, cover of ericaceous shrubs can be significantly higher on these sites (Lafleur et al. 2010), which has been cited as having a negative impact on black spruce growth (Inderjit and Mallik 1996; Mallik 2003).

Management implications

The declining area of tamarack forest in northern Minnesota due to site conversion to other forest types as well as widespread insect-induced mortality (Hanberry et al. 2013; McKee and Aukema 2015) is now a major concern for forest managers. Finding appropriate measures and opportunities to regenerate this species in light of climate change should be of critical importance, given it is now limited to wetland sites

(Hanberry et al. 2013). The results from this work are consistent with past research documenting successful tamarack regeneration following harvesting of lowland sites (Duncan 1952). Although the low seedling densities documented in the clearcuts examined in this study speak to the importance of maintaining adjacent or onsite seed sources through the use of strip clearcutting or group seed-tree methods. These harvest patterns may also represent a more natural analog to the historic, patchy nature of fire and stand-scale disturbance in these systems, as several areas within the tamarack swamps in the study area had stringers of surviving tamarack interspersed with fire-killed trees (Fig. 4.1).

The initial findings from areas experiencing complete tamarack mortality from fire indicate that restoration of tamarack to these sites may prove difficult given the loss of suitable seedbed conditions and tamarack seed source, and the general shift in vegetation towards a marsh-like state. Aerial seeding is frequently employed to reforest tamarack in large harvest blocks and areas impacted by eastern larch beetle; however, it is unlikely these methods will be successful in the burned sites given current elevated water tables and competition from dense graminoids and cattails. Long-term monitoring of these areas for changes in water table dynamics and development of suitable seedbed conditions will be important for determining if and when reforestation efforts might be applied to restore tamarack to these systems.

The positive influence of fire on regeneration in black spruce bog sites is consistent with a large body of early silvicultural research that highlighted the benefits of prescribed fire as a site preparation tool in these systems (Johnston 1971). Consistent

with this historic work, prescribing burning was historically used as a management tool on harvested back spruce sites in northern Minnesota; however, this method is no longer employed. The cessation of applying prescribed fires was largely due to the cost of this practice as well as the risk involved given peat fires can be difficult to extinguish despite extensive moisture and firefighting attempts, and can smolder for long periods of time (Rein et al. 2008). The beneficial microsite conditions documented following the North Minnie fire and past work with prescribed burning (Johnston 1971; Aksamit and Irving 1984) suggest that the reintroduction of a light, but limited prescribed fire regime to these systems should be considered as an option for sustaining black spruce on the landscape. Importantly, this reintroduction would need to acknowledge potential shifts in growing season moisture availability associated with climate change and its influence on fuel conditions to minimize the scale and intensity of burning that might occur following ignition.

An additional consideration regarding the use of prescribed fire are the benefits this method provides in terms of serving as an effective method for controlling the spread of eastern dwarf mistletoe, a serious parasitic disease of black spruce in northern Minnesota (Johnston 1971; Geils et al. 2002; Baker et al. 2006). Currently, eastern dwarf mistletoe is controlled using large block clearcuts in which all stems greater than 1.3 m are felled to reduce the impacts of this disease on the growth of individuals regenerating into the harvested areas. This approach may reduce mistletoe impacts on the regenerating stand; however, it does not provide similar benefits in terms of eradicating dwarf mistletoe from the given site and does not create the same level of suitable seedbed

conditions. Moreover, the patterns of vegetation development observed following harvesting in this work suggest that current practices may largely serve to maintain a high level of competing ericaceous shrubs (Malik 2003) creating challenging conditions for regeneration of these areas.

Study limitations and research recommendations

Throughout the course of this study a number of knowledge gaps and research needs were identified which fell outside the scope of this study. Additionally, several limitations with the study design and approach were recognized and are outlined below.

First, given the limitations of remotely-sensed fire severity assessments for quantifying belowground impacts of fire in peatland communities, fire-severity classifications were verified in the field and adjusted where necessary. The lack of information on pre-fire site conditions and uncertainty regarding the degree to which the dNBR fire severity map reflected an accurate range of fire conditions resulted in fire severity being assessed *ad hoc* in the field. For these reasons, two additional measures of fire severity were developed for each plot. Given the recognized importance of organic matter consumption on ecological recovery after fire disturbance (Rowe 1983), additional research is needed to construct field-based measures of fire severity for forested peatland systems—akin to the Composite Burn Index (CBI; Key and Benson 2006) used for uplands. Currently, there has been limited research or attempts at creating a consistent approach for classifying fire severity for lowland systems (Kasischke et al. 2008).

Measurements of adventitious roots on tamarack and black spruce have been shown to be reliable indicators of where the surface of the peat layer was prior to burning

(Kasischke et al. 2008; Veverica et al. 2012). Limited testing of this approach in the present study suggests that these measurements could be a valuable component to include in future fire severity assessments of organic matter, or peat, consumption. The narrow time frame for data collection in this study prevented the collection of a sufficient number of measurements of adventitious roots to draw consistent conclusions on fire severity relationships; however, future work focused on this metric will be important in assisting ongoing efforts aimed at quantifying fire impacts in forested peatlands.

Aerial seeding is frequently employed for reforesting lowland conifer communities; however, this study was restricted to harvested stands in which this practice was excluded. The use of a wider range of harvested sites that included those with aerially seeding would provide insight into whether disturbance from post-harvest is indeed creating a receptive seedbed. For this study, because sampling took place in clearcuts without direct seeding, a lack of nearby seed may have limited the results of this study. Furthermore, the sampling design constraints of excluding aerial seeded sites limited the number of potential harvest study areas in which to draw inferences.

A lack of information on vegetation abundance and composition prior to disturbance precluded making any direct inferences on changes in vegetation communities resulting from disturbance and is necessary to support the assumption that differences observed after disturbance are a direct result of the effects of fire and harvest. An attempt was made to account for this by selecting undisturbed forests found on sites with similar stand ages, overstory tree stocking, peat depth, microtopography and canopy

composition to the sampled disturbed sites; however, pre-disturbance differences in vegetation as a potential driver of observed trends cannot be excluded.

Finally, further research is needed to fully understand the regeneration dynamics of lowland tamarack systems. Very little data currently exists with respect to the seedbed requirements, recruitment patterns, and appropriate silvicultural systems for sustaining tamarack on minerotrophic sites. Given the many factors currently affecting this species, there are numerous opportunities for future research examining how tamarack will adapt to increased temperatures and ongoing outbreaks of eastern larch beetle. There is also a critical need for the development of silvicultural systems to enhance and maintain this resource given its continued decline from the landscape.

Figure



Fig. 4.1. Stringers of unburned tamarack in the North Minnie fire, Minnesota, USA. Photo taken by Gretchen Mehmel, Red Lake Wildlife Management Area manager for the MN DNR.

References

- Ahlgren, C. E. 1960. Some Effects of Fire on Reproduction and Growth of Vegetation in Northeastern Minnesota. *Ecology* 41:431-445.
- Ahlgren, I. F., and C. E. Ahlgren. 1960. Ecological Effects of Forest Fires. *Botanical Review* 26:483-533.
- Allen, J. L., and B. Sorbel. 2008. Assessing the differenced Normalized Burn Ratio's ability to map burn severity in the boreal forest and tundra ecosystems of Alaska's national parks. *International Journal of Wildland Fire* 17:463-475.
- Bauer, I. E., L. D. Gignac, and D. H. Vitt. 2003. Development of a peatland complex in boreal western Canada: lateral site expansion and local variability in vegetation succession and long-term peat accumulation. *Canadian Journal of Botany* 81:833-847.
- Baker, F. A., and K. R. Knowles. 2004. Case study: 36 Years of dwarf mistletoe in a regenerating black spruce stand in northern Minnesota. *Northern Journal of Applied Forestry* 21:150-153.
- Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography* 19:134-143.
- Baselga, A., D. Orme, S. Villeger, J. De Bortoli and F. Leprieur. 2013. betapart: Partitioning beta diversity into turnover and nestedness components. R package version 1.3. <http://CRAN.R-project.org/package=betapart>
- Belyea, L. R. and Malmer, N. 2004. Carbon sequestration in peatland: patterns and mechanisms of response to climate change. *Global Change Biology*, 10: 1043–1052. doi:10.1111/j.1529-8817.2003.00783.x
- Benscoter, B. W., R. Kelman-Wieder, and D. H. Vitt. 2005. Linking microtopography with post-fire succession in bogs. *Journal of Vegetation Science* 16:453-460.
- Benscoter, B. W., D. K. Thompson, J. M. Waddington, M. D. Flannigan, B. M. Wotton, W. J. de Groot, and M. R. Turetsky. 2011. Interactive effects of vegetation, soil moisture and bulk density on depth of burning of thick organic soils. *International Journal of Wildland Fire* 20:418-429.
- Bradof, K.L. 1992. Impact of ditching and Road Construction. In: *The Patterned Peatlands of Minnesota*. H.E. Wright, Coffin, B.A., Aaseng, N. (Eds.) Pages 173-185. University of Minnesota Press, Minneapolis.
- Brown, C. D. and J. F. Johnstone (2012). Once burned, twice shy: Repeat fires reduce seed availability and alter substrate constraints on *Picea mariana* regeneration. *Forest Ecology and Management* 266: 34-41.

- Brumelis, G., and T. J. Carleton. 1988. The Vegetation of postlogged black spruce lowlands in central Canada. Trees and tall shrubs. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 18:1470-1478.
- Burns, R. M. & B. H. Honkala, 1990. *Sylvics of North America: 2. Hardwoods*. Agriculture Handbook 654. US Department of Agriculture, Washington, DC.
- Busque, D., and D. Arseneault. 2005. Fire disturbance of larch woodlands in string fens in northern Québec. *Canadian Journal of Botany* 83:599-609.
- Charron, I., and D. F. Greene. 2002. Post-wildfire seedbeds and tree establishment in the southern mixedwood boreal forest. *Canadian Journal of Forest Research* 32:1607-1615.
- Chen, H. Y. H., and J. R. Wang. 2006. Post-harvest Regeneration of Lowland Black Spruce Forests in Northeastern Ontario. *New Forests* 31:115-129.
- Clark, J.S., L. Iverson, C.W. Woodall, C.D. Allen, D.M. Bell, D.Bragg, A.W. D'Amato, F.W. Davis, M. Hersh, I. Ibanez, S.T. Jackson, S. Matthews, N. Pederson, M. Peters, M. Schwartz, K. Waring, and N.E. Zimmermann. In press. The impacts of increasing drought on forest dynamics, structure, and biodiversity. *Global Change Biology*.
- Chrosiewicz, Z. 1976. Burning for black spruce regeneration in a lowland cutover site in Southeastern Manitoba. Northern Forest Research Centre, Canadian Forestry Service, Dept. of the Environment.
- Cocke, A. E., Fule, P.Z., and Crouse, J.E. (2005). Comparison of burn severity assessments using Differenced Normalized Burn Ratio and ground data. *International Journal of Wildland Fire* 14: 189-198.
- Curtis, J.T. 1959. *Vegetation of Wisconsin: An Ordination of Plant Communities*. University of Wisconsin Press, Madison, WI. 657 pp.
- Dale, V. H., L. A. Joyce, S. McNulty, R. P. Neilson, M. P. Ayres, M. D. Flannigan, P. J. Hanson, L. C. Irland, A. E. Lugo, C. J. Peterson, D. Simberloff, F. J. Swanson, B. J. Stocks and B. M. Wotton . 2001. Climate change and forest disturbances. *Bioscience* 51(9): 723-734.
- Daubenmire, R. 1968. *Plant Communities. A Textbook of Plant Synecology*. Harper and Row, New York.
- Davis, M.B. and R.G. Shaw. 2001. Range shifts and adaptive responses to quaternary climate change. *Science*, 292. pp. 673–679.
- DesRochers, A., and R. Gagnon. 1997. Is ring count at ground level a good estimation of black spruce age? *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 27:1263-1267.
- Dufrêne, M. and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67. 345–366.

- Duguid, M. C., and M. S. Ashton. 2013. A meta-analysis of the effect of forest management for timber on understory plant species diversity in temperate forests. *Forest Ecology and Management* 303:81-90.
- Duncan, D. P. 1954. A Study of Some of the Factors Affecting the Natural Regeneration of Tamarack (*Larix Laricina*) in Minnesota. *Ecology* 35:498-521.
- Dussart, E., and S. Payette. 2002. Ecological impact of clear-cutting on black spruce-moss forests in southern; *Ecoscience* 9:533-543.
- Dyrness, C. T., and R. A. Norum. 1983. The effects of experimental fires on black spruce forest floors in interior Alaska. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 13:879-893.
- Fenton, N. J., and Y. Bergeron. 2007. Sphagnum community change after partial harvest in black spruce boreal forests. *Forest Ecology and Management* 242:24-33.
- Fenton, N., N. Lecomte, S. Légaré, and Y. Bergeron. 2005. Paludification in black spruce (*Picea mariana*) forests of eastern Canada: Potential factors and management implications. *Forest Ecology and Management* 213:151-159.
- Fenton, N., L. I., T. Work, J. Jacobs, H. Bescond, P. Drapeau, and Y. Bergeron. 2013. Lessons learned from 12 years of ecological research on partial cuts in black spruce forests of northwestern Québec. *The Forestry Chronicle* 89.
- Flinn, M. A., and R. W. Wein. 1977. Depth of underground plant organs and theoretical survival during fire. *Canadian Journal of Botany* 55:2550-2554.
- Franklin, J. F., R. J. Mitchell, and B. Palik. 2007. Natural disturbance and stand development principles for ecological forestry. USDA Forest Service General Technical Report NRS-19.
- Frelich, L. E., 2002. *Forest dynamics and disturbance regimes*. Cambridge University Press, New York, NY.
- Frelich, L. E. and P. B. Reich (2010). Will environmental changes reinforce the impact of global warming on the prairie-forest border of central North America? *Frontiers in Ecology and the Environment*. 8: 371-378.
- Kasischke, E.S., M. R. T., Roger D. Ottmar, Nancy H. F. French, Elizabeth E. Hoy, and Evan S. Kane. 2008. Evaluation of the composite burn index for assessing fire severity in Alaskan black spruce forests. *International Journal of Wildland Fire* 17:515-526.
- Galatowitsch, S., Frelich, L., & Phillips-Mao, L. 2009. Regional climate change adaptation strategies for biodiversity conservation in a midcontinental region of North America. *Biological Conservation*, 142(10), 2012-2022.
- Geils, B.W., J.C. Tovar and B. Moody. 2002. Mistletoes of North American conifers. USDA Forest Service, Gen. Tech. Rep. RMRS-GTR-98, 120 p

- Gilliam, F. S. 2007. The Ecological Significance of the Herbaceous Layer in Temperate Forest Ecosystems. *Bioscience* 57:845-858.
- Girard, F., S. Payette, and R. Gagnon. 2009. Origin of the lichen–spruce woodland in the closed-crown forest zone of eastern Canada. *Global Ecology and Biogeography* 18:291-303.
- Glaser, P.H. 1987. The Ecology of Patterned Boreal Peatlands of Northern Minnesota: A community profile. U.S. Fish & Wildlife Service. Tech. Rep. 85(7.14). 98 pp.
- Gorham, E. 1991. Northern Peatlands: Role in the Carbon Cycle and Probable Responses to Climatic Warming. *Ecological Applications* 1:182–195.
- Greene, D. F., J. C. Zasada, L. Sirois, D. Kneeshaw, H. Morin, I. Charron, and M. J. Simard. 1999. A review of the regeneration dynamics of North American boreal forest tree species. *Canadian Journal of Forest Research*. 29:824-839.
- Greene, D. F., J. Noël, Y. Bergeron, M. Rousseau, and S. Gauthier. 2004. Recruitment of *Picea mariana*, *Pinus banksiana*, and *Populus tremuloides* across a burn severity gradient following wildfire in the southern boreal forest of Quebec. *Canadian Journal of Forest Research* 34:1845-1857.
- Greene, D. F., S. E. Macdonald, S. Haeussler, S. Domenicano, J. Noël, K. Jayen, I. Charron, S. Gauthier, S. Hunt, E. T. Gielau, Y. Bergeron, and L. Swift. 2007. The reduction of organic-layer depth by wildfire in the North American boreal forest and its effect on tree recruitment by seed. *Canadian Journal of Forest Research* 37:1012-1023.
- Grieg-Smith, P. 1983. *Quantitative Plant Ecology*. 3rd edition. Blackwell Scientific Publications, Oxford.
- Griffen, K. O. 1977. Paleocological aspects of the Red Lake Peatland, northern Minnesota. *Canadian Journal of Botany* 55:172-192.
- Groot, A., and Adams, M.J. 1994. Direct seeding black spruce on peatlands: fifth-year results. *For. Chron.* 70:585–593.
- Groot, A. 1996. Regeneration and surface condition trends following forest harvesting on peatlands. NODA Tech. Rep. TR-26. 12 p. + append.
- Gustafsson, L., S. C. Baker, J. Bauhus, W. J. Beese, A. Brodie, J. Kouki, D. B. Lindenmayer, A. Löhmus, G. M. Pastur, C. Messier, M. Neyland, B. Palik, A. Sverdrup-Thygeson, W. J. A. Volney, A. Wayne, and J. F. Franklin. 2012. Retention forestry to maintain multifunctional forests: a world perspective. *Bioscience* 62:633-645
- Hanberry B., B.J.Palik, S.H. Hong. 2013. Winning and Losing Tree Species of Reassembly in Minnesota’s Mixed and Broadleaf Forests. *PLoS One* 8.
- Harvey B. and Brais S. 2002. Effects of mechanized careful logging on natural regeneration and vegetation competition in the southeastern Canadian boreal forest. *Can. J. For. Res.* 32: 653–666.

- Hébert, F., N. Thiffault, J.-C. Ruel, and A. D. Munson. 2010. Ericaceous shrubs affect black spruce physiology independently from inherent site fertility. *Forest Ecology and Management* 260:219-228.
- Heinselman, M. L. 1961. Black Spruce on the Peatlands of Former Glacial Lake Agassiz and Adjacent Areas in Minnesota: a Study of Forest Sites, Bog Processes, and Bog Types. P.h.D. thesis. University of Minnesota.
- Heinselman, M. L. 1963. Forest Sites, Bog Processes, and Peatland Types in the Glacial Lake Agassiz Region, Minnesota. *Ecological Monographs* 33:327-374.
- Heinselman, M. L. 1970. Landscape Evolution, Peatland Types, and the Environment in the Lake Agassiz Peatlands Natural Area, Minnesota. *Ecological Monographs* 40:235-261.
- Heinselman, M. 1981. Fire and Succession in the Conifer Forests of Northern North America. Pages 374-405 in D. West, H. Shugart, and D. Botkin, editors. *Forest Succession*. Springer New York.
- Hulme, P.E. 2005. Adapting to climate change: is there scope for ecological management in the face of a global threat? *Journal of Applied Ecology*, 42. pp. 784–794.
- Inderjit, and A. U. Mallik. 1996. Growth and physiological responses of Black Spruce (*Picea mariana*) to sites dominated by *Ledum groenlandicum*. *Journal of Chemical Ecology* 22:575-585.
- Inderjit, and A. U. Mallik. 1996. Growth and physiological responses of Black Spruce (*Picea mariana*) to sites dominated by *Ledum groenlandicum*. *Journal of Chemical Ecology* 22:575-585.
- Inderjit, and A. U. Mallik. 1997. Effects of *Ledum groenlandicum* amendments on soil characteristics and black spruce seedling growth. *Plant Ecology* 133:29-36.
- IPCC [Intergovernmental Panel on Climate Change]. 2007. Climate change 2007: the physical science basis. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, and H.L. Miller, editors. Cambridge University Press, England, United Kingdom.
- Iverson, L. R., A. M. Prasad, S. N. Matthews, and M. Peters. 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *Forest Ecology and Management* 254:390-406. <http://www.treesearch.fs.fed.us/pubs/13412>
- Janssen, C. R. 1967. Stevens Pond: A Postglacial Pollen Diagram from a Small Typha Swamp in Northwestern Minnesota, Interpreted from Pollen Indicators and Surface Samples. . *Ecological Monographs* 37:145-172.
- Jayen, K., A. Leduc, and Y. Bergeron. 2006. Effect of fire severity on regeneration success in the boreal forest of northwest Québec, Canada. *Ecoscience* 13:143-151.

- Jeglum, J. K. 1981. Black spruce seedling growth and nutrition on Sphagnum and feather moss peats from a northern Ontario peatland. iv + 20 pp.
- Johnson, E. A. 1992. Fire and vegetation dynamics: Studies from the North American boreal forest. Cambridge University Press, Cambridge.
- Johnston, W. F. 1971. Broadcast burning slash favors black spruce reproduction on organic soil in Minnesota. *The Forestry Chronicle* 47:33-35.
- Johnston, W. F. 1977. Manager's handbook for black spruce in the north-central states. General Technical Report NC-34. St. Paul, MN: U.S. Dept. of Agriculture, Forest Service, North Central Forest Experiment Station.
- Johnstone, J., and F. S. Chapin, III. 2006. Effects of Soil Burn Severity on Post-Fire Tree Recruitment in Boreal Forest. *Ecosystems* 9:14-31.
- Johnstone, J. F., and E. S. Kasischke. 2005. Stand-level effects of soil burn severity on postfire regeneration in a recently burned black spruce forest. *Canadian Journal of Forest Research* 35:2151-2163.
- Johnstone, J., L. Boby, E. Tissier, M. Mack, D. Verbyla, and X. Walker. 2009. Postfire seed rain of black spruce, a semiserotinous conifer, in forests of interior Alaska. *Canadian Journal of Forest Research* 39:1575-1588.
- Johnstone, J. F., T. N. Hollingsworth, F. S. Chapin, and M. C. Mack. 2010. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Global Change Biology* 16:1281-1295.
- Kasischke, E.S., M. R. T., Roger D. Ottmar, Nancy H. F. French, Elizabeth E. Hoy, and Evan S. Kane. 2008. Evaluation of the composite burn index for assessing fire severity in Alaskan black spruce forests. *International Journal of Wildland Fire* 17:515-526.
- Keeley, J. E. 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. *International Journal of Wildland Fire* 18:116-126.
- Kemball, K. J., G. G. Wang, and Q.-L. Dang. 2005. Response of understory plant community of boreal mixedwood stands to fire, logging, and spruce budworm outbreak. *Canadian Journal of Botany* 83:1550-1560.
- Key, C., and N. Benson. 2006. Landscape Assessment (LA) Sampling and Analysis Methods. USDA Forest Service Gen. Tech. Rep. RMRS-GTR-164-CD.
- Knowles, P., Perry, D. J., and H. A. Foster. 1992. Spatial Genetic Structure in Two Tamarack [*Larix laricina* (Du ROI) K. Koch] Populations with Differing Establishment Histories. *Evolution* 46(2): 572-576.
- Kuhry, P. 1994. The Role of Fire in the Development of *Sphagnum*-Dominated Peatlands in Western Boreal Canada. *Journal of Ecology* 82:899-910.

- Kuhry, P., B. J. Nicholson, L. D. Gignac, D. H. Vitt, and S. E. Bayley. 1993. Development of *Sphagnum*-dominated peatlands in boreal continental Canada. *Canadian Journal of Botany* 71:10-22.
- Lafleur, B., D. Paré, N. Fenton, and Y. Bergeron. 2011. Growth and nutrition of black spruce seedlings in response to disruption of Pleurozium and Sphagnum moss carpets in boreal forested peatlands. *Plant and Soil* 345:141-153.
- Lavoie, C., and S. Pellerin. 2007. Fires in temperate peatlands (southern Quebec): past and recent trends. *Canadian Journal of Botany* 85:263-272.
- Magnan, G., M. Lavoie, and S. Payette. 2012. Impact of fire on long-term vegetation dynamics of ombrotrophic peatlands in northwestern Québec, Canada. *Quaternary Research* 77:110-121.
- Mallik, A. U. 2003. Conifer Regeneration Problems in Boreal and Temperate Forests with Ericaceous Understory: Role of Disturbance, Seedbed Limitation, and Keystone Species Change. *Critical Reviews in Plant Sciences* 22:341-366.
- McCune, B., and P. Lesica. 1992. The Trade-off between Species Capture and Quantitative Accuracy in Ecological Inventory of Lichens and Bryophytes in Forests in Montana. *The Bryologist* 95:296-304.
- McCune, B. and M.J. Mefford. 2011. Multivariate analysis of ecological data, Version 5.10. MjM Software Design, Gleneden Beach, Oregon.
- McKee, F. R., and B. H. Aukema. 2015. Influence of temperature on the reproductive success, brood development and brood fitness of the eastern larch beetle *Dendroctonus simplex* LeConte. *Agricultural and Forest Entomology* 17:102-112.
- McRae, D.J., Duchesne, L.C., Freedman, B., Lynham, T. J. and S. Woodley. 2001. Comparisons between wildfire and forest harvesting and their implications in forest management. *Environmental Reviews* 9: 223-260.
- MNDNR. 1997. Forest development manual. Minnesota Department of Natural Resources, Division of Forestry, Saint Paul, MN.
- MN DNR. 2003. Field guide to the native plant communities of Minnesota: The Laurentian Mixed Forest Province. Ecological Land Classification Program, Minnesota County Biological Survey, and Natural Heritage and Nongame Research Program. St. Paul, MN, US.
- MNDNR. 2008. Regeneration Monitoring: Procedures and Standards. Division of Forestry, Minnesota Department of Natural Resources, St. Paul, MN.
- MN DNR. 2013a. Subsection Forest Resource Management Plan- Agassiz Lowlands: Strategic Direction and Stand Selection Results. Minnesota Department of Natural Resources, Division of Forestry, Saint Paul, MN.

- MN DNR. 2013b. Tamarack assessment report. Division of Forestry, Minnesota Department of Natural Resources, St. Paul, MN.
- MN DNR. Minnesota Climatology Working Group, State Climatology Office. Published online, retrieved on Nov. 2, 2013 from http://climate.umn.edu/doc/climate_monitor.htm
- Moul, E. T., and M. F. Buell. 1955. Moss Cover and Rainfall Interception in Frequently Burned Sites in the New Jersey Pine Barrens. *Bulletin of the Torrey Botanical Club* 82:155-162.
- Nguyen-Xuan, T., Y. Bergeron, D. Simard, J. W. Fyles, and D. Paré. 2000. The importance of forest floor disturbance in the early regeneration patterns of the boreal forest of western and central Quebec: a wildfire versus logging comparison. *Canadian Journal of Forest Research* 30:1353-1364.
- Nyland, R. D. 2007. *Silviculture : concepts and applications*. Long Grove, Ill. : Waveland Press, Long Grove, Ill.
- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P.R. Minchin, R.B. O'Hara, G. L. Simpson, P. Solymos, M. Henry, H. Stevens and H. Wagner. 2015. *vegan: Community Ecology Package*. R package version 2.3-2.
- O'Hara, R. B., and D. J. Kotze. 2010. Do not log-transform count data. *Methods in Ecology and Evolution* 1:118-122.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climatic change. *Annual Review of Ecology and Systematics*, 37. pp. 637–669
- Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. Compounded perturbations yield ecological surprises. *Ecosystems* 1:535-545.
- Paquette, M., C. Boudreault, N. Fenton, D. Pothier, and Y. Bergeron. 2016. Bryophyte species assemblages in fire and clear-cut origin boreal forests. *Forest Ecology and Management* 359:99-108.
- Perera, A. H., and W. Cui. 2010. Emulating natural disturbances as a forest management goal: Lessons from fire regime simulations. *Forest Ecology and Management* 259:1328-1337.
- Pothier, D. 2000. Ten-year results of strip clear-cutting in Quebec black spruce stands. *Canadian Journal of Forest Research* 30:59-66.
- R Core Team, 2014. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rein, G., N. Cleaver, C. Ashton, P. Pironi, and J. L. Torero. 2008. The severity of smouldering peat fires and damage to the forest soil. *Catena* 74:304-309.
- Renard, S. M., S. Gauthier, N. J. Fenton, B. Lafleur, and Y. Bergeron. 2016. Prescribed burning after clearcut limits paludification in black spruce boreal forest. *Forest Ecology and Management* 359:147-155.

- Roberts, M. R. 2004. Response of the herbaceous layer to natural disturbance in North American forests. *Canadian Journal of Botany* 82:1273-1283.
- Robroek, B.J.M., Limpens, J., Breeuwer, A. & Schouten, M.G.C. (2007) Effects of water level and temperature on performance of four Sphagnum mosses. *Plant Ecology* 190, 97–107.
- Rowe, J. S., and G. W. Scotter. 1973. The Ecological Role of Fire in Natural Conifer Forests of Western and Northern America: Fire in the boreal forest. *Quaternary Research* 3:444-464.
- Rowe, J. S., 1983. Concepts of fire effects on plants, individuals and species. Pages 135–153 in R. W. Wein & D. A. MacLean (eds.). *The Role of Fire in Northern Circumpolar Ecosystems*. John Wiley & Sons, New York, New York.
- Ryan, K.C., 2002. Dynamic interactions between forest structure and fire behavior in boreal ecosystems. *Silva Fennica*, 36(1), pp.13-39.
- Rydin, H. 1986. Competition and niche separation in Sphagnum. *Can. J. Bot.* 64: 1817–1824.
- Rydin, H., and J. K. Jeglum. 2013. *The Biology of Peatlands*. 2nd edition. Oxford University Press, Oxford.
- Turetsky, M., Wieder, K., Halsey, L., & Vitt, D. 2002. Current disturbance and the diminishing peatland carbon sink. *Geophysical Research Letters*, 29(11). doi: 10.1029/2001gl014000
- Turetsky, M. R., B. D. Amiro, E. Bosch, and J. S. Bhatti. 2004. Historical burn area in western Canadian peatlands and its relationship to fire weather indices. *Global Biogeochemical Cycles* 18.
- Turetsky, M. R. and V. St. Loius. 2006. Disturbance in Boreal Peatlands. In *Boreal Peatland Ecosystems*. R.K.Wieder and D.H.Vitt (Eds.) Springer-Verlag. Berlin.
- Turetsky, M. R., M. C. Mack, T. N. Hollingsworth, and J. W. Harden. 2010. The role of mosses in ecosystem succession and function in Alaska's boreal forest *Canadian Journal of Forest Research* 40:1237-1264.
- Turner, M. G., W. H. Romme, R. A. Reed & G. A. Tuskan, 2003. Post-fire aspen seedling recruitment across the Yellowstone (USA) landscape. *Landscape Ecology*, 18: 127–140.
- Schimmel, J., and A. Granström. 1996. Fire Severity and Vegetation Response in the Boreal Swedish Forest. *Ecology* 77:1436-1450.
- Soverel, N. O., D. D. B. Perrakis, and N. C. Coops. 2010. Estimating burn severity from Landsat dNBR and RdNBR indices across western Canada. *Remote Sensing of Environment* 114:1896-1909.
- Uchytil, Ronald J. 1991. *Larix laricina*. In: *Fire Effects Information System*, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: <http://www.fs.fed.us/database/feis/> [2015, December 10].

- Ulrich, W., and M. Almeida-Neto. 2012. On the meanings of nestedness: back to the basics. *Ecography* 35:865-871.
- Veverica, T. J., E. S. Kane, and E. S. Kasischke. 2012. Tamarack and black spruce adventitious root patterns are similar in their ability to estimate organic layer depths in northern temperate forests. *Canadian Journal of Soil Science* 92:799-802.
- Viereck, L.A. and W.F. Johnson. 1990. *Picea mariana*. In: *Silvics of North America*, volume 1: Conifers. R.M. Burns and B.H. Honkala (ed.). USFS Agriculture Handbook 654, Washington D.C., pp. 227-237.
- Viglas, J. N., C. D. Brown, and J. F. Johnstone. 2013. Age and size effects on seed productivity of northern black spruce. *Canadian Journal of Forest Research* 43:534-543.
- Veilleux-Nolin, M., and S. Payette. 2012. Influence of recent fire season and severity on black spruce regeneration in spruce–moss forests of Quebec, Canada. This article is one of a selection of papers from the 7th International Conference on Disturbance Dynamics in Boreal Forests. *Canadian Journal of Forest Research* 42:1316-1327.
- Vitt, D. H., and N. G. Slack. 1984. Niche diversification of *Sphagnum* relative to environmental factors in northern Minnesota peatlands. *Canadian Journal of Botany* 62:1409-1430.
- Waddington J. M., Morris P. J., Kettridge N., Granath G., Thompson D. K. and Moore P. A. 2015. Hydrological feedbacks in northern peatlands, *Ecohydrol.* 113–127.
- Wang, G. G., and K. J. Kembell. 2005. Effects of fire severity on early development of understory vegetation. *Canadian Journal of Forest Research* 35:254-262.
- Wein, R. W., 1983. Fire behaviour and ecological effects in organic terrain. Pages 81–93 in R. W. Wein & D. A. MacLean (eds.). *The Role of Fire in Northern Circumpolar Ecosystems*. John Wiley & Sons, New York, New York.
- WDNR. 2006. *Silviculture handbook*. State of Wisconsin, Department of Natural Resources, Madison, WI.
- Zasada, J. C., R. A. Norum, R. M. Vanveldhuizen, and C. E. Teutsch. 1983. Artificial regeneration of trees and tall shrubs in experimentally burned upland black spruce feather moss stands in Alaska. *Canadian Journal of Forest Research*. 13:903-913.
- Zoltai, S. C., L. A. Morrissey, G. P. Livingston, and W. J. Groot. 1998. Effects of fires on carbon cycling in North American boreal peatlands. *Environmental Reviews* 6:13-24.
- Zuur, A., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed effects models and extensions in ecology with R*. Springer Science & Business Media.

Appendix A. Canopy and ground layer consumption class descriptions used for field assessments of fire severity.

	Description
Substrate Consumption Class	0 Unburned
	1 Most peat unburned, with only occasional spot fires and few hummocks singed or charred. Mosses largely all identifiable. Microtopography remains largely intact. Burned out tree bases are rare.
	2 Most hummocks at least superficially singed or charred, with many mosses still identifiable. Occasional deep burnouts around tree bases, where only a small amount of roots are exposed immediately surrounding tree base (<30% of trees).
	3 More than 50% of microtopography, or fibric peat, still remains where upper peat surface has only been superficially singed on upper hummocks, but where mosses are no longer unrecognizable in those areas. 30-60% of trees bases have deep burnouts, forming many interconnected areas of lawns between trees with many surface roots exposed.
	4 Less than 50% of microtopography, or fibric peat, surface remains, where considerable reduction of peat has occurred exposing areas occasional areas of poorly-decomposed peat. Hummocks are significantly charred or reduced. Most tree bases (60-90%) have deep burnouts around boles leaving many roots exposed. Lawns are common, often with <i>Polytrichum</i> or <i>Marchantia</i> or other colonizing bryophytes.
	5 Extensive areas of peat consumed where less than 30% of original upper peat surface remains in small patches. Many areas of underlying, highly-decomposed peat exposed, with a significant reduction of hummocks. Majority (>90%) of tree bases have expansive burning around boles where most roots are now exposed. A significant amount of water-filled hollows.
	6 Upper peat surface mostly or entirely consumed (<10% remains). All tree bases exposed. No microtopography remains, except for small patches of lawn. Majority of bryophytes are colonizing species colonizing tree roots. No <i>Sphagnum</i> remains.

Canopy Consumption Class		Description
	0	No tree mortality
	1	Tree deceased with no needles/branches consumed, scorch height evident on bole
	2	Tree deceased with all needles and some secondary and tertiary branches consumed
	3	Tree deceased with all needles and tertiary branches consumed, few secondary branches remain
	4	Tree deceased with all needles, tertiary, and secondary branches consumed, >30% of primary branches remaining
	5	Tree deceased with all needles, tertiary, and secondary branches consumed, <30% of primary branches remaining
	6	Tree deceased with all needles and branches consumed, bole charring present

Appendix B. Correlations (Kendall's τ) between the understory vascular and non-vascular species composition and non-metric multidimensional scaling Axes 1 and 2 in Figure 3.1 and 3.2 for a) black spruce bog sites and b) rich tamarack swamp sites. Values in bold have significant correlations with axes scores ($P < 0.05$).

NPC	Species	Axis 1	Axis 2	Species	Axis 1	Axis 2
a) BSB	<i>Andromeda polifolia</i>	0.01	-0.52	<i>Picea mariana</i>	0.56	0.17
	<i>Aulacomnium palustre</i>	0.33	0.25	<i>Pleurozium schreberi</i>	-0.35	0.54
	<i>Betula papyrifera</i>	0.46	0.19	<i>Polytrichum strictum</i>	0.13	-0.63
	<i>Carex aquatilis</i>	0.39	0.06	<i>Populus tremuloides</i>	0.34	-0.52
	<i>Carex magellanica</i>	0.39	0.30	<i>Ptilium crista-castrensis</i>	-0.44	0.32
	<i>Dicranum polysetum</i>	-0.42	0.39	<i>Rhododendron groenlandicum</i>	-0.47	-0.01
	<i>Epilobium leptophyllum</i>	0.49	0.24	<i>Salix discolor</i>	0.44	-0.21
	<i>Epilobium</i> spp. (wide-leaved)	0.54	0.28	<i>Salix planifolia</i>	-0.38	-0.51
	<i>Equisetum arvense</i>	0.44	0.31	<i>Solidago uliginosa</i>	0.44	0.31
	<i>Equisetum sylvaticum</i>	0.42	0.32	<i>Sphagnum angustifolium</i>	0.11	0.50
	<i>Eriophorum angustifolium</i>	0.48	0.21	<i>Sphagnum magellanicum</i>	0.03	0.50
	Fire bryophyte group	0.18	-0.56	<i>Vaccinium angustifolium</i>	-0.52	-0.09
	<i>Marchantia aquatica</i>	0.03	-0.62			
NPC	Species	Axis 1	Axis 2	Species	Axis 1	Axis 2
b) RTS	<i>Agrostis scabra</i>	0.56	-0.00	<i>Lysimachia thyrsiflora</i>	0.35	-0.05
	<i>Alnus incana</i>	-0.28	0.40	<i>Maianthemum canadense</i>	-0.24	0.18
	<i>Aulacomnium palustre</i>	-0.28	-0.43	<i>Marchantia aquatica</i>	0.69	-0.08
	<i>Calamagrostis canadensis</i>	0.32	-0.32	<i>Mitella nuda</i>	-0.50	0.20
	<i>Campanula aparinoides</i>	0.51	0.04	<i>Orthilia secunda</i>	-0.47	-0.43
	<i>Campylium stellatum</i>	-0.41	-0.26	<i>Plagiomnium ellipticum</i>	-0.55	-0.07
	<i>Carex chordorrhiza</i>	0.45	-0.29	<i>Pleurozium schreberi</i>	-0.54	-0.28
	<i>Carex diandra</i>	0.49	-0.17	<i>Polytrichum strictum</i>	0.42	0.16

NPC	Species	Axis 1	Axis 2	Species	Axis 1	Axis 2
RTS,	<i>Carex interior</i>	0.43	-0.11	<i>Populus tremuloides</i>	0.62	0.20
Cont.	<i>Carex lacustris</i>	0.33	0.47	<i>Pyrola asarifolia</i>	-0.40	-0.21
	<i>Carex leptalea</i>	-0.23	0.27	<i>Rhododendron groenlandicum</i>	-0.54	-0.23
	<i>Carex magellanica</i>	-0.25	-0.57	<i>Rubus arcticus</i>	-0.01	-0.52
	<i>Carex pseudocyperus</i>	0.39	-0.28	<i>Rubus pubescens</i>	-0.24	0.51
	<i>Carex tenuiflora</i>	0.35	-0.24	<i>Rumex britannica</i>	0.27	-0.27
	<i>Carex trisperma</i>	-0.24	0.54	<i>Salix discolor</i>	0.32	0.42
	<i>Cicuta bulbifera</i>	0.51	-0.19	<i>Salix pedicellaris</i>	0.01	-0.53
	<i>Climacium dendroides</i>	-0.48	0.04	<i>Salix petiolaris</i>	0.43	0.34
	<i>Cornus sericea</i>	-0.44	0.06	<i>Salix serissima</i>	0.46	-0.20
	<i>Epilobium</i> spp. (wide-leaved)	0.42	0.08	<i>Scutellaria galericulata</i>	-0.15	0.46
	<i>Epilobium leptophyllum</i>	0.01	0.51	<i>Sphagnum angustifolium</i>	-0.55	0.05
	<i>Epilobium palustre</i>	-0.29	-0.52	<i>Sphagnum magellanicum</i>	-0.32	-0.13
	<i>Fire group</i>	0.73	0.02	<i>Sphagnum warnstorffii</i>	-0.30	-0.41
	<i>Fragaria virginiana</i>	-0.22	0.33	<i>Stellaria longifolia</i>	0.53	-0.10
	<i>Galium triflorum</i>	0.02	0.61	<i>Symphyotrichum puniceum</i>	-0.19	0.38
	<i>Helodium blandowii</i>	-0.26	-0.18	<i>Thuidium delicatulum</i>	-0.44	0.04
	<i>Larix laricina</i>	-0.30	0.18	<i>Trientalis borealis</i>	-0.20	0.34
	<i>Linnaea borealis</i>	-0.36	-0.03	<i>Typha</i> spp.	0.64	0.05
	<i>Lonicera oblongifolia</i>	-0.23	-0.39	<i>Vaccinium oxycoccos</i>	-0.36	-0.25
	<i>Lonicera villosa</i>	-0.42	0.05	<i>Vaccinium vitis-idaea</i>	-0.40	0.06