



Early response of ground layer plant communities to wildfire and harvesting disturbance in forested peatland ecosystems in northern Minnesota, USA



Erika R. Rowe^{a,*}, Anthony W. D'Amato^b, Brian J. Palik^c, John C. Almendinger^d

^a Department of Forest Resources, University of Minnesota, St. Paul, MN 55108, USA

^b Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, VT 05495, USA

^c USDA Forest Service Northern Research Station, Grand Rapids, MN 55744, USA

^d Minnesota Department of Natural Resources, Grand Rapids, MN 55744, USA

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ABSTRACT

A rare, stand-replacing fire in northern Minnesota, USA provided the opportunity to compare the effects of wildfire and timber harvesting in two peatland forest communities, nutrient-poor black spruce (*Picea mariana*) bogs (BSB) and nutrient-rich tamarack (*Larix laricina*) swamps (RTS). We found the response between the two communities and their corresponding vegetation to be highly sensitive to different types and severity of disturbance, ranging from modest shifts in ground layer vascular plants and bryophyte species abundance, to wholesale plant community transformation resulting from the removal of the upper peat surface. Fire 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. Our results also suggest that ecosystem recovery will be rapid after low-severity fire in these areas, given that localized areas of peat combustion created suitable microsites for black spruce seedling establishment ensuring this species will remain a component of the post-fire communities. In contrast, tamarack regeneration was only documented in harvested RTS sites. For BSB, there was spatial heterogeneity in peat consumption as a result of fire behavior interacting with varying moisture conditions throughout peat hummocks and hollows. Light to moderate burning created suitable black spruce seedbeds by reducing cover of *Sphagnum* moss and the dominant ericaceous shrub *Rhododendron groenlandicum*, and increasing the cover of pioneering mosses, such as *Polytrichum strictum*. In RTS sites, fire typically consumed the entire upper peat surface, resulting in homogenization of community composition and retrogression towards marsh-like conditions dominated by cattails (*Typha* spp.). These findings underscore the importance of accounting for post-fire microsite heterogeneity when developing silvicultural systems for emulating natural disturbance processes in conifer forests with a naturally accumulated surface peat layer. In addition, the state shifts observed in areas experiencing high severity fire suggest that increases in fire frequency and severity may create significant challenges to maintaining forested conditions in these areas, particularly in RTS.

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1. Introduction

As the ecological importance of ground layer plant communities is increasingly acknowledged, the impacts of forest harvesting on these communities has received increased attention (Gilliam, 2007). Management approaches are also more commonly integrating aspects of natural disturbance regimes, such as disturbance fre-

quency and severity, to satisfy ecologically-based objectives (Long, 2009). Yet, the response of the ground layer to a range of disturbances continues to be a challenging element to predict. Given the higher number of species and life-history strategies of ground layer plants relative to the overstory (Roberts, 2004; Gilliam, 2007), a better understanding of how harvests and natural disturbances affect ecosystem structure and composition is needed. Furthermore, these concepts are still in their infancy with regard to the extensive forested peatlands in North America, where deep peat and varying moisture conditions contribute to the complexity of predicting ground layer plant community response to disturbance.

* Corresponding author at: Minnesota Department of Natural Resources, 500 Lafayette Road, Box 25, St. Paul, MN 55155, USA.

E-mail address: erika.rowe@state.mn.us (E.R. Rowe).

Stand-replacing wildfire, though rare, has been an important, historical disturbance influencing forest dynamics in boreal landscapes for millennia, with the Agassiz Lake Plain landscape shaped by many of these disturbances (Heinselman, 1968, 1970). However, due to fire suppression, disturbance regimes have shifted from wildfire to clearcutting as the primary disturbance (Pidgen and Mallik, 2013). Clearcutting-based regeneration methods are widely employed in many regions, including much of the managed area of the boreal peatlands (Locky and Bayley, 2007), where this approach has been suggested as a surrogate for stand-replacing fire events and for encouraging the regeneration of shade-intolerant tree species, such as tamarack (*Larix laricina* (Du Roi) K. Koch; Nyland, 2007). Yet, little is understood as to how post-disturbance recovery of the ground layer differs between clearcutting and stand-replacing disturbances, like fire, in these ecosystems. Despite similarities in levels of overstory disturbance between stand-replacing fires and clearcut harvests, i.e., significant tree mortality (or removal, in the case of harvest), there are also key differences, such as the amount of live and dead-tree legacies and the level of soil or peat disturbance (cf. Roberts, 2004). With wildfire, there may be considerable spatial differences in the residual peat layer resulting from moisture gradients in hummocks and hollows (Benscoter et al., 2005), 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 also increase pH and nitrogen mineralization rates in more severely burned areas (Dyrness and Norum, 1983; McRae et al., 2001), whereas harvesting has less impact on nutrient cycling relative to wildfire, with logging largely removing macronutrients contained in tree biomass (Brumelis and Carleton, 1988; McRae et al., 2001; Roberts, 2004; Kembell et al., 2005). These important differences between natural and anthropogenic disturbances have the potential to generate diverging ecosystem responses, and thus post-disturbance patterns of vegetation recovery, including both vascular and nonvascular plants (Roberts, 2004; McRae et al., 2001; Franklin et al., 2007; Johnstone et al., 2010; Fenton et al., 2013; Pidgen and Mallik, 2013).

Examining the influence of disturbance processes on the presence of ericaceous shrubs is also an important consideration in peatland communities, because these shrubs are known to 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), can regenerate vigorously from belowground root rhizomes post-disturbance (Viereck and Johnson, 1990; Mallik, 2003). Given the comparatively low levels of ground layer disturbance associated with harvesting relative to wildfire, post-harvest areas generally lack the suitable seedbeds for conifer regeneration that fire creates, i.e., reduced peat microtopography and ericaceous competition (Mallik, 2003; Hébert et al., 2010; Lafleur et al., 2011), with several studies documenting increases in ericaceous cover following harvesting in black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb) communities (Groot 1996; Dussart and Payette 2002).

To compare post-disturbance plant community and regeneration patterns between fire and harvest, this study takes advantage of a rare wildfire 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 on wildfire in lowland conifer peatlands. This region represents the southernmost extent for boreal peatlands in North America and is uniquely situated to examine the impacts of wildfire and forest harvesting as these ecosystems are projected to be significantly impacted by

changes in future climate and altered disturbance regimes (Kasischke and Turetsky, 2006; Galatowitsch et al., 2009; Brown and Johnstone, 2012; Moritz et al., 2012).

The overall objective of this study was to quantify differences in seedling regeneration associated with post-disturbance seedbed condition, as well as ground layer plant community composition, two growing seasons after wildfire and clearcut harvesting disturbances in two forested peatland types. Many of the vascular and nonvascular species compositional differences following these two disturbance types are related to differences in ground layer disturbance associated with microsite conditions. By relating early vegetation development observed following wildfires and clearcut harvesting to the level of disturbance, we sought to address the following questions: (1) how does disturbance severity, as well as type, affect early regeneration success of conifer seedlings in nutrient-rich tamarack swamps and nutrient-poor, black spruce bogs; (2) how 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?

2. Methods

2.1. Study area

The study area is located primarily in the Red Lake Wildlife Management Area (WMA) in Beltrami and Lake of the Woods counties, Minnesota, USA (Fig. 1). A few harvested sites were also located in the neighboring Beltrami and Pine Island State Forests, as the WMA had a limited number of recent clearcuts that met our criteria, thus requiring us to expand our search. This entire region was formerly occupied by Glacial Lake Agassiz and is characterized by flat (topographic relief is less than 15 m), poorly drained soils of lacustrine origin that have developed through paludification into the most extensive boreal peatlands in the lower United States (Glaser, 1987).

The climate for this region is characterized as mid-continental, where annual precipitation is substantially more than evaporation with the water table at or close to the surface, thus inhibiting decomposition of plant material. 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, annual 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 98–111 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>).

This study focused on two forested peatland communities: nutrient-poor black spruce bogs (BSB), and nutrient-rich tamarack swamps (RTS). Black spruce-dominated bogs in the study area occur on deep peat (>1 m), which isolates the plant rooting zone from the underlying mineral-rich groundwater. Surface water is typically acidic (pH < 4.2), with nutrient inputs supplied primarily by atmospheric precipitation, limiting species diversity to a small subset adapted to tolerate these conditions. Tamarack swamps also occur on well-developed peat, although less so (typically over 40 cm) than bogs. These communities are influenced by mineral-rich groundwater (pH 5.5–7), thus species diversity is much higher than in black spruce bogs. These communities were selected because they represent the two plant communities most affected by the North Minnie wildfire and they are commonly managed for forest products.

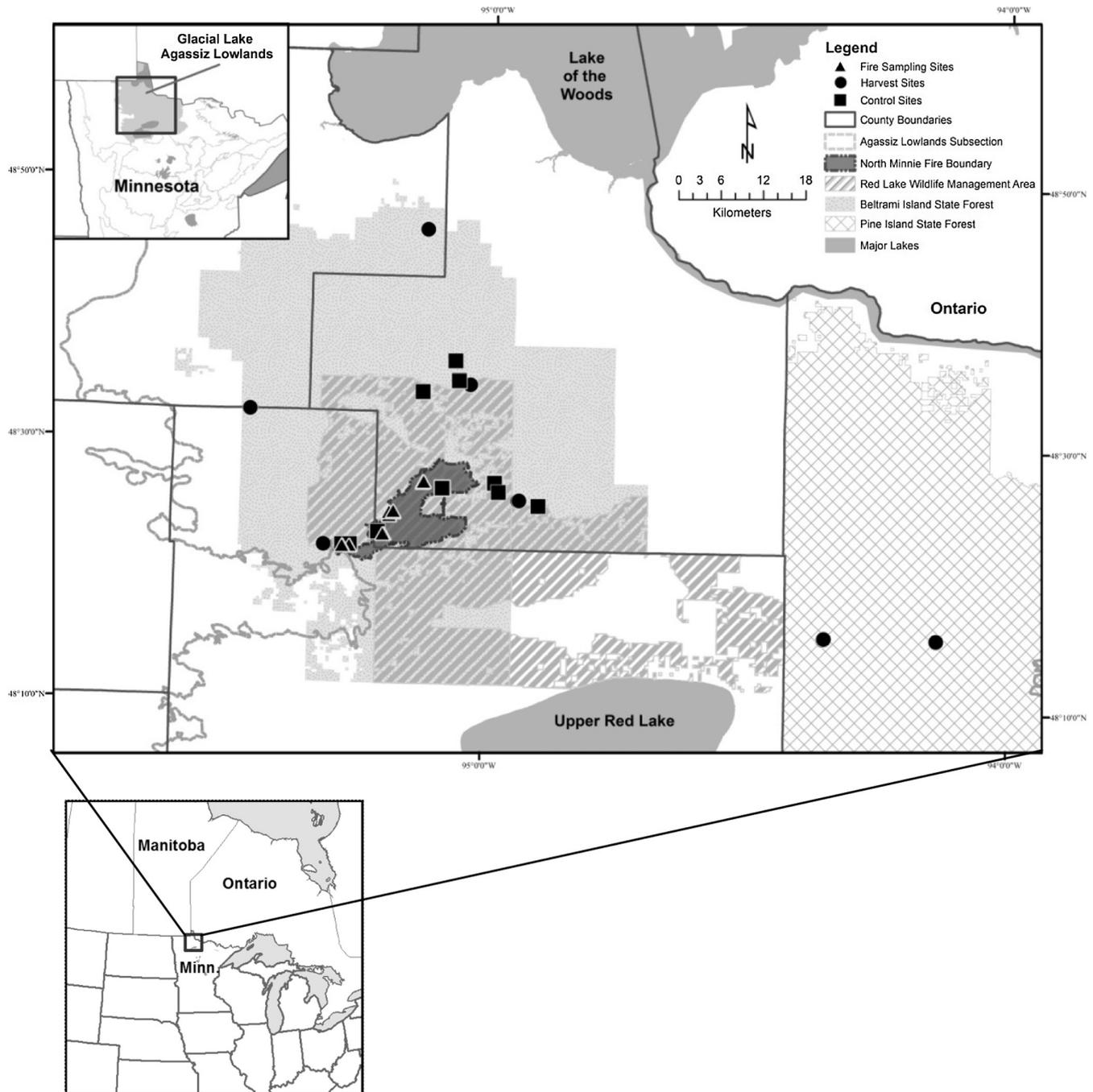


Fig. 1. Location of harvest, fire, and control plots in northern Minnesota, U.S.A. with the North Minnie fire area in dark grey.

2.2. Site selection

A differenced Normalized Burn Ratio (dNBR; Banskota and Falkowski, unpublished data 2013) map of the study area was created to initially identify a pool of candidate sites representing three different fire severity categories (low, moderate, and high). With the aid of this remotely sensed data, as well as field reconnaissance, a total of five disturbance conditions (low, moderate, and high fire severity, harvested and undisturbed) were sampled across the two peatland communities described above (Table 1). Each burn severity had at least two replications and each replication had at least two plots per site. Undisturbed controls and harvested sites had 1–3 plots per site depending on size of the area. Harvested

plots were replicated across three BSB clearcuts and four RTS clearcuts, with each replication (or clearcut) representing 1–2 plots.

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). Because the dNBR approach has primarily been used to remotely sense fire severity for upland coniferous forests, its effectiveness to assess forested peatlands and peat consumption has been more limited (Allen and Sorbel, 2008; Kasischke et al., 2008; Keeley, 2009). Therefore,

Table 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.

Community	Treatment groups					Total
	Undisturbed (control)	Low severity fire	Mod severity fire	High severity fire	Harvested	
BSB	6	4	4	–	6	20
RTS	7	2	3	4	5	21
Total	13	6	7	4	11	41

fire-severity classes were verified in the field, aided by two measures of fire severity that were constructed to quantify tree canopy consumption and peat consumption (c.f., Greene et al., 2007; Kasischke et al., 2008; Collier and Mallik, 2010). However, we found that quantifying peat consumption was a difficult characteristic to measure consistently, primarily because of the well-developed peat (>1 m) in BSB, where this measurement was most relevant. Alternatively, a qualitative assessment of peat consumption was constructed. For further details on how categories of fire severity were verified in the field for both BSB and RTS sites, see Rowe (2015).

To ensure that stand age and composition of forest sites were similar prior to selection, we reviewed aerial photography and compiled forest inventory data from the Minnesota Department of Natural Resources, which included information on dominant canopy species, stand age, site index and density. Several stands ages were also confirmed based on increment cores collected from adjacent, undisturbed sites. From this information we were able to determine that prior to disturbance (both fire and harvest), stand ages ranged from 90 to 180 years for BSB sites and 50 to 115 years for RTS sites. Harvested plots were selected from recent clearcuts in the Beltrami Island and Pine Island State Forests that were harvested the same year as the North Minnie Fire (winter harvests in 2012) and prescribed for natural regeneration, thus they had not received aerial seeding. Clearcut size for BSB sites ranged 8.5–22 ha and 8–29 ha for RTS. Unburned sites were selected from areas of the landscape spanning similar age ranges and were typically located either adjacent to disturbed sites or from nearby stands that were identified as the same community type.

For each stand within the study, representative plant communities of burned and harvested areas were delineated and plots were randomly selected in ArcGIS. Individual plots were located at least 90 m from the impacts of roads or ditches and at least 60 m away from another plot. 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 harvested areas prior to data collection.

2.3. Field measurements

Plots were sampled during the second growing season following the North Minnie Fire using a series of 11.3 m (400 m²) fixed-radius plots. To evaluate tree regeneration, ericaceous shrub abundance and seedbed condition (microtopography), six-1 m² nested quadrats were placed along one of three transects at 4 and 10 m, emanating from within the larger, fixed-radius 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). 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 lawns (see Rydin and Jeglum, 2013). Each quadrat also included a smaller, nested 0.5 m² plot, where bryophyte species were identified and their percent cover was visually estimated (see McCune and Lesica, 1992).

2.4. Statistical analysis

Mixed model analysis of variance (ANOVA) was used to examine the impact of disturbance severity levels (i.e., low, moderate, and high fire severity, harvested and undisturbed) 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. For RTS sites, all ericaceous species were analyzed together because *Rhododendron* makes up the vast majority of this total cover. All species observed in the *Sphagnum* sect. *Acutifolia* (e.g., *S. fuscum*, *S. rubellum*, *S. capillifolium*, *S. russowii*, *S. subtile*) for the BSB plots were grouped together for ANOVAs, as these species largely consist of hummock-forming *Sphagnum*, several of which are notoriously difficult to tell apart without further microscopic cellular differentiation. For the RTS plots, where diversity of *Sphagnum* species was much higher, and the abundance of any one species was fairly low, all *Sphagnum* species were grouped together for ANOVAs.

Analyses of conifer seedling count data were conducted with generalized linear mixed models (GLMMs) with a negative binomial distribution and a logarithmic link function to determine the effect of disturbance on seedling density. A GLMM 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).

For all ANOVAs and GLMMs, disturbance type was treated as a fixed effect and site as a random effect. 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 GLMM model – see above). All analyses were performed in R version 3.1.2 (R Core Team, 2014).

Non-metric multidimensional scaling (NMS) was used to examine the variation in community composition for both forest community types (i.e., black spruce bogs and rich tamarack swamps) within and among the main disturbance categories (i.e., undisturbed, fire, harvest) for all ground layer species (including bryophytes). Fire severity levels were grouped together as a single

disturbance category to aid in the interpretability of ordination results. NMS was performed using PC-ORD version 6.0 (McCune and Mefford, 2011), 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 < 0.001).

Multi-response permutation procedures (MRPP) in PC-ORD were used to test whether there was a significant difference between disturbance categories (i.e., harvest, fire, undisturbed) based on species composition. Sørensen's distance metrics were also used for MRPP, which was followed by indicator species analysis (ISA; Dufrene and Legendre, 1997) to determine which species were significantly associated with a particular disturbance category. 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.

3. Results

3.1. Seedling regeneration

For black spruce bog (BSB) plots, the abundance of spruce seedlings (stems·m⁻²) was significantly affected by disturbance type, with seedling densities significantly higher in low severity fire plots compared to moderate levels of fire, as well as harvested and undisturbed control plots (Table 2). Harvested plots were no different than controls or moderate severity fire 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 2).

For the rich tamarack swamp (RTS) plots, only harvest disturbance had a significant increase in tamarack seedling densities (stems·m⁻²). All remaining disturbance categories were not significantly different from each other and had mean seedling counts closer to zero (Table 3). Similar to the BSB plots, aspen seedlings also increased significantly for RTS burned plots compared to undisturbed and harvested plots; however, significant increases

were only found for the moderate and high severity levels of fire (Table 3).

3.2. Bryophytes and microtopography

Total *Sphagnum* cover in the BSB plots was significantly reduced by fire at both low and moderate fire severities compared to undisturbed controls and harvested plots. This overall reduction in cover was considerably greater for moderate fire severity plots (Table 2). In examining individual species or group cover, *Sphagnum angustifolium* (Warnstorff) Jensen, 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, as well as with harvest disturbance, with no significant difference between these two disturbance categories (Table 2). Cover for *Sphagnum magellanicum* Brid., a species characteristic of lower hummocks and lawns, had significantly lower cover primarily at the moderate fire severity, compared to undisturbed controls and harvests (Table 2). In contrast to *Sphagnum* cover, *Polytrichum strictum* Brid., a post-fire colonizing moss species, had significantly increased cover relative to controls and harvested plots for the BSB sites (Table 2). There was no difference in cover of *P. strictum* between harvested and control areas.

Disturbance also influenced moss community structure at RTS plots, 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). Post-fire bryophyte cover increased significantly in moderate and high fire severity plots compared with controls or harvested plots (Table 3). These post-fire mosses consisted of *Ceratodon purpureus* (Hedw.) Brid., *Funaria hygrometrica* Hedwig, *Pohlia nutans* (Hedw.) Lindberg, *Polytrichum strictum*, and *Ptychostomum pseudotriquetrum* (Hedw.) Spence 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 plots, due in large part to substantial variation in documented cover of hummocks, hollows and lawns

Table 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 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 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
<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
<i>Andromeda polifolia</i> cover (%)	1.3(0.8) ^a	3.5(0.7) ^a	1.3(0.3) ^a	0.3(0.2) ^a	5.2	0.03
<i>Kalmia polifolia</i> cover (%)	6.6(2.2) ^a	10.3(3.8) ^a	4.4(1.6) ^a	2.3(1.0) ^a	2.1	0.2
<i>Chamaedaphne calyculata</i> cover (%)	6.5(3.4) ^a	17.8(6.3) ^a	3.2(1.6) ^a	5.4(3.5) ^a	2.7	0.11
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) ^a	2.1(0.1) ^b	1.7(0.1) ^{ab}	1.9(0.2) ^b	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

Table 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 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 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
Vascular 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*.

within assigned disturbance classes (Table 2). Conversely, microtopographic features for the RTS plots were significantly impacted by disturbance with fire reducing total cover of hummocks significantly, relative to controls and harvests (Table 3). 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. Mean percent cover of hollows was similar among fire severity categories, but significantly higher than hollow cover in 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).

3.3. Ericaceous shrubs

Total combined ericaceous cover for the BSB plots was not significantly affected by disturbance; however, in examining cover of individual species, as well as their stem densities, *Rhododendron* was significantly reduced at low levels of fire severity (Table 2). This reduction was not statistically different from harvested plots. Conversely, *Andromeda polifolia* had a slight increase in stem densities and cover at low levels of fire severity disturbance relative to the other categories. Although only a slight increase, it was found to be a statistically significant increase over other disturbance categories.

For RTS plots, fire and harvest significantly reduced the total mean ericaceous cover at all levels of fire severity, relative to controls; however, there were no differences between fire categories and harvested plots in terms of ericaceous cover (Table 3).

3.4. 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 plots 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 2). Bryophyte species richness and diversity (H') for BSB plots, on the other hand, did not appear to be affected by disturbance, as no significant differences were found (Table 2).

A similar, but reverse trend was found for the RTS plots, where no differences were detected between vascular plant species for

both richness and diversity between disturbance groups (Table 3). The differences in community composition for RTS plots suggest that changes in the cover and frequency of ground layer species after fire and harvest are offset by increases in other species, leading to little net change in richness or diversity in the understory following disturbance. While species richness for RTS plots was highly variable, ranging from 19 to 42 species, there was no clear relation to disturbance for mean species richness. In contrast, significant differences were detected for bryophyte species richness and diversity with fire and harvest disturbance having the most notable reductions in mean cover for species richness (Table 3).

3.5. Ground layer 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 (Fig. 2a). These disturbance categories were captured by axis one and two of the ordination, which accounted for 42% and 27% of the total variance (77%; Fig. 2a). Harvested plots had high positive first-axis scores largely due to greater species richness. Species significantly correlated with this portion of axis one were willow-herbs (*Epilobium* spp.), bog birch (*Betula papyrifera* Marshall), pussy willow (*Salix discolor* Pursh) and the cotton-grass *Eriophorum angustifolium* Honck. (Appendix A). The negative end of axis one (i.e., undisturbed controls) was significantly correlated with a higher abundance of advance regeneration of *Picea mariana* through layering, ericaceous species such as blueberry (*Vaccinium angustifolium* Aiton) and *Rhododendron*, as well as the mosses *Dicranum polysetum* Sw. and *Ptilidium crista-castrensis* (Hedw.) De Not. (Fig. 2a; Appendix A).

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 harvest and control plots (Appendix A). Species that differentiated either end of axis two were primarily bryophytes with *Polytrichum strictum* and other post-fire, colonizing mosses, such as *Ceratodon purpureus*, significantly correlated with the negative portion of the axis (i.e., fire disturbance), whereas the feathermoss *Pleurozium schreberi* (Brid.) Mitt. was more strongly associated with the positive end of this axis (i.e., harvests and controls; Fig. 2a).

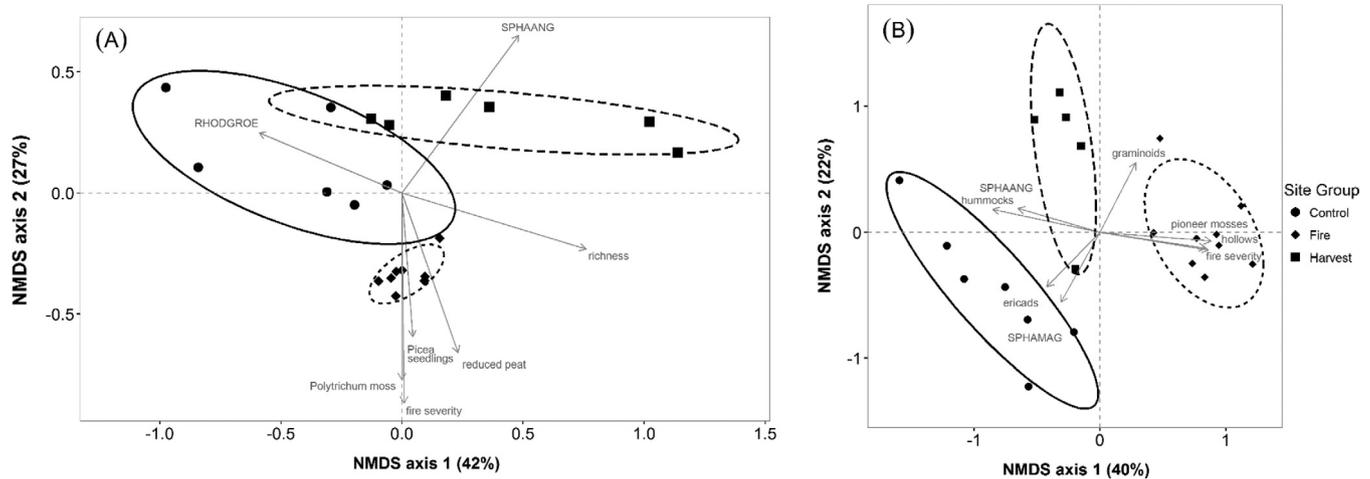


Fig. 2. Non-metric multidimensional scaling (NMS) ordination of ground layer species composition across disturbance treatments for (a) black spruce bog and (b) rich tamarack swamp. Arrows indicate the nature and strength of significant correlations of variables with the ordination axes with 80% confidence ellipses around plots from each disturbance group. See Appendix A for species correlations with NMS axes 1 and 2. SPHAANG = *Sphagnum angustifolium*; SPHAMAG = *Sphagnum magellanicum*; RHODGROE = *Rhododendron groenlandicum*.

Several species were identified as significant indicators of a given disturbance category for BSB (per Indicator Species Analysis, $p < 0.1$; Table 4). Graminoid species, including *Carex trisperma*, *C. chordorrhiza*, *Eriophorum angustifolium*, and the moss *Sphagnum angustifolium* were indicators of 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* L.), although both species were low in cover. 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-idaea* L.).

For the RTS plots, the post-disturbance understory species composition was even more discretely 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. 2b). The three disturbance categories were clustered within their respective groups 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 severity gradient with fire plots on the positive end and control plots on the negative end of this axis. Fire plots were strongly and negatively correlated with increased disturbance severity and an increase in hollows and exposed, or combusted peat. Species significantly correlated with the positive end of axis one consisted of trembling aspen seedlings, post-fire colonizing bryophytes, and cattails (Appendix A). The negative portion of axis one was significantly correlated with a greater amount 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* (L.) House) and the feathermoss *Pleurozium schreberi*.

The second axis explained 22% of the variation in understory species composition with disturbance groups not as clearly demarcating either end of the axis. The positive end of axis two, which was slightly more associated with harvest plots, was characterized by three-seeded bog sedge (*Carex trisperma* Dewey), lake sedge (*Carex lacustris* Willd.), bog willow-herb (*Epilobium leptophyllum* Raf.), fragrant bedstraw (*Galium triflorum* Michx.) and speckled

alder. The negative portion of the axis was more strongly associated with a higher abundance of boreal bog sedge (*Carex magellanica* Lam.), bog willow (*Salix pedicellaris* Pursh.) and arctic raspberry (*Rubus arcticus* L.).

Several species were identified as significant indicators of a given disturbance category for the RTS plots (per Indicator Species Analysis, $p < 0.1$; Table 4) and both the NMS ordination and Indicator Species Analysis showed that fire plots were associated strongly with post-fire colonizing mosses, whereas harvests were not associated with any one particular group of moss indicators. Harvest disturbance, however, had several significant vascular plant indicators, including dwarf raspberry (*Rubus pubescens* Raf.), pussy willow (*Salix discolor*), red-stemmed aster (*Symphotrichum puniceum*) and tamarack seedlings. Indicator species related to fire disturbance were the liverwort *Marchantia polymorpha*, followed by other post-fire colonizing species such as *Ceratodon purpureus*, *Funaria hygrometrica*, and *Ptychostomum pseudotriquetrum*. Vascular plants associated with fire were cattails, wide-leaved willow-herbs (*Epilobium ciliatum* or *E. glandulosum*), and seedlings of trembling aspen. Indicator species for undisturbed plots included the forbs one-sided pyrola and marsh willow-herb (*Epilobium palustre* L.) and graminoids such as *Carex magellanica*. Mosses identified as significant indicators for undisturbed plots included *Sphagnum warnstorffii*, and the feathermoss *Pleurozium schreberi*.

4. Discussion

The main objectives of the present study were to examine differences in vegetation composition following wildfire and clearcut harvesting and determine how level of disturbance impacted seedling establishment in *Picea mariana* and *Larix laricina*-dominated peatland forests. Similar to previous comparative studies, burned and harvested stands had distinct post-disturbance plant communities (Nguyen-Xuan et al., 2000), with bryophytes as the primary drivers of these differences. Disturbance severity was most pronounced in tamarack swamps as a result of fire consuming a significant amount of the peat substrate. Most notable was the lack of tamarack seedling regeneration and a shift in composition towards dominance by wind-dispersed species, and a lower abundance of residual vascular plant species. In contrast, black spruce bogs (BSB) showed increased spatial heterogeneity as a result of fire

Table 4Indicator 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.

Community	Disturbance category	Species	IV	p-Value	
(a) ABSB	Undisturbed	<i>Vaccinium vitis-idaea</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	
		Other post-fire bryophytes (<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	
	(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 magellanica</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)	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>Symphotrichum puniceum</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>Symphotrichum 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			

behavior in the well-developed microtopography in these systems, creating a variety of seedbed conditions, particularly at lower levels of fire severity, and facilitating seedling recruitment. Harvest disturbance had less impact on both communities, where ground layer plant composition and seedbed conditions were generally more similar to undisturbed controls, especially for BSB plots.

4.1. Disturbance effects on black spruce bogs

Black spruce-dominated bog communities have been considered fairly resilient to fire, where changes in both vegetation and microtopography are relatively short-lived, particularly following low severity events where combustion does not entirely consume

the peat horizon down to the water table (Wein, 1983; Kuhry, 1994; Bencoter and Vitt, 2008; Magnan et al., 2012). In the current study, this resilience appears evident at low levels of fire severity, where spruce seedling densities were significantly higher than in harvest and control plots. Fire also increased spatial heterogeneity in the peat substrate, which likely promoted seedling establishment, as the majority of spruce seedlings were documented in microsites where fire had reduced the peat and other vegetation. A greater abundance of colonizing mosses also increased on recently reduced peat, with residual species, primarily ericaceous shrubs, persisting on unburned hummocks. These low, moist areas provide a stable environment just above the water table (Johnstone and Chapin, 2006; Brown and Johnstone, 2012) that is optimal for seedling growth and recruitment (Chrosiewicz, 1976; Charron and Greene, 2002; Jayen et al., 2006; Johnstone and Kasischke, 2005; Greene et al., 2007). However, as fire severity increased, the amount of open, water-filled hollows also increased, leading to a higher frequency of unsuitable seedbeds for seedling establishment, at least in the short-term.

Despite the increase in trembling aspen seedlings following fire, this response likely had no effect on the establishment of black spruce seedlings or other vegetation. Aspen is known for its ability to disperse its seeds over great distances (Burns and Honkala, 1990) so its presence in the study sites is not surprising, as it is a common species in the adjacent upland forests. However, its presence is expected to be an ephemeral component given the perennially high water table in this bog community and the low tolerance of aspen to prolonged inundation and nutrient-poor conditions. Furthermore, because the fire did not consume the peat down to mineral soil, a deciduous-dominated successional trajectory is unlikely (e.g., Johnstone et al., 2010).

The increases in black spruce seedling regeneration observed in burned areas relative to harvests reflected an influx of black spruce seed released from semi-serotinous cones after fire. While the majority of larger black spruce clearcuts in Minnesota are aerially seeded, smaller clearcuts, such as those examined in this study rely on natural regeneration from adjacent, uncut areas. Despite this prescription, the sites in this study clearly showed regeneration was limited, where a relatively homogenous *Sphagnum*-dominated substrate lacked the variability in microsites suitable for seedling establishment. The lower abundance of black spruce regeneration following harvesting was consistent with findings from other work that has demonstrated reduced seed supply and lack of suitable microsites limits regeneration in these systems (Chrosiewicz, 1976; Charron and Greene, 2002; Jayen et al., 2006; Johnstone and Chapin, 2006; Greene et al., 2007), particularly with increasing clearcut size (Pothier, 2000). The present study provides additional evidence that harvesting does not create comparable disturbance, relative to fire, for regeneration of seedlings or reducing competition. Although the majority of harvests in lowland conifer forests in Minnesota are carried out during winter months to minimize disturbance to the organic layer, rutting can still occur particularly on skid trails (Groot and Adams, 1994); however, this ground layer disturbance is not comparable to the microsites created by fire.

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). Although there were no significant differences between disturbance types (harvest and fire) in the total cover of ericaceous shrubs in BSB plots, a finding consistent with other work examining black spruce-dominated peatlands (Renard et al., 2016), cover of *Rhododendron* was significantly lower following fire and harvest disturbance relative to controls. These patterns suggest that disturbance generates at least an initial reduction in cover of this species. However, ericaceous and dwarf shrub species typical of forested

peatlands, such as *Rhododendron* and bog birch (*Betula pumila* L.), often resprout quickly after disturbance and thus have a competitive advantage over other plants that establish from seed (Flinn and Wein, 1977; Rowe, 1983). 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), despite its documented ability to recover after disturbance from belowground rhizomes (Flinn and Wein, 1977).

Slight differences were also found between the two disturbance types (fire and harvest) relating to vascular and nonvascular species responses. Although no significant differences in bryophyte species richness or diversity were found, all indicators of fire disturbance were largely colonizing moss species as total *Sphagnum* cover was significantly reduced with increasing fire severity. This was particularly true for *S. angustifolium* and *S. magellanicum*. Hollows and hummock margins occupied by loose colonies of mosses tolerant of wetter conditions, such as *S. angustifolium* and *S. magellanicum*, are more prone to desiccation when the water table drops below the peat surface and are more completely consumed by fire than hummock mosses (Bencoter et al., 2005; Thompson and Waddington, 2013). Hummocks, despite being higher above the water table, are more resistant to desiccation and combustion because the densely-packed hummock-forming species typical of the group *Sphagnum* sect. *Acutifolium* are able to transport and retain water more effectively. Therefore, with light combustion only minor singeing of hummock interiors occurs enabling them to quickly revegetate (Bencoter and Vitt, 2008), and our observations were consistent with this pattern.

Fire-reduced peat lawns that were approximately 10 cm or less above the water table showed increases in cover of the colonizing moss *Polytrichum strictum*. These lawns also corresponded, at least indirectly, with the majority of black spruce seedling recruitment. *Polytrichum*, along with turfs of *Ceratodon purpureus* –another pioneer moss species commonly found in post-fire bog sites, may provide partial insulation to new seedling roots and intercept rainfall and moisture (Moul and Buell, 1955; Ahlgren and Ahlgren, 1960). Large turfs of *Polytrichum* may serve as a proxy for identifying microsites where seedlings would have a greater level of germination success, as other studies have also found higher black spruce seedling regeneration associated with *Polytrichum* (Askamit and Irving, 1984; Charron and Greene 2002; Greene et al., 2004; Jayen et al., 2006; Johnstone and Chapin 2006; Veilleux-Nolin and Payette 2012).

Similar increases in *Polytrichum* were not observed following harvest disturbance, suggesting that harvest did not create similar levels of ground layer disturbance and vegetation removal to enable *Polytrichum* to colonize or increase to any great degree. In contrast, harvesting had little effect on total cover of *Sphagnum* and we found that winter harvesting instead allowed for the expansion of *Sphagnum* lawns composed largely of *S. angustifolium*. Several studies have documented that dense *Sphagnum* carpets are unfavorable substrates for black spruce seedlings due in part to lower nutrient availability (Jeglum, 1981; Groot and Adams, 1994; Lavoie and Pellerin, 2007; Lafleur et al., 2011), but also fast growing species, such as *S. angustifolium*, can quickly outpace and cover new seedlings (Jeglum, 1981; Groot and Adams, 1994). The increased cover of *S. angustifolium* is reflective of this species' tolerance to a wide array of environmental conditions relative to other *Sphagnum* species, as well as its capacity to increase growth in lower, wetter conditions (Andrus et al., 1983; Vitt and Slack, 1984; Bencoter et al., 2005; Fenton and Bergeron, 2006), which are often found following harvest. Microclimatic changes as a result of increased light availability with the removal of the canopy, direct impacts to substrate microtopography, and possibly slash deposition, may have created conditions for *S. angustifolium*

to have a competitive advantage (c.f., Fenton and Bergeron 2006; 2007). These results are similar to those found in other post-fire, paludified black spruce forests where total cover of *Sphagnum* was significantly less than in clearcut areas (Renard et al., 2016).

Lastly, the slight, but significant increase found for vascular plant species richness and diversity for both low severity fire and harvest plots, was likely due to the addition of newly colonizing wind-dispersed species, while at the same time, maintaining species that resprout after disturbance through vegetative means, as with ericaceous shrubs. With low severity fire, modest increases in the heterogeneity of habitat conditions, and as well as other abiotic changes (nutrient availability and soil moisture; Benschoter and Vitt 2008), likely initiated these modest increases in diversity. The fact that harvest was associated with an increase in bog birch, willow-herbs, and pussy willow – the latter two species dispersed by wind, suggests that enough ground layer disturbance was created by this disturbance type to allow for opportunists such as these to rapidly colonize these newly created habitats. However, this may be misleading since the majority of species associated with harvest disturbance were graminoids, particularly the abundant mats consisting of the rhizomatous species *Carex trisperma*, *C. chordorrhiza*, and *Eriophorum angustifolium*, which may have created barriers for black spruce seedling establishment. The reasons for which *C. trisperma* – a species more associated with shaded bogs and swamps (Anderson et al., 1996) – increased in such abundance once the canopy was removed is unclear, but is understandably related to its life-history characteristics and its presence prior to disturbance.

4.2. Disturbance effects on rich tamarack swamps

In contrast to BSB, higher seedling regeneration rates were observed for RTS harvests where increased light conditions from the removal of the canopy and disturbance to the ground layer created a mosaic of seedbed conditions. Unlike BSB, where no differences were found in total cover of *Sphagnum* (despite a change in species abundance) between harvest and controls, RTS harvest plots had significantly lower cover than controls and also contained bare, organic soil that likely benefited seedling establishment. However, the effect of fire was more acute for the rich tamarack swamps, where a shallow peat horizon was more effectively reduced, and in some cases entirely consumed. This resulted in a system-level change in ecological function and homogenization of community composition that resulted in retrogression towards marsh-like conditions with little to no tamarack regeneration. The lack of seedling establishment in burned plots was limited by the complete or near removal of a suitable tamarack seedbed due to significant reductions in the organic layer and increased expansion of deep water-filled hollows following fire. Tamarack seedlings cannot tolerate more than a week of submergence; favoring instead, a moist but unsaturated substrate for germination and preferably with areas of fine mosses over *Sphagnum* (Duncan, 1954; Viereck and Johnson, 1990).

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 a limiting factor in post-fire recruitment of this species, as it solely relies on wind-dispersed seed from surviving trees to regenerate burned stands (Duncan, 1954; Busque and Arseneault, 2005; Viereck and Johnson, 1990). Given the limited dispersal distances associated with tamarack (\leq two mature tree heights; Duncan, 1954; Viereck and Johnson, 1990), it is not well adapted to rapidly reseed large burns. The areas affected by fire were significantly greater in size (>30 ha) compared to harvested

sites, limiting the levels of tamarack seed reaching suitable germination areas from adjacent, unburned stands.

Palynological studies have shown that large-scale, peat-removing fire events have historically resulted in complete stand-level mortality in these minerotrophic systems generating concomitant ecosystem-level shifts in vascular and nonvascular plant species composition (Griffen, 1977; Heinselman, 1968). The retrogression we observed to an open *Typha-Cyperaceae* dominated wetland is consistent with this previous work examining lowland forest ontogeny. In all but the lowest levels of fire severity, the shift in ground layer vegetation to a *Typha* and graminoid-dominated wetland, with herbaceous species typical of marshes and wet meadows and bryophytes dominated by brown moss assemblages, is characteristic of earlier stages in forested peatland development. The duration of these earlier, successional wet meadow or rich fen phases, however, can last for centuries with timing dependent upon local hydrology and other allogenic factors (Griffen, 1977; Bauer et al., 2003; Heinselman, 1968; Janssen, 1967; Kuhry et al., 1993; Kuhry, 1994), suggesting that reforestation of these areas will remain challenging for the foreseeable future.

Like black spruce bogs, harvesting in these tamarack swamps is carried out in winter months. However, tamarack swamps were clearly different in their response to harvest disturbance, possibly relating to pre-disturbance abiotic factors such as a higher water table, lower peat depths and less developed surface microtopography compared to bogs. These differences resulted in a higher variety of substrate conditions in post-harvested RTS plots and likely benefited seedling recruitment, while at the same time increasing overall bryophyte species diversity. Harvest disturbance was associated with values slightly higher than for undisturbed controls. Although total *Sphagnum* cover was significantly lower for harvest in RTS plots compared to controls, it was still much higher than for burned plots. The remaining *Sphagnum* cover for harvest plots was again heavily dominated by *S. angustifolium*. Similar to BSB plots, this higher cover of *S. angustifolium* was likely related to the removal of the canopy and increased light conditions, as well as other changes related to hydrology and microtopography, as this species is more tolerant of a wider range of environmental conditions (Andrus et al., 1983; Andrus, 1986; Gignac, 1992; Vitt and Slack, 1984). Undisturbed RTS plots were dominated largely by *S. warnstorffii*, a shade-tolerant species associated with minerotrophic, lowland conifer forests with a narrow pH and temperature range (Gignac, 1992; Vitt and Slack, 1984).

The lack of differences in vascular plant species richness and diversity between RTS disturbance types was reflective of high levels of species turnover following disturbance as opposed to persistence of predisturbance taxa. For example, the severe disturbance created by fire allowed for an entirely different set of species to establish in the wetter environment that ensued with peat consumption. These new species were largely characterized by life-history strategies that depend on wind-dispersed seed for regeneration, e.g., cattails and willow-herbs. Harvest disturbance was characterized by both wind-dispersed species (pussy willow, red-stemmed aster, tamarack seedlings), as well as species that depend on regeneration from aboveground vegetative sources (dwarf raspberry, *Rhododendron*), reflecting a lower impact to the substrate layer. While significant differences were found between disturbance types for ericaceous shrub cover (*Rhododendron* is the dominant species), where fire eliminated almost all cover, it is typically much lower in RTS communities predisturbance and likely did not significantly influence seedling regeneration to any great degree. Similar to BSB, RTS harvest plots had high cover of graminoid species, but RTS also had high deciduous shrub cover, compared to fire and control plots. The ground layer species responses documented in both fire and harvest RTS plots were consistent with models of a disturbance severity spectrum following

canopy removal (Roberts, 2004), where fire was obviously at the extreme end of the spectrum in this case.

5. Conclusion

The results of this study lend further support to the prevailing notion that the type and degree of forest floor disturbance is an important element in driving the dynamics of tree regeneration and ground layer community composition in lowland conifer forests (Roberts, 2004; Fenton et al., 2005). Although the results of this study should be interpreted with a degree of caution given the low replications for each disturbance type due to difficult access and short study duration, the overall trends suggest a need for further evaluations of whether forest harvesting regimes are approximating natural disturbance processes in these systems. 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 (Bose et al., 2014). Further research is also needed on a more extensive suite of harvesting conditions that includes aerial seeding to examine how substrate and post-disturbance vegetation changes influence seedling regeneration and long-term establishment.

While stand-replacing fires impacted these communities historically, they were rare. Most studies agree that wetland and peatland forests were more often affected by light surface fires (Heinselman, 1968; Kuhry, 1994; Busque and Arseneault, 2005). Despite the challenges and costs of using prescribed fire in these ecosystems, earlier studies have shown that incorporating low severity fire is highly effective at increasing the success of black spruce regeneration and spatial heterogeneity of ground layer composition and reducing organic peat soils (Johnston, 1971; Chrosciewicz, 1976; Askamit and Irving, 1984; McRae et al., 2001; Renard et al., 2016). Additionally, fire can reduce the levels of ericaceous phenolic compounds that inhibit seed germination and seedling growth of conifers in these systems (Bloom and Mallik, 2006; Mallik, 2003) and serve as an effective method for controlling eastern dwarf mistletoe, a serious parasitic disease of black spruce in northern Minnesota (Johnston, 1971; Geils et al., 2002; Baker and Knowles, 2004). While it is not feasible to introduce prescribed fire after clearcutting as a routine practice, and

compound disturbances such as these have the potential to create divergent communities (Pidgen and Mallik, 2013), its use as a site preparation method prior to direct seeding should at least be considered in areas where mistletoe is detected prior to harvest. Introducing low severity, prescribed fires in these areas would more effectively emulate the chemical and biological processes of natural disturbance (Dyrness and Norum, 1983) in these managed ecosystems.

While the environment created by fire in the tamarack swamps examined in this study is likely not a desirable condition to emulate through management, the dramatic shifts in vegetation conditions we observed are consistent with general successional patterns reconstructed via palynological work in this region and across Canada (e.g., Janssen, 1967; Griffen, 1977; Kuhry et al., 1993). Increases in drought severity and frequency may result in future large-scale fire events that could generate compound disturbance effects, disrupting autogenic successional processes in these lowland systems and creating significant challenges to the long-term maintenance of these communities on the landscape. Additional research is needed to understand whether the North Minnie fire area, as well as future disturbance events, will continue to follow historical, successional trajectories in the face of current and future climate patterns, as well the recent, unprecedented outbreaks of eastern larch beetle in the region (Crocker et al., 2016). Examining the long-term recovery of the areas impacted by the North Minnie fire will be critical for informing appropriate management responses to these future disturbances (cf. Lindenmayer et al., 2016).

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Appendix A

Correlations (Kendall's τ) between the understory vascular and non-vascular species composition and non-metric multidimensional scaling Axes 1 and 2 in Fig. 2 for (a) black spruce bog sites (BSB) and (b) rich tamarack swamp (RTS) 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			

Appendix A (continued)

NPC	Species	Axis 1	Axis 2	Species	Axis 1	Axis 2
(b) RTS	<i>Agrostis scabra</i>	0.56	−0.00	<i>Lysimachia thyriflora</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>Campylopus 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
	<i>Carex interior</i>	0.43	−0.11	<i>Populus tremuloides</i>	0.62	0.20
	<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 pedicularis</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
	Fire bryophyte group	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 oxycoccus</i>	− 0.36	−0.25
	<i>Lonicera villosa</i>	− 0.42	0.05	<i>Vaccinium vitis-idaea</i>	− 0.40	0.06

References

- Ahlgren, I.F., Ahlgren, C.E., 1960. Ecological effects of forest fires. *Bot. Rev.* 26, 483–533.
- Allen, J.L., Sorbel, B., 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. *Int. J. Wildl. Fire* 17, 463–475.
- Anderson, D.S., Davis, R.B., Rooney, S.C., Campbell, C.S., 1996. The ecology of sedges (Cyperaceae) in Maine Peatlands. *Bull. Torrey Bot. Club* 123 (2), 100–110.
- Andrus, R.E., 1986. Some aspects of Sphagnum ecology. *Can. J. Bot.* 64 (2), 416–426.
- Andrus, R.E., Wagner, D.J., Titus, J.E., 1983. Vertical zonation of Sphagnum mosses along hummock-hollow gradients. *Can. J. Bot.* 61 (12), 3128–3139.
- Askamit, S.E., Irving, F.D., 1984. Prescribed burning for lowland black spruce regeneration in northern Minnesota. *Can. J. For. Res.* 14 (1), 107–113.
- Baker, F.A., Knowles, K.R., 2004. Case study: 36 years of dwarf mistletoe in a regenerating black spruce stand in northern Minnesota. *North. J. Appl. Forest.* 21, 150–153.
- Bauer, I.E., Gignac, D.L., Vitt, D.H., 2003. Development of a peatland complex in boreal western Canada: lateral site expansion and local variability in vegetation succession and long-term peat accumulation. *Can. J. Bot.* 81 (8), 833–847.
- Benscoter, B.W., Kelman-Wieder, R., Vitt, D.H., 2005. Linking microtopography with post-fire succession in bogs. *J. Veg. Sci.* 16, 453–460.
- Benscoter, B.W., Vitt, D.H., 2008. Spatial patterns and temporal trajectories of the bog ground layer along a post-fire chronosequence. *Ecosystems* 11 (7), 1054–1064.
- Bloom, R., Mallik, A., 2006. Relationships between ericaceous vegetation and soil nutrient status in a post-fire *Kalmia angustifolia*-black spruce chronosequence. *Plant Soil* 289, 211–226.
- Bose, A.K., Harvey, B.D., Brais, S., Beaudet, M., Leduc, A., 2014. Constraints to partial cutting in the boreal forest of Canada in the context of natural disturbance-based management: a review. *Forestry* 87, 11–28.
- Brown, C.D., Johnstone, J.F., 2012. Once burned, twice shy: repeat fires reduce seed availability and alter substrate constraints on *Picea mariana* regeneration. *For. Ecol. Manage.* 266, 34–41.
- Brumelis, G., Carleton, T.J., 1988. The vegetation of postlogged black spruce lowlands in central Canada. Trees and tall shrubs. *Can. J. For. Res.* 18, 1470–1478.
- Burns, R.M., Honkala, B.H., 1990. *Sylvics of North America: 2. Hardwoods*. Agriculture Handbook 654. US Department of Agriculture, Washington, DC.
- Busque, D., Arseneault, D., 2005. Fire disturbance of larch woodlands in string fens in northern Québec. *Can. J. Bot.* 83, 599–609.
- Charron, I., Greene, D.F., 2002. Post-wildfire seedbeds and tree establishment in the southern mixedwood boreal forest. *Can. J. For. Res.* 32, 1607–1615.
- Chrosiewicz, Z., 1976. Burning for black spruce regeneration in a lowland cutover site in Southeastern Manitoba. *Can. J. For. Res.* 6, 179–186.
- Collier, L.C., Mallik, A.U., 2010. Does post-fire abiotic habitat filtering create divergent plant communities in black spruce forests of eastern Canada? *Oecologia* 164 (2), 465–477.
- Crocker, Susan J., Liknes, Greg C., McKee, Fraser R., Albers, Jana S., Aukema, Brian H., 2016. Stand-level factors associated with resurging mortality from eastern larch beetle (*Dendroctonus simplex* LeConte). *For. Ecol. Manage.* 375, 27–34.
- Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* 67, 345–366.
- 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., Payette, S., 2002. Ecological impact of clear-cutting on black spruce-moss forests in southern Québec. *Ecoscience* 9, 533–543.
- Dyrness, C.T., Norum, R.A., 1983. The effects of experimental fires on black spruce forest floors in interior Alaska. *Can. J. For. Res.* 13, 879–893.
- Fenton, N., Lecomte, N., Légaré, S., Bergeron, Y., 2005. Paludification in black spruce (*Picea mariana*) forests of eastern Canada: potential factors and management implications. *For. Ecol. Manage.* 213, 151–159.
- Fenton, N.J., Bergeron, Y., 2006. Facilitative succession in a boreal bryophyte community driven by changes in available moisture and light. *J. Veg. Sci.* 17, 65–76.
- Fenton, N.J., Bergeron, Y., 2007. Sphagnum community change after partial harvest in black spruce boreal forests. *For. Ecol. Manage.* 242, 24–33.
- Fenton, N., Work, L.T., Jacobs, J., Bescond, H., Drapeau, P., Bergeron, Y., 2013. Lessons learned from 12 years of ecological research on partial cuts in black spruce forests of northwestern Québec. *For. Chron.* 89, 350–359.
- Flinn, M.A., Wein, R.W., 1977. Depth of underground plant organs and theoretical survival during fire. *Can. J. Bot.* 55, 2550–2554.
- Franklin, J.F., Mitchell, R.J., Palik, B., 2007. Natural disturbance and stand development principles for ecological forestry. USDA Forest Service General Technical Report NRS-19.
- Galatowitsch, S., Frelich, L., Phillips-Mao, L., 2009. Regional climate change adaptation strategies for biodiversity conservation in a midcontinental region of North America. *Biol. Cons.* 142 (10), 2012–2022.

- Geils, B.W., Tovar, J.C., Moody, B., 2002. Mistletoes of North American conifers. USDA Forest Service, Gen. Tech. Rep. RMRS-GTR-98, 120 p.
- Gignac, L., 1992. Niche structure, resource partitioning, and species interactions of mire bryophytes relative to climatic and ecological gradients in Western Canada. *The Bryologist* 95 (4), 406–418.
- Gilliam, F.S., 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. *Bioscience* 57, 845–858.
- Glaser, P.H., 1987. The ecology of patterned boreal peatlands of northern Minnesota: a community profile. U.S. Fish Wildl. Serv. Tech. Rep. 85 (7.14), 98.
- Greene, D.F., Noël, J., Bergeron, Y., Rousseau, M., Gauthier, S., 2004. Recruitment of *Picea mariana*, *Pinus banksiana*, and *Populus tremuloides* across a burn severity gradient following wildfire in the southern boreal forest of Quebec. *Can. J. For. Res.* 34, 1845–1857.
- Greene, D.F., Macdonald, S.E., Haeussler, S., Domenicano, S., Noël, J., Jayen, K., Charron, I., Gauthier, S., Hunt, S., Gielau, E.T., Bergeron, Y., Swift, L., 2007. The reduction of organic-layer depth by wildfire in the North American boreal forest and its effect on tree recruitment by seed. *Can. J. For. Res.* 37, 1012–1023.
- Griffen, K.O., 1977. Paleoeological aspects of the Red Lake Peatland, northern Minnesota. *Can. J. Bot.* 55, 172–192.
- Groot, A., 1996. Regeneration and surface condition trends following forest harvesting on peatlands. NODA Tech. Rep. TR-26. 12 p.
- Groot, A., Adams, M.J., 1994. Direct seeding black spruce on peatlands: fifth-year results. *For. Chron.* 70, 585–593.
- Hébert, F., Thiffault, N., Ruel, J.C., Munson, A.D., 2010. Ericaceous shrubs affect black spruce physiology independently from inherent site fertility. *For. Ecol. Manage.* 260, 219–228.
- Heinselman, M.L., 1968. Forest sites, bog processes, and peatland types in the glacial lake Agassiz region. *Ecol. Monogr.* 33, 327–374.
- Heinselman, M.L., 1970. Landscape evolution, peatland types, and the environment in the Lake Agassiz Peatlands Natural Area, Minnesota. *Ecol. Monogr.* 40, 235–261.
- Inderjit, Mallik, A.U., 1996. Growth and physiological responses of black spruce (*Picea mariana*) to sites dominated by *Ledum groenlandicum*. *J. Chem. Ecol.* 22, 575–585.
- Jayen, K., Leduc, A., Bergeron, Y., 2006. Effect of fire severity on regeneration success in the boreal forest of northwest Québec, Canada. *Ecoscience* 13, 143–151.
- 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. *Ecol. Monogr.* 37, 145–172.
- Jeglum, J.K., 1981. Black Spruce Seedling Growth and Nutrition on Sphagnum and Feather Moss Peats from a Northern Ontario Peatland. Canadian Forestry Service, Great Lakes Forest Research Centre, Sault Ste. Marie, Ontario. Information Report O-X-326.
- Johnston, W.F., 1971. Broadcast burning slash favors black spruce reproduction on organic soil in Minnesota. *For. Chron.* 47, 33–35.
- Johnstone, J., Chapin III, F.S., 2006. Effects of soil burn severity on post-fire tree recruitment in boreal forest. *Ecosystems* 9, 14–31.
- Johnstone, J.F., Kasischke, E.S., 2005. Stand-level effects of soil burn severity on postfire regeneration in a recently burned black spruce forest. *Can. J. For. Res.* 35, 2151–2163.
- Johnstone, J.F., Hollingsworth, T.N., Chapin, F.S., Mack, M.C., 2010. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Glob. Change Biol.* 16, 1281–1295.
- Kasischke, E., Turetsky, M., 2006. Recent changes in the fire regime across the North American boreal region – spatial and temporal patterns of burning across Canada and Alaska. *Geophys. Res. Lett.* 33, L09703.
- Kasischke, E.S., Ottmar, Roger D., French, Nancy H.F., Hoy, Elizabeth E., Kane, Evan S., 2008. Evaluation of the composite burn index for assessing fire severity in Alaskan black spruce forests. *Int. J. Wildl. Fire* 17, 515–526.
- Keeley, J.E., 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. *Int. J. Wildl. Fire* 18, 116–126.
- Kemball, K.J., Wang, G.G., Dang, Q.L., 2005. Response of understory plant community of boreal mixedwood stands to fire, logging, and spruce budworm outbreak. *Can. J. Bot.* 83, 1550–1560.
- Key, C., Benson, N., 2006. Landscape Assessment (LA) Sampling and Analysis Methods. USDA Forest Service Gen. Tech. Rep. RMRS-GTR-164-CD.
- Kuhry, P., 1994. The role of fire in the development of sphagnum-dominated peatlands in Western Boreal Canada. *J. Ecol.* 82, 899–910.
- Kuhry, P., Nicholson, B.J., Gignac, L.D., Vitt, D.H., Bayley, S.E., 1993. Development of Sphagnum-dominated peatlands in boreal continental Canada. *Can. J. Bot.* 71, 10–22.
- Lafleur, B., Paré, D., Fenton, N., Bergeron, Y., 2011. Growth and nutrition of black spruce seedlings in response to disruption of *Pleurozium* and *Sphagnum* moss carpets in boreal forested peatlands. *Plant Soil* 345, 141–153.
- Lavoie, C., Pellerin, S., 2007. Fires in temperate peatlands (southern Quebec): past and recent trends. *Can. J. Bot.* 85, 263–272.
- Lindenmayer, D., Messier, Sato, C., 2016. Avoiding ecosystem collapse in managed forest ecosystems. *Front. Ecol. Environ.* 14, 561–568.
- Locky, D.A., Bayley, S.E., 2007. Effects of logging in the southern boreal peatlands of Manitoba, Canada. *Can. J. For. Res.* 37, 649–661.
- Long, J.N., 2009. Emulating natural disturbance regimes as a basis for forest management: a North American view. *For. Ecol. Manage.* 257, 1868–1873.
- Magnan, G., Lavoie, M., Payette, S., 2012. Impact of fire on long-term vegetation dynamics of ombrotrophic peatlands in northwestern Québec, Canada. *Quatern. Res.* 77, 110–121.
- Mallik, A.U., 1995. Conversion of temperate forests into heaths—role of ecosystem disturbance and ericaceous plants. *Environ. Manage.* 19, 675–684.
- Mallik, A.U., 2003. Conifer regeneration problems in boreal and temperate forests with ericaceous understory: role of disturbance, seedbed limitation, and keystone species change. *Crit. Rev. Plant Sci.* 22, 341–366.
- McCune, B., Lesica, P., 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., Grace, J., 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, OR.
- McCune, B., Mefford, M.J., 2011. PC-ORD. Multivariate Analysis of Ecological Data. Version 6. MjM Software, Gleneden Beach, Oregon, U.S.A.
- McRae, D.J., Duchesne, L.C., Freedman, B., Lynham, T.J., Woodley, S., 2001. Comparisons between wildfire and forest harvesting and their implications in forest management. *Environ. Rev.* 9, 223–260.
- Moritz, M.A., Parisien, M.-A., Batllori, E., Krawchuk, M.A., VanDorn, J., Ganz, D.J., Hayhoe, K., 2012. Climate change and disruptions to global fire activity. *Ecosphere* 3 (6), 49.
- Moul, E.T., Buell, M.F., 1955. Moss cover and rainfall interception in frequently burned sites in the New Jersey Pine Barrens. *Bull. Torrey Bot. Club* 82, 155–162.
- Nguyen-Xuan, T., Bergeron, Y., Simard, D., Fyles, J.W., Paré, D., 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. *Can. J. For. Res.* 30, 1353–1364.
- Nyland, R.D., 2007. Silviculture: Concepts and Applications. Waveland Press, Long Grove, IL.
- O'Hara, R.B., Kotze, D.J., 2010. Do not log-transform count data. *Methods Ecol. Evol.* 1, 118–122.
- Pidgen, K., Mallik, A.U., 2013. Ecology of compounding disturbances: the effects of prescribed burning after clearcutting. *Ecosystems* 16 (1), 170–181.
- Pothier, D., 2000. Ten-year results of strip clear-cutting in Quebec black spruce stands. *Can. J. For. Res.* 30, 59–66.
- R Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rein, G., Cleaver, N., Ashton, C., Pironi, P., Torero, J.L., 2008. The severity of smouldering peat fires and damage to the forest soil. *CATENA* 74, 304–309.
- Renard, S.M., Gauthier, S., Fenton, N.J., Lafleur, B., Bergeron, Y., 2016. Prescribed burning after clearcut limits paludification in black spruce boreal forest. *For. Ecol. Manage.* 359, 147–155.
- Roberts, M.R., 2004. Response of the herbaceous layer to natural disturbance in North American forests. *Can. J. Bot.* 82, 1273–1283.
- Rowe, J.S., 1983. Concepts of fire effects on plants, individuals and species. In: Wein, R.W., MacLean, D.A. (Eds.), *The Role of Fire in Northern Circumpolar Ecosystems*. John Wiley & Sons, New York, NY, pp. 135–153.
- Rowe, E.R., 2015. Effects of fire and harvesting on tree regeneration and ground layer vegetation in forested peatland communities in northern Minnesota. Master's Thesis. University of Minnesota.
- Rydin, H., Jeglum, J.K., 2013. *The Biology of Peatlands*. Oxford University Press, Oxford.
- Soverel, N.O., Perrakis, D.D.B., Coops, N.C., 2010. Estimating burn severity from Landsat dNBR and RdNBR indices across western Canada. *Remote Sens. Environ.* 114, 1896–1909.
- Thompson, D.K., Waddington, J.M., 2013. Peat properties and water retention in boreal forested peatlands subject to wildfire. *Water Resour. Res.* 49, 3651–3658.
- Viereck, L.A., Johnson, W.F., 1990. *Picea mariana* (Mill.) B.S.P., black spruce. In: Burns, R.M., Honkala, B.H. (Eds.), *Silvics of North America*. U.S. Department of Agriculture, Forest Service, Washington, DC, pp. 227–237.
- Veilleux-Nolin, M., Payette, S., 2012. Influence of recent fire season and severity on black spruce regeneration in spruce–moss forests of Quebec, Canada. *Can. J. For. Res.* 42, 1316–1327.
- Vitt, D.H., Slack, N.G., 1984. Niche diversification of Sphagnum relative to environmental factors in northern Minnesota peatlands. *Can. J. Bot.* 62, 1409–1430.
- Wein, R.W., 1983. Fire behaviour and ecological effects in organic terrain. In: Wein, R.W., MacLean, D.A. (Eds.), *The Role of Fire in Northern Circumpolar Ecosystems*. John Wiley & Sons, New York, NY, pp. 81–93.
- Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer Science & Business Media.