Does fire severity difference create divergent plant communities in black spruce-*Kalmia* forests of eastern Canada?

By

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Abstract

After fire, some conifer-ericaceous plant communities in Western Europe and eastern North America have demonstrated divergent succession from traditional conifer stand replacement to Ericaceae-dominated community states. Divergence may be of function of species‟ responses to changes in fire severity as determined by the amount of residual organic matter (ROM) remaining after fire. ROM depth may act as an abiotic habitat filter to conifer species by physically inhibiting species establishment or through chemical afterlife effects in the unburned organic matter. If post-fire community assembly is predominantly determined by ROM depth, then post-fire species composition and their functional traits should correspond with the depth and distribution of ROM. But if species interactions are the primary constraint on community assembly, then post-fire species composition and their functional traits should be independent of the depth and distribution of ROM. I tested these predictions in black spruce (*Picea mariana* (Mill.) B.S.P.)-*Kalmia* (*Kalmia angustifolia* L.) plant communities of eastern Newfoundland among three post-fire plant community types (heath, wood savannah and forest) with similar pre-fire stand types (forest).

To determine if the three communities were similar prior to fire, I reconstructed stand types by sampling unburned portions of adjacent stands and by compiling pre-fire forest resource inventory data. I quantified post-fire differences in species composition by determining percent cover of all vegetation along three 20 x 1 m belt transects in replicated 20 x 20 m plots. From the species list, I compiled functional trait information from the literature for each species, and weighted traits by the total cover of species that possessed a given trait. Species and trait response (total abundance, richness and diversity) was then compared using one-way ANOVA. Indicator analysis was also performed to characterize species and functional traits among communities. I estimated fire severity as ROM by taking soil cores sampled contiguously in one 20 x 1m belt transect from the replicated 20 x 20 m plots in each community. ROM was estimated by the depth of organic matter not consumed by the most recent fire under the uppermost charcoal layer. Multivariate ordination (Canonical correspondence analysis) and exponential growth and decay models were then used to test the effect of ROM on species composition and their functional traits.

I found that the relative importance of abiotic and biotic filtering in post-fire community assembly was a function of ROM. When ROM was less than 2 cm, abiotic filtering favored the establishment of black spruce and other seed regenerating species, leading to black spruce recovery. When ROM was greater than 2 cm, substrate conditions and biotic interactions favored *Kalmia* and other vegetatively regenerating species, resulting in successional divergence. Also, when abiotic filtering was the predominant habitat constraint, it controlled species composition and functional traits directly by filtering species mode of regeneration, and indirectly through differences in the dominant species‟ performance between the heath and forest. The independence of species composition and functional traits to shallow ROM in the wood savannah suggests that priority effects may play an important role in determining the relative importance of abiotic vs. biotic filtering when ROM is around a threshold value (~2 cm).

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1. Introduction

1.1 Natural wildfire and plant community assembly theory

Classical theory on secondary succession suggests that temporal changes in species composition are deterministic and converge on a single climax community as a result of species interactions under shared environment conditions (Clements, 1916; Connell and Slayter, 1977; Grime, 1979; Tilman, 1985). Historically, many naturally disturbed plant communities have followed deterministic patterns of succession, resulting in recovery of pre-disturbance species composition, structure and function (Bear et al., 2002; Chase, 2003; Buhk et al., 2006). This is particularly true in boreal forest plant communities where the dominant and intermittent effects of natural wildfire have controlled the distribution of vegetation mortality and substrate characteristics (Rowe, 1983; Halpern, 1989; Sirois and Payette, 1991; Johnson 1992; Payette, 1992; Neary et al., 2005; Wang and Kemball, 2005; Johnstone and Chapin, 2006; Lecomte et al., 2006), typically leading to convergence on stand recovery (Van Cleve et al., 1991; Bergeron, 2000; Johnstone and Kasischke, 2005). Post-fire convergence has been largely attributed to fire cycles that are shorter than the life span of the dominant tree species, which promotes post-fire compositions similar to pre-fire states (Johnson, 1992). Also, fire releases recalcitrant nutrients in undecomposed forest floor biomass, and creates favourable seedbed conditions for fire-adapted conifers (Scheuner et al., 2004).

However, a growing number of plant communities including those of the boreal forest have diverged from their pre-disturbance conditions towards alternate community endpoints (*sensu* Payette and Delwaide, 2003; Didham and Watts, 2005). Traditional succession theory falls short of explaining community divergence because it fails to consider the external constraints on species colonization and establishment prior to species interactions. Community assembly theory on the other hand provides a promising framework to explain post-disturbance divergence because it focuses on the external constraints and inherent ecosystem processes influencing the regional species pool before and after species establish (Diamond, 1975; Chase, 2003; Snyder and Chesson, 2004).

Community assembly begins with species dispersal and is influenced by species‟ ability to colonize a site after it has been disturbed (Hughes et al., 1994). But once species have reached a locality, how is their establishment limited? Community assembly theory proposes that species are constrained by habitat filters. Filters limit the range of potentially successful colonizers by favouring or inhibiting species‟ characteristics and functional attributes through abiotic and biotic conditions in the local environment (Diamond, 1975; Wilson and Whittaker, 1995; Weiher and Keddy, 1999; Cornwell et al., 2006; Ackerly and Cornwell, 2007). Abiotic filters represent the physiochemical conditions of the post-disturbance environment, such as the amount and distribution of suitable seedbed, biotic legacy effects from previously dominant species, soil pH and nutrient availability (Keddy, 1992; Weiher and Keddy, 1999). Therefore, if the degree or distribution of abiotic habitat filters varies throughout a regional species pool, successional divergence can occur because species have responded differently to those environmental conditions (Chase, 2003; Platt and Connell, 2003). Biotic filters represent the affect that early colonizers can have on their neighbours and on later establishing species through interactions such as facilitation, inhibition and tolerance (Connell and Slayter, 1977) and competition for resources (Tilman, 1985). So, even if environmental conditions are similar among the regional species pool, community divergence may occur due to differences in the sequence of species invasions and the nature of species‟ impact once they have colonized and established a disturbed area (Noble and Slayter, 1980; Chase, 2003; Didham and Watts, 2005).

Although community endpoints are determined by a combination of abiotic influences and biotic processes over time and by stochasticity in the natural environment (Hubbell, 2001; Cornwell et al., 2006), the severity of a disturbance influences the relative importance of abiotic and biotic filters in early post-disturbance ecosystems (Sousa, 1984; Frelich and Reich, 1999). This is true in fire-prone ecosystems, where successional divergence has been linked to changes in natural fire regime characteristics (see Schimmel and Granstrom, 1996; Payette and Delwaide, 2003; Jasinski and Payette, 2005; Johnstone and Kasischke, 2005; Johnstone and Chapin, 2006) such as the frequency of wildfire (Fox and Fox, 1986; Collins, 1992; Laughlin and Grace, 2006), intensity of burning (Alexander, 1982; Morrison and Renwick, 2000; Kennard and Gholz, 2001; de Groot et al., 2004; Green et al., 2004), or extent and pattern of fire impacts (Turner et al., 1997; Johnson et al., 1998; Schroeder, 2000; Bonnet et al., 2005). However, fire severity is believed to have the strongest ecological impact on post-fire plant regeneration patterns due to the marked differences between high and low severity fires‟ influences on abiotic and biotic filters (Rowe, 1983; Van Wagner, 1983; Schimmel and Granstrom, 1996; DeBano et al., 1998; Frelich and Reich, 1999; Turner et al., 1999; Brown, 2000; Ryan, 2002; Rydgren et al., 2004; Johnstone and Kasischke, 2005; Neary et al., 2005; Wang and Kemball, 2005; Johnstone and Chapin, 2006; Lecomte et al., 2006).

By burning deep into the organic horizon, severe fire directly influences the relative importance of sexual vs. vegetative recruitment by exposing or consuming buried seeds and spores stored in the soil seed bank, and consuming vegetative propagules, for instance, rhizomes (Rowe, 1983; Schimmel and Granstrom, 1996; Greene et al., 2007). Complete organic matter removal benefits immigrating species by removing competition from sprouting and seed banking vegetation (Whittle et al., 1997; Wang and Kemball, 2005), increasing soil nutrient cycling by reducing organic soils to mineral-rich ash (Chrosciewicz, 1974, 1976; Thomas and Wein, 1985; Bonan and Shugart, 1989; Bergeron, 2000; Cote et al., 2003; Scheuner et al., 2004; Ruel et al., 2004), and neutralizing the soil engineering effects associated with dominant woody shrubs (Wardle et al., 1998; Gallet et al., 1999; Mallik, 2003). Severe fire acts as an abiotic filter of species regeneration traits through the effects of seedbed conditions on colonizing vegetation (Chrosciewicz, 1974, 1976; Thomas and Wein, 1984). Shallow substrate depths created by severe fire favour recruitment of small-seeded boreal conifers by reducing the distance that roots must grow before they reach moisture near the mineral soil horizon (Greene et al., 1999; 2004). Non-severe fire leaves behind high residual organic matter (ROM) because of incomplete duff combustion. The ROM becomes susceptible to high moisture loss, which can lead to desiccation of germinating plants before their roots are able to reach the moist mineral soil horizon (Greene et al., 1999; 2004). Also, incomplete duff combustion stimulates vegetative regeneration of rhizomes surviving in the remaining duff layer, which may accentuate biotic interactions in the early post-fire condition.

Thus, fire severity operates as a driving force on the evolution of species‟ life histories by filtering the functional attributes of immigrating or existing species that are capable of thriving under the abiotic and biotic conditions after fire (Sousa, 1984; Pausas and Lavorel, 2003). Deterministic and convergent patterns of species composition, structure and function have typically resulted from high severity fire (Johnson, 1992; Neary et al., 2005); however the long-term effects of altered fire severity patterns on post-fire community assembly in the boreal forest are unclear. A reduction in fire severity due to human activity such as fire suppression may play a key role in successional divergence among boreal forest plant communities. If so, changes in fire severity should also be reflected in changes in the functional attributes of the species of the divergent plant communities (Bond and Keeley, 2005).

1.2 Successional divergence in the boreal forest of eastern Canada: The case of *Picea mariana* and *Kalmia angustifolia*

After fire, some conifer-ericaceous plant communities in western Europe and eastern North America diverge from traditional conifer stand replacement to Ericaceae-dominated community states (i.e. Mallik, 1995; Latham, 2003; Mallik, 2003; Nilsson and Wardle, 2005; Lagerstrom et al., 2007). Post-fire Ericaceae dominance is particularly problematic in eastern Canada between the coniferous tree species black spruce (*Picea mariana* (Mill.) B.S.P.) and the ericaceous shrub *Kalmia* (*Kalmia angustifolia* L.) (Bloom and Mallik, 2004, 2006; Thiffault and Jobidon, 2006). Among black spruce-*Kalmia* associations, post-fire departure from stand replacement produces one of two species assemblages, *Kalmia* heath or *Kalmia*-lichen wood savannah. *Kalmia* heath is characterized by a relatively uniform, low growing and multi-stemmed stratum of *Kalmia* and other ericaceous plants, with *Cladonia* and *Cladina* lichen-mats dominating the forest floor (Bloom, 2001; Mallik, 2003). Scattered spruce may be present in *Kalmia* heath, although they are characteristically stunted with chlorotic needles (Power, 2000; Bloom, 2001). *Kalmia*-lichen wood savannah (also referred to as lichen woodland) is structurally intermediate between black spruce-*Kalmia* forest and *Kalmia* heath as it is comprised of sparsely scattered black spruce islands with no more than 40% canopy closure in expanses of *Kalmia* heath (Payette, 1992).

The mechanisms responsible for deviation from stand recovery in black spruce-*Kalmia* communities are unclear, however many studies have focused on the autecology of *Kalmia* to explain regeneration failure and how *Kalmia* inhibits black spruce establishment through species interactions. Damman (1971, 1974) was one of the first to study *Kalmia* dominance and identified that the slow decomposition of *Kalmia* biomass increases duff accumulation, which locks up soil nutrients and reduces site fertility. *Kalmia* further reduces the bioavailability of nutrients to black spruce by decreasing nitrogen mineralization rates through accumulation of recalcitrant litter (Bradley et al., 2000). Intense competition for nutrients significantly reduces spruce growth (Yamasaki et al., 2002), and becomes magnified as the post-fire dominance of *Kalmia* increases with time (Bloom and Mallik, 2006).

Kalmia also influences physiochemical conditions in the post-fire environment by releasing phenolic compounds from decomposed litter into the organic horizon. Phenolics interfere with black spruce root formation, significantly reducing its potential for post-fire establishment (Zhu and Mallik, 1994, 2006; Inderjit and Mallik, 1996). The tannins and phenolics in *Kalmia* litter also reduce soil enzyme activity (Joanisses et al., 2007) and obstruct mycorrhizal colonization of black spruce roots (Titus et al., 1995; Yamasaki et al., 1998). These processes are critical for nutrient uptake in black spruce, and may also be contributing to reduced black spruce establishment in the presence of *Kalmia*.

Very few studies have considered the role of fire and how changes to fire severity may be influencing the abiotic filtering mechanisms of black spruce before it interacts with *Kalmia*. In eastern and Atlantic Canada where black spruce-*Kalmia* associations are abundant, improved efficiency in fire suppression has dramatically decreased the incidence of high severity fire, resulting in most fires being small and not thoroughly burned (Power, 2001). Bloom (2001) studied some of these communities in their early post-fire condition and found that one year after fire, only 10% of burned surfaces had mineral soil exposed seedbed suitable for black spruce seed germination and seedling establishment, and that suitability decreased with time since fire.

Kalmia quickly colonized the remaining seedbed surfaces characterized by thick ROM and surface charred organic matter through aggressive vegetative regeneration (Mallik and Bloom, 2005; Bloom, 2001). Bloom (2001) linked these early seedbed conditions to *Kalmia* heath formation and abiotic constraints on black spruce establishment. Payette et al. (2000) also studied the recent fire history of lichen-woodlands and found that they too are divergent communities of black spruce forests due to the abiotic conditions created by repeated fire and insect defoliation events.

The objectives of my study are to determine i) the effect of fire severity as determined by ROM on the origin of *Kalmia* heath and *Kalmia*-lichen wood savannah, and ii) if the post-fire plant communities represent divergent community states. If post-fire community assembly is predominantly determined by ROM (abiotic habitat filter), then post-fire species composition and functional traits should correspond to the depth and distribution of ROM. But if species interactions are the primary constraint on community assembly, then post-fire species composition and functional traits should be independent of the depth and distribution of ROM.

To test these predictions, I first determined if *Kalmia* heath and *Kalmia*-lichen wood savannah were similar stand types (black spruce-*Kalmia* forest) prior to disturbance. Knowledge of pre-fire composition was important to determine if differences in community assembly were related to pre-fire stand types. I compared species composition and their functional traits to characterize the differences among the plant communities. I then quantified the depth and distribution of ROM and used that as a proxy for early post-fire substrate conditions. I tested the effect of ROM on species composition and functional traits to determine the relative importance of abiotic and biotic filters on community assembly. Finally, I determined seed availability, and tested seed germination and seedling establishment of black spruce and *Kalmia* on high and low severity substrate conditions (shallow vs. deep ROM). The experiment was performed to test the regeneration response of the dominant species to ROM.

2. Materials and Methods

2.1 Study area

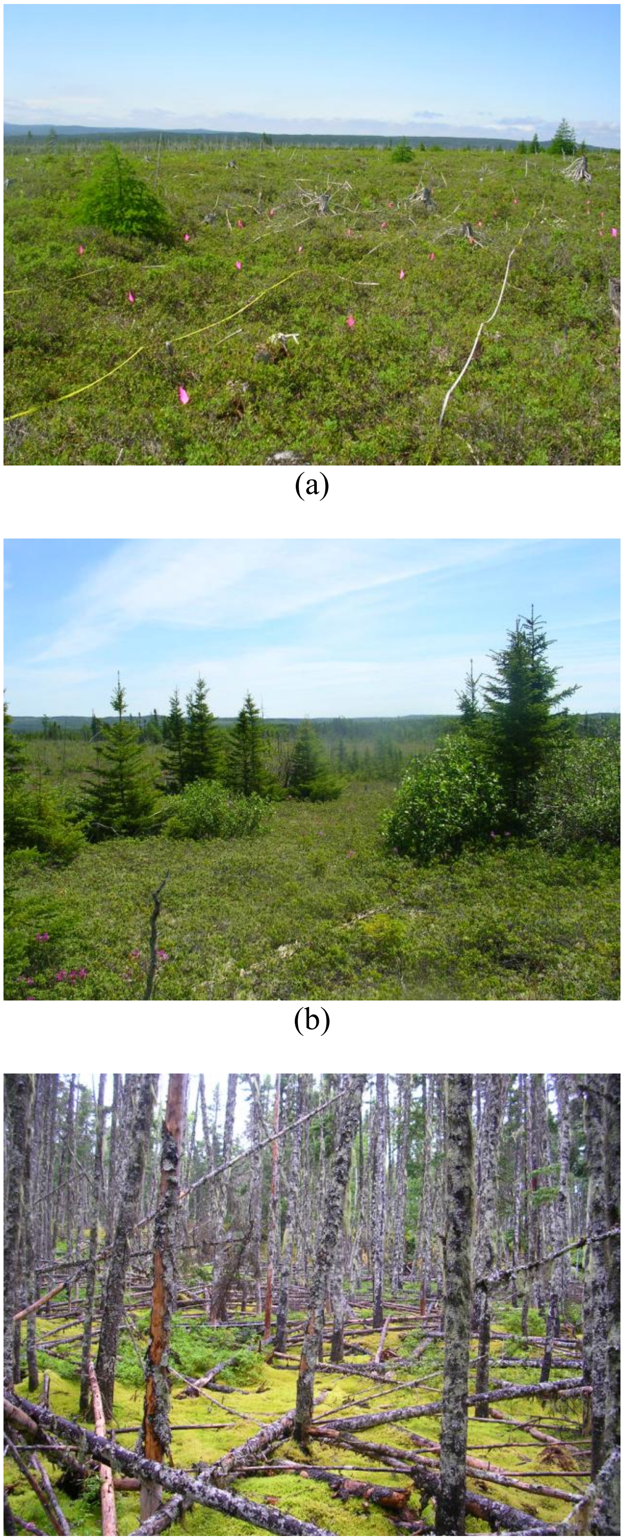
The study was conducted in the greater Terra Nova National Park (TNNP) ecosystem located in the east-central and north shore ecoregion of Newfoundland, Canada (48 33° N latitude, 53 58.8° W longitude) (Rowe, 1972; Damman, 1974). Climatic conditions are both continental and maritime, due to prevailing westerly winds and close proximity to the Atlantic Ocean. Summers are brief and cool with regional mean summer temperatures averaging 12.5 °C and mean annual precipitation ranging from 1000-1300 mm (Power, 2000, 2005).

TNNP is nearly 80% forested and stands are similar to that of the mainland boreal forests of Canada. Forests are dominated by black spruce and balsam fir (*Abies balsamea* (L.) Mill.) mixed with mainly white birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.) and to a lesser extent, larch (*Larix laricina* (du Roi) Koch), and red maple (*Acer rubrum* L.). Black spruce communities are among the most common in the Terra Nova region, occupying 52% of total forest cover. The dominant sub-canopy species associated with black spruce forests and barrens is *Kalmia*, and black spruce-*Kalmia* associations occupy nearly 50 % of the land base in TNNP (Power, 1996, 2000, 2005; Bloom and Mallik, 2004). Other ericaceous shrubs such as Labrador tea (*Rhododendron groenlandicum* (Oeder) K.A. Kron & W.S. Judd), rhodora (*Rhododendron canadense* (L.) Torr.) and blueberry (*Vaccinium angustifolium* Aiton) are also strongly associated with these forest types (Power, 2000; Bloom, 2001).

Evidence of burning from peat and lake sediment deposits (MacPherson, 1995) and the regular occurrence of charcoal macrofossils in the organic soil horizons (Power, 1996, 2000) indicates a long history of fire in shaping the Terra Nova landscape. High severity fire has historically facilitated black spruce recovery, producing even-aged stands throughout the region (Bloom and Mallik, 2006). In recent years, improved fire detection and suppression have reduced the frequency and severity of stand replacing fires and corresponded with an increase in *Kalmia* dominance (Power, 2000).

2.1.1 Site selection

Three replicates of *Kalmia*-heath, *Kalmia*-lichen-wood savannah and black spruce-*Kalmia* forest (herein referred to as heath, wood savannah and forest) (Figure 1a-c) were studied to test the hypotheses (Figure 2). Due to a limited number of recent fire events in the greater Terra Nova ecosystem, time since fire was not equal among the plant communities. However, at least one replicate from each plant community type was similar in successional age (≈ 40 yrs). One additional site was used to conduct the field experiments. The experimental site differed from all others in that time since disturbance was less than five years. This post-fire age was selected to test how the early post-fire condition influences plant community assembly. Examination of soil profiles confirmed that these locations had similar organic and mineral soil characteristics (Meades and Moore, 1994).



(a)

(b)

(c)

Figure 1. Representative site types of a) *Kalmia* heath b) *Kalmia*-lichen wood savannah and c) black spruce-*Kalmia* forest in the greater Terra Nova ecosystem.

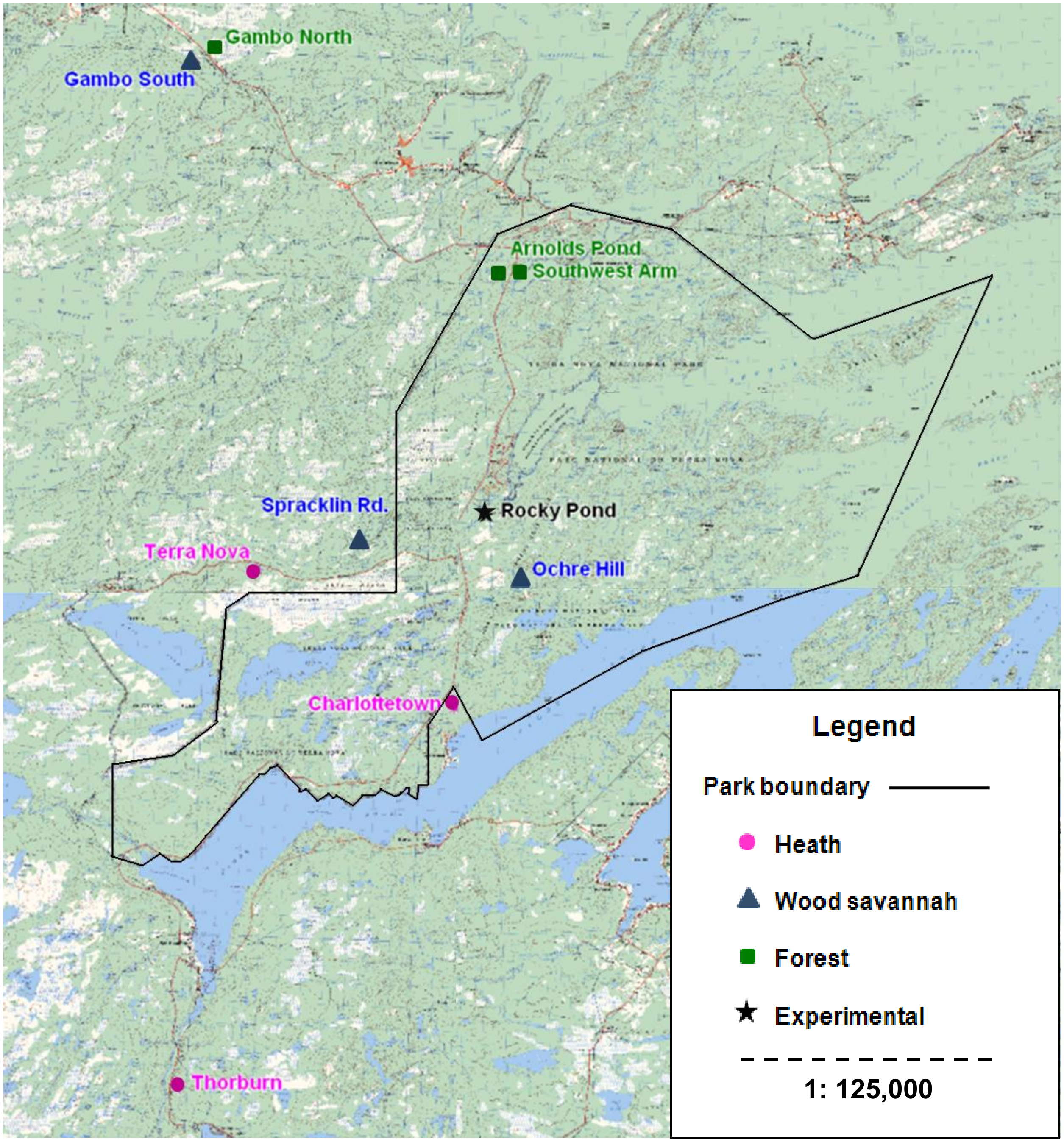


Figure 2. Locations of nine survey sites and one experimental site in the greater Terra Nova ecosystem.

2.2 Study design

2.2.1 Pre-fire stand reconstruction

Unburned stands adjacent to heath, wood savannah and forest communities were surveyed to determine if the plant communities originated from similar pre-fire black spruce-*Kalmia* forests. Basal area (m^2/ha) of all black spruce trees was estimated in one 20 x 20 m sampling plot in each community type. Field basal area was compiled with pre-fire forest resource inventory data (FRI) to describe the canopy species, age, height, and canopy density of study sites prior to disturbance (TNNP and provincial forestry records, Gambo and Clarenville District offices). Two mature forests (Arnold"s Pond and Southwest Arm) and two mature wood savannah (Spracklin Road and Ochre Hill) sites were burned before forest resource inventory data were collected. Yet since the distribution of black spruce forests in the region is a function of regularly occurring fire, there is adequate reason to believe that their pre-fire stand types had originated from stand replacing fire (Power, 2000). Since the wood savannahs are displaced from their typical northern range (Power, 2005), and because they are adjacent to mature black spruce-*Kalmia* stands, it is possible that at some point they originated from black spruce-feathermoss forest. To ensure that the black spruce islands were not remnants from a pre-fire wood savannah state, 10 random tree cores were collected using an increment corer from black spruce islands in the two mature wood savannah sites (Spracklin Rd. and Ochre Hill). Tree age was determined by counting the number of annual growth rings under 40x magnification. The average age and standard deviation of black spruce islands was estimated at 64.75 ± 28.64 and 84.54 ± 7.24 years for Spracklin Road and Ochre Hill respectively. Since current FRI data estimates their stand ages between 41-80 and 81-100 yrs respectively, the tree ring cores suggest that the islands were not remnants from the pre-fire forest condition and established after the most recent fire.

2.2.2 Plant community composition & performance

In the summer of 2006 and 2007, three 20 x 20 m sample plots were randomly established in each study site. Their locations were determined by overlaying topographic maps of each study site with a 100 x 100 m grid (Touratech QV; version 3). The corners of each cell in the grid represented potential sampling locations and were converted to GPS waypoints. To remove edge effects of historic fire boundaries, waypoints greater than 100 m from stand/fire boundaries were randomly selected for plot establishment. I also avoided establishing plots on slopes greater than 10%. In each sampling plot, three 20 x 1 m contiguous belt transects were randomly established in the west-east direction (Figure 3). Each belt transect was divided into 1 x 1 m quadrats and surveyed continuously to estimate species abundance of all vascular and non-vascular plants (N=60/plot, 180/site). Plants were identified to species level, however species were grouped to genera when abundances were <1%. A descriptive trait matrix based on species functional attributes was compiled for the species list using on-line plant databases and other published literature (see results for citation). The trait matrix was categorized by, i) species morphology, physiology and phenology (MPP), ii) species performance, iii) species‟ effect on the environment, and iv) environmental attributes. In total, 77 descriptive traits were considered, however the traits could be summarized into 14 sub-categories under the above four soft trait categories, i) species lifeform, Raunkiaer lifeform, successional status, architecture, regeneration strategy and mycorrhizal symbiont, ii) growth rate, C:N ratio, fertility requirements, shade, drought and fire tolerance, iii) allelopathy and iv) root concentration in soil (Weiher et al., 1999; Violle et al., 2007). Trait distribution was evaluated among plant communities by adding the total abundance of species in each sample plot that possessed any of the 77 traits. Covariation in trait data was summarized for each of the 14 sub-categories using principal component analysis

(PCA; PC-ORD v. 5). PCA yielded 14 composite variables, each being a cumulative representative of all the traits in each sub-category. Weighted trait abundances were standardized in a variance-covariance matrix before summarizing into 14 composite variables.

Performance of black spruce and *Kalmia* was estimated based on productivity of each species to further characterize species function among plant communities. To estimate live *Kalmia* productivity, stem density, mean stem height (cm) and basal diameter (mm) of stems was measured in the bottom right quadrant of each 1 x 1 m quadrat along one 20 x 1 m belt transect (N=20/plot, 60/site). Productivity (1) was based on estimates of stem volume (Bloom, 2001):

(1) $$\text{Stem volume} = (\pi\ (d/2)^{2} \times h) / (3 \times n)$$

Where: d = mean stem diameter

h = mean stem height, and

n = stem density

Along the same transect, productivity of black spruce was calculated as basal area (2) of living stems (N=20/plot, 60/site):

(2) $$\text{Basal area} = \sum ((dbh)^{2} \times 7.58 \times 10^{-5})$$

Where: dbh = diameter at breast height (cm)

Basal diameter was used to estimate basal area when stems did not reach breast height. To ensure an accurate estimate of productivity in the wood savannah, I selected transects that ran through no less than two black spruce islands. Due to significant variation in dead, above ground ericaceous stems, I measured the total abundance of dead ericaceous stems along each transect to estimate standing dead biomass among sample plots and plant communities.

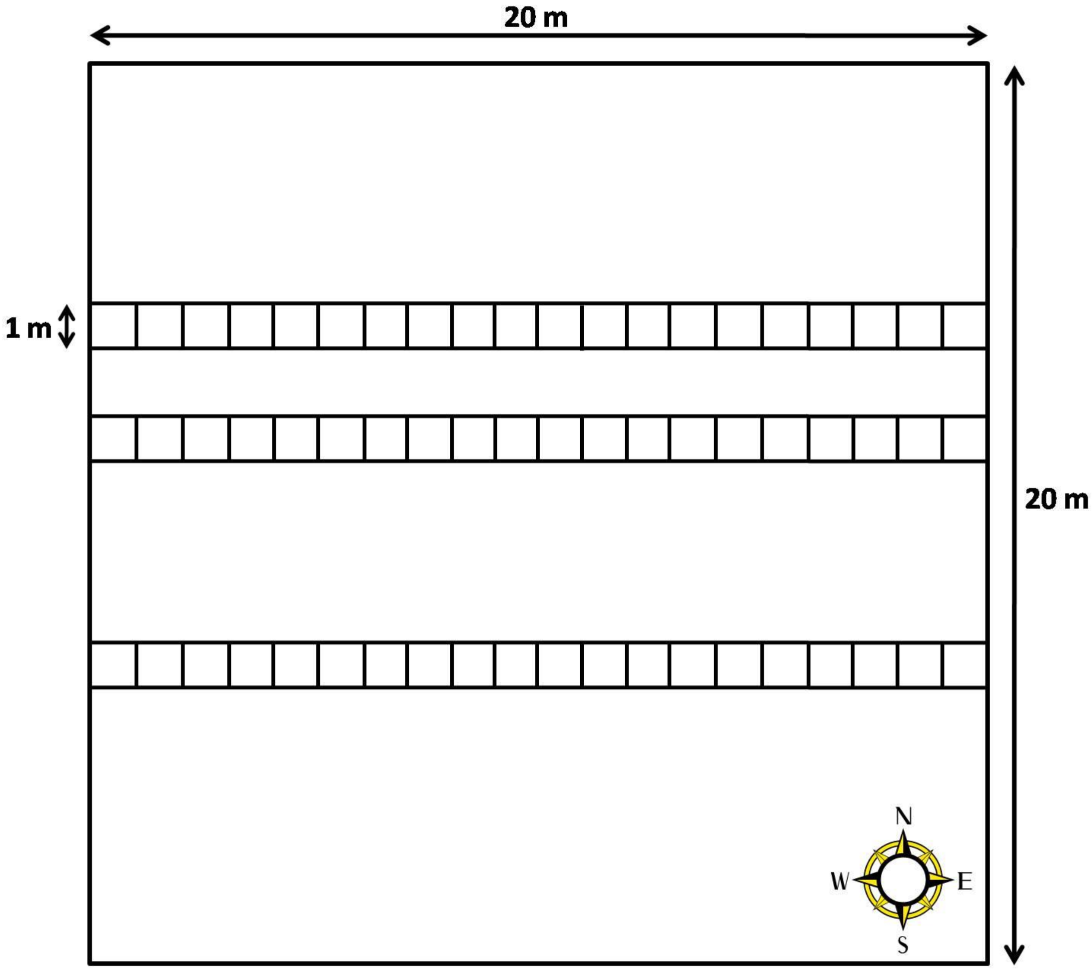


Figure 3. Layout of the replicated 20 x 20 m sample plots in each study site. Horizontal belts represent the 20 x 1 m belt transect that were established randomly and sampled continuously with 1 x 1 m quadrats in the west-east direction.

2.2.3 Fire severity and current substrate conditions

Generally speaking, classifications of fire severity and early post-fire conditions should consider characteristics of fire behaviour (fire intensity), estimates of depth of burn (duff consumption) and visual characteristics of the ground surface effect (charring and fuel consumption) (Ryan and Noste, 1985; Miyanishi and Johnson, 2002; Ryan, 2002; Neary et al., 2005; Lecomte et al., 2006). However, it was not possible to determine the exact depth of organic matter in pre-fire stands. Therefore, TNNP fire weather records were compiled (*sensu* Bloom, 2001) to compare the fire conditions of each post-fire plant community. Fire severity was determined from the residual organic matter (ROM) depth by quantifying the average thickness of organic matter (duff) that was not consumed by the last fire (see Nguyen-Xuan et al., 2000; Lecomte et al., 2006).

Thickness of the ROM layer was estimated by *in situ* analysis of soil cores consecutively sampled from each 1 x 1 m quadrat along one 20 x 1m belt transect (N=20/plot; 60/site). Intact soil cores were sampled down to the Ae mineral soil horizon using a 40 cm long, 5.5 cm diameter Eijkelkamp split tube sampler (Hoskin Scientific, Burlington, Ontario). The cores were removed from the sampler in the field and analysed to determine the depth of charcoal position within the soil profile. ROM was then estimated as the depth of organic matter above the Ae mineral soil horizon and below the most recent charcoal layer. Multiple charcoal layers were not encountered in the samples; I therefore assumed the absence of multiple fire events in these plots.

To compare the current substrate conditions in each plant community, mean depth of organic matter (DOM) was consecutively sampled in 1 x 1 m quadrats along three 20 x 1 m belt transects (N=60/plot; 180/site). Three measures of DOM were averaged for each quadrat to summarize the within quadrat variability. Soil cores were taken with a simple auger (from the Oh to the Ae mineral soil horizon) and measured to the nearest 0.1 cm. Soil moisture (SM) was also estimated in the organic horizon in each quadrat by averaging three instantaneous readings (± 0.05 $m^3.m^{-3}$) from a Theta Probe moisture meter (N=60/plot; 180/site) (Model # ML2x, Hoskin Scientific, Burlington, Ontario). Moisture readings were taken two days after rainfall between 11:00 am and 1:00 pm to reduce diurnal variation in the data.

Since it was not possible to determine the initial change in organic matter depth after each fire event, the amount of organic matter consumed in each study site was quantified by laboratory analysis of charcoal content in the organic horizon. Three soil cores were randomly sampled from post-fire sample plots in each study site using an Eijkelkamp split tube sampler. Since wood savannah study sites were characterized by two distinct microsites (black spruce islands and *Kalmia* heath), cores were sampled in pairs; one from the inside of black spruce islands and the other from the surrounding heath (N=9 in *Kalmia* heath, N=18 in *Kalmia*-lichen wood savannah, and N=9 black spruce-*Kalmia* forest). Cores were transferred from the sampler into 40 cm long, 5.2 cm diameter PVC pipe, and stored frozen until they were cold-transported back to the Lakehead University Plant Ecology lab. The cores remained frozen for one month prior to charcoal analysis.

The cores were semi-thawed and cut into uniform, 2 cm thick samples (approximately 47.53 cm^3) using a sharp serrated saw. Samples were cut from the upper-most surface of the organic horizon down to the organic-Ae mineral soil horizon interface. I estimated charcoal content by modifying the method described by Lecomte et al. (2006). Each 2 cm section was deflocculated by submerging the section in a 2% solution of NaOH and heating in a 60 °C water bath for 24 hrs. Once cooled to touch, the soil was gently sieved through wire mesh to retain soil particles ranging from 2-0.5 mm, which is the average size range for most charcoal particles after wildfire (Zackrisson et al., 1996). Location of the organic-Ae mineral soil horizon interface was determined for each soil core by recording the depth at which a soil sample retained > 25% mineral soil particles above the 2 mm wire mesh (Lecomte et al., 2006). Sieved particles were then bleached in a 10-20% solution of HCl to better distinguish charcoal from other suspended organics.

The samples were then poured into a 14.5 cm diameter Pyrex Petri dish fitted with a 1-cm^2 grid and observed under 6-40x magnification. The abundance of charcoal was estimated for each 2 cm soil section by estimating the percentage of charcoal particles present relative to the total sample. Charcoal abundances were assigned to one of 13 rank abundance classes, 0 (not visible), 1 (<2%), 2 (2-5%), 3 (5-10%), 4 (11-20%), 5 (21-30%) and so on up to abundance class 12 (91-100%). Abundance class 13 was assigned to samples in which both charcoal and ash (indicating complete soil combustion) were present.

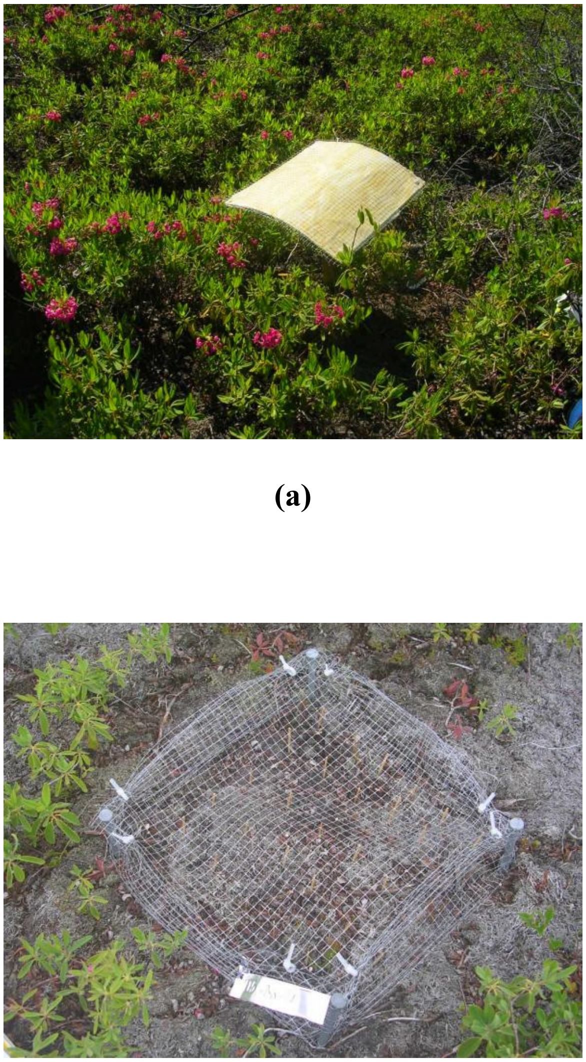
2.2.4 Seed supply and seedbed condition

In early June 2007, 20 seed traps were randomly established throughout the experimental study site. Power (2005) determined that black spruce seed rain was more prevalent at the burn edges than within the interior of this sites, therefore I established five 80 m transects beginning at the fire boundary extending into the interior of the burn. Four seed traps were spaced at 20 m intervals along each transect. Traps were constructed from a 30 cm tall wooden post fitted with a 30 x 30 cm vinyl tile surface (Figure 4a). Tiles were covered with wax paper and coated with Tanglefoot (Halifax Seed Company). The vinyl surface was overlaid with a 1 x 1 cm wire mesh grid to aid in determining the number of seeds/unit area. While pit traps and seed boxes are commonly used to measure conifer seed rain, they are not as successful at capturing the small seeds characteristic of some woody shrubs like *Kalmia*. Therefore, erected adhesive seed traps were used to ensure capture of all aerial seeds, both small and large. Traps were visited weekly to monitor seed captures and to repair or replace damaged surfaces.

From June to August, none of the 20 seed traps contained seed, and by early August the traps were being disturbed frequently by black bears (*Ursus americanus* Pallas). However, I was able quantify seed production of *Kalmia* after flowering in mid-late August. I randomly established 20, 1 x 1 m sampling plots in the burn edge and interior, and counted the total number of fruits both retained and freshly fallen from *Kalmia* within each plot. Ten samples of fruit were collected from each plot to quantify the number of seeds/fruit/m^2. Fruits were observed under 40x magnification to determine average seed production, and mean seed count from each plot was used to estimate *Kalmia* seed production/ha.

During the same time period, a seeding trial was established to test the effects of low and high burn severity substrates on seed germination and seedling establishment of black spruce and *Kalmia*. A 2 x 2 factorial design was replicated in 20 random locations. Each seeding location consisted of two paired subplots; one for black spruce and *Kalmia* at high burn severity, and the other for black spruce and *Kalmia* at low burn severity. High severity burn microsites were characterized by exposed mineral soil located under former black spruce islands. Surface-charred lichen mats with intact duff layers characterized the adjacent low severity burn microsites. Each subplot was 30 x 30 cm, and was protected from seed predation by 10 cm high, 1 cm^2, wire-mesh screening (Figure 4b). In each subplot, 30 black spruce seeds were planted in grid formation and marked with toothpicks. Black spruce seeds used in this study were collected from the TNNP area by Wooddale provincial tree nursery. Germination tests showed that the seeds had > 95% viability. Since *Kalm*ia seeds are too small to mark their location, the seed of 10 fruits were scattered in each 30 x 30 cm subplot, approximating 150 seeds per subplot. *Kalmia* seeds were collected from the experimental site, and were 45% viable. The seedbed subplots were surveyed weekly for 14 weeks to determine the rate of germination.

After 14 weeks, neither species had germinated on either of the microsites. To determine if germination failure was a function of field conditions, I collected ten, 15 x 15 cm substrate samples of each microsite type and seeded each sample with 15 black spruce seeds. The samples were placed in plastic Tupperware containers, stored indoors and moistened with 200 ml water prior to seeding. The samples were sprayed with 20 ml water and surveyed for spruce germinates daily. *Kalmia* was excluded from the indoor seeding trial because its predominant mode of regeneration is vegetative.



(a)

(b)

Figure 4. Erected seed traps (a) and seeding subplots (b) (both 30 x 30 cm) established in the early post-fire field experiment.

2.2.5 Statistical analyses

Abundance of all vegetation was summarized at the sample plot level, and is reported for each site in Appendix 1. Cover values for each species were summed to estimate the total abundance of species in each plot. Species richness was calculated as the total number of different species in each sample plot and species diversity was calculated as the inverse of Simpson‟s Index (3).

$$D=1/\sum(n/N)^2 \tag{3}$$

Where n = the total abundance of a particular species

N = the total abundance of all species

Mean representation of traits was calculated for each plant community by constructing two matrices, i) a species x plot, and ii) a species x trait matrix. The matrices were combined in a trait x plot matrix by adding the percentage cover of all vegetation in each plot that possessed a given trait (Appendix 2) (Mallik et al., 2001). The matrix can be described as a weighted trait matrix, where trait values are a function of species abundance and occurrence (Walker et al., 2007). Total abundance, richness and diversity of traits were then calculated from the trait x plot matrix as described for species cover data. Species and trait response (abundance, richness and diversity) in addition to estimates of standing dead biomass and black spruce and *Kalmia* productivity were compared among plant communities using one-way analysis of variance (ANOVA) and Tukey post-hoc multiple comparisons (SPSS version 16.0). Kolomogorv-Smirnoff and Levene‟s tests were used to test the assumptions of normality and equal variance. Of these variables, it was necessary to Ln-transform standing dead biomass to meet the assumptions of ANOVA. Equal variances were not assumed for comparisons of black spruce and *Kalmia* productivity. To contrast the differences in species and trait composition among plant communities, I performed indicator species analysis (ISA; PC-ORD version 5.0). ISA calculated the proportional abundance of a particular species or trait in each community relative to their abundance in all groups to estimate their importance in each post-fire plant community.

Measures of ROM and charcoal content were averaged at the plot level. The degree of organic matter consumption by fire was summarized for each site by averaging the rank relative abundance (RAB) of charcoal in each soil core. Fire severity and charcoal content were then compared among plant communities using one-way ANOVA and Tukey post-hoc multiple comparisons tests (SPSS version 16.0). ANOVA and Tukey post-hoc tests were also used to compare DOM and SM among plant communities. The following transformations were performed in order to meet assumptions of normality and equal variance: 1/√ (ROM), √ (charcoal content) and 1/SM. ROM depth was plotted against transect length in each plant community to profile ROM distribution. A thematic diagram was constructed for each soil core to compare charcoal concentration among plant communities.

Canonical correspondence analysis (CCA) was performed on species abundance and environmental data (ROM, charcoal content, DOM, and SM) to examine the relationship between community composition and fire severity (PC-ORD v. 5.0). I then modelled the significant differences in species and trait response (i.e. abundance, richness and diversity) as a function of ROM. Significant principal components of the 14 summarized trait sub-categories were also modelled as a function of ROM to test abiotic filtering of functional traits. Scatterplots of species and trait response to ROM indicated that the variables were not linearly related. However, I anticipated that there would be a shift in species composition and functional traits corresponding to some critical depth of ROM. I had reason to accept the notion that species and traits may exponentially respond (either positively or negatively) to changes in ROM. Therefore, exponential growth and decay regression models were used to model the relationships (SigmaPlot v. 10.0). Although variation in ROM was not continuously sampled across communities, I assumed that black spruce-*Kalmia* forest sites represented the pre-fire condition among plant communities. Therefore, ROM and vegetation response were analyzed along a continuous scale among the plant communities.

The seed germination and seedling establishment trial yielded few data, and consequently the results were largely descriptive. However, I performed a t-test to determine if black spruce seed germination under laboratory conditions was different among high and low severity post-fire substrate conditions using SPSS v. 16.0.

3. Results

3.1 Pre-fire stand reconstruction

Pre-fire FRI data were available for 5 of the 9 study sites (Table 1). Among these sites, all stands were dominated by black spruce canopy ranging in age from 41-120 yrs. Black spruce heights were estimated between 9.6-18.5 m, although the majority were between 12.5 and 15.6 m. Most canopies reached 50-75% closure and had an estimated basal area between 22.40-40.46 m^2/ha. FRI data from black spruce forests adjacent to Ochre Hill and Spracklin Road wood savannah are consistent with the other 5 study sites. Although tree height was variable among sites, the data provides reasonable evidence to suggest that pre-fire site conditions were structurally and compositionally representative of typical black spruce-*Kalmia* forests in this region.

3.2 Community composition

3.2.1 Species characteristics among plant communities

Species were nearly two times more abundant in the wood savannah and forest than in the heath ($F_{2,26}=11.412$, $p<0.001$), although the heath supported 10-15 more species than the wood savannah and forest ($F_{2,26}=23.411$, $p<0.001$). Species diversity was similar among the heath and wood savannah, but significantly lower in the forest ($F_{2,26}=7.322$, $p=0.003$) (Figure 5). Higher total species abundance was a function of high shrub and lichen cover in the wood savannah and tree and pleurocarpous moss cover in the forest (Figure 6a). Trends towards higher species richness in the heath and lower diversity in the forest were a function of more lichen species in the heath and wood savannah (Figure 6b).

Table 1. Pre-fire stand characteristics of post-fire heath, wood savannah and forest communities.

Post-fire community	Site name	Stand type[a]	Age (yrs)	Height (m)	Canopy closure (%)	Field estimated bS basal area (m^2/ha)$_{\text{As}}$[b]
Heath	Thorburn	bS -wB	81-100	9.6-12.5, 12.6-15.5	26-50, 51-75	35.25
	Charlottetown	bS-KSph	61-80	15.6-18.5	>75, 26-50	45.23
	Terra Nova Rd.	bS	61-80	9.6-12.5	51-75	22.40
Wood Savannah	Gambo South	bS	61-80	9.6-12.5, 12.6-15.5	51-75	40.46
	Spracklin Rd.	bS$_{\text{As}}$	41-60$_{\text{As}}$	6.6-9.5$_{\text{As}}$	26-50$_{\text{As}}$	NA
	Ochre Hill	bS$_{\text{As}}$	81-120$_{\text{As}}$	12.3-15.5$_{\text{As}}$	NA	28.30
Forest	Gambo North	bS	61-80	9.6-12.5, 12.6-15.5	51-75	40.46
	Arnold‟s Pond	bS$_{\text{As}}$	NA	NA	NA	NA
	Southwest Arm	bS$_{\text{As}}$	NA	NA	NA	NA

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[a] The first species in each stand type represents that dominant species, such as bS (black spruce) in this case. Hyphenated species such as wB (white birch), K (*Kalmia*) and Sph (*Sphagnum*) represent the secondary dominant or primary understory species of the stand.

[b] As refers to basal area estimates that were calculated from "adjacent stands".

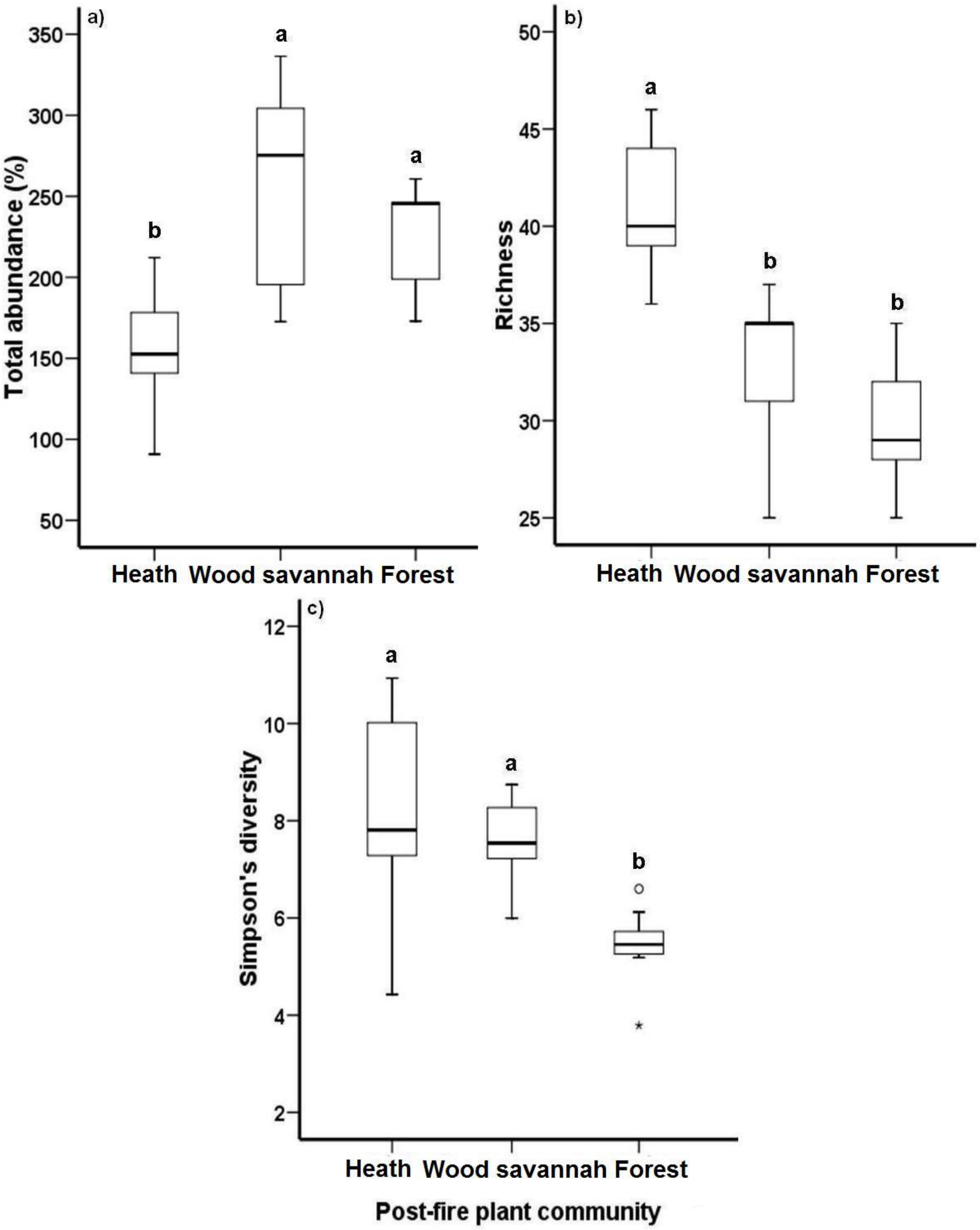

Figure 5. Post-fire ANOVA and Tukey post-hoc multiple comparison test comparing (a) total mean abundance ($F_{2,26}$=11.412, p<0.001), (b) richness ($F_{2,26}$=23.411, p<0.001) and (c) diversity ($F_{2,26}$=7.322, p=0.003) of species among heath, wood savannah and forest communities. Error bars represent 95% confidence intervals, and the solid lines in each box depict the sample median. Different letters above each box represent significant differences among communities.

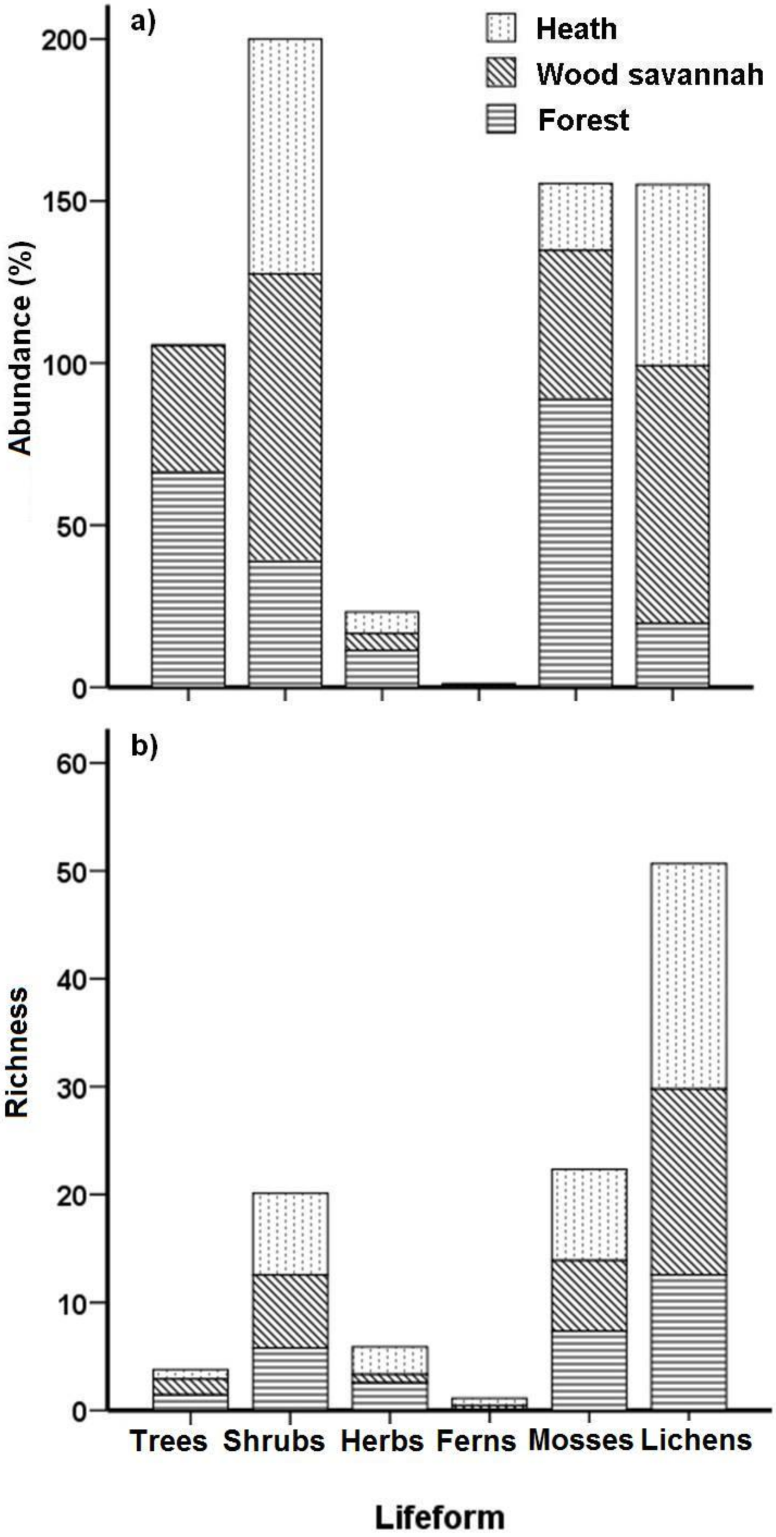

Figure 6. (a) Total mean species abundance and (b) richness of plant lifeforms represented in heath, wood savannah and forest communities. Bars represent the proportion of lifeforms among communities.

The heath and wood savannah differed significantly in species composition from the forest community (Table 2). These communities were both represented by a dwarf ericaceous shrub canopy (*Kalmia angustifolia*, *Rhododendron canadense, R. groenlandicum* and *Vaccinium angustifolium*) and lichen bed at the soil surface (*Cladina* and *Cladonia* spp.). Unlike the wood savannah, the heath had greater abundance and frequency of the shrub *Amelanchier* spp., acrocarpous mosses (*Ceratodon purpurea, Dicranum acutifolium*, *D.undulatum* and *Polytrichum juniperinum*) and fruticose lichens (*Cladonia crispata*, *C. sulphurina* and *C. gracilis*). The forest was strongly characterized by black spruce canopy with epiphytic lichens such as *Bryoria* spp., *Parmelia sulcata* and *Hypogymnia physodes*. Ground layer shrubs (*Gaultheria hispidula*), herbaceous plants (*Linnaea borealis, Clintonia borealis*), and pleurocarpous mosses (*Pleurozium schreberi, Hylocomium splendens*, *Ptilium crista-castrensis*) dominated the forest floor (Table 2).

Table 2. Indicator species analysis of species abundance (%) data between (a) heath vs. forest and (b) wood savannah vs. forest plant communities. Importance values (IV) represent the faithfulness of species to each community and are supported by the significance value *p*. *P*-values <0.05 indicate significant indicator species among plant communities.

Lifeform	Heath$_a^*$ and wood savannah$_b^*$ species	IV	*P*-value	Forest species	IV	*P*-value
Trees	_ _ _	_ _ _	_ _ _	*Picea mariana*	99.3$_a$ 62.8$_b$	<0.001$_a$ <0.001$_b$
Shrubs	*Amelanchier* spp.	95.6$_a$	<0.001$_a$	*Gaultheria hispidula*	66.6$_a$ 65.5$_b$	0.011$_a$ 0.032$_b$
	Kalmia angustifolia	64.6$_a$ 68.9$_b$	0.028$_a$ 0.001$_b$	_ _ _	_ _ _	_ _ _
	Rhododendron canadense	92.9$_a$ 94.9$_b$	<0.001$_a$ <0.001$_b$	_ _ _	_ _ _	_ _ _
	Rhododendron groenlandicum	86.0$_a$ 97.7$_b$	0.001$_a$ <0.001$_b$	_ _ _	_ _ _	_ _ _
	Vaccinium angustifolium	82.1$_a$ 78.5$_b$	0.001$_a$ 0.003$_b$	_ _ _	_ _ _	_ _ _
Herbs	_ _ _	_ _ _	_ _ _	*Linnaea borealis*	55.6$_a$ 55.6$_b$	0.025$_a$ 0.027$_b$
	_ _ _	_ _ _	_ _ _	*Clintonia borealis*	55.6$_b$	0.027$_b$
Bryophytes	*Ceratodon purpurea*	84.7$_a$	0.003$_a$			
	Dicranum acutifolium	77.8$_a$	0.002$_a$	*Ptilium crista-castrensis*	99.8$_a$ 98.2$_b$	<0.001$_a$ 0.001$_b$
	Dicranum undulatum	66.7$_a$	0.009$_a$	Leafy liverwort	94.9$_a$	<0.001$_a$
	Dicranum spp. (wavy)	66.7$_b$	0.007$_b$	*Pleurozium schreberi*	88.7$_a$	0.001$_a$
	Polytrichum juniperinum	64.2$_a$	0.041$_a$	*Hylocomium splendens*	87.4$_a$ 82.0$_b$	0.005$_a$ 0.005$_b$

Table 2
continued.

Lichens	*Cladonia cornuta*	99.6_a	$<0.001_a$	*Dicranum polysetum*	63.9_a	0.042_a
		65.1_b	0.027_b			
	Cladina stellaris	98.8_a	$<0.001_a$	*Cladonia coniocrea*	87.9_a	$<0.001_a$
		99.8_b	$<0.001_b$		75.8_b	0.005_b
	Cladonia crispata	98.5_a	$<0.001_a$	*Bryoria* spp.	85.8_a	0.028_a
	Cladina mitis	98.7_a	$<0.001_a$	*Parmelia sulcata*	86.4_a	0.007_a
		97.3_b	0.001_b			
	Cladonia borealis/cristatella	98.8_a	$<0.001_a$	*Hypogymnia physodes*	81.8_a	$<0.001_a$
	Cladonia sulphurina	93.7_a	$<0.001_a$			
	Cladina rangiferina	93.7_a	$<0.001_a$			
		92.3_b	$<0.001_b$			
	Cladonia gracilis	91.3_a	$<0.001_a$			
	Parmeliopsis ambigua	69.2_a	$<0.016_a$	_ _ _	_ _ _	_ _ _
		93.8_b	$<0.001_b$			
	Cetraria spp.	80.5_b	0.009_b	_ _ _	_ _ _	_ _ _
	Buellia punctata	71.7_a	0.027_a			
	Cladonia verticillata	55.6_a	0.031_a			

[*] a=Heath vs. forest, b=Wood savannah vs. forest.

3.2.2 Trait characteristics among plant communities

Traits were nearly two times more abundant in the wood savannah and forest community than in the heath ($F_{2,26}=20.568$, $p<0.001$), and trait diversity significantly higher by five times in the wood savannah ($F_{2,26}=12.602$, $p<0.001$). However, the richness of traits was similar among plant communities ($F_{2,26}=3.299$, $p=0.054$) (Figure 7).

Although the number of traits was similar among communities, their composition in the heath and wood savannah differed significantly from the forest community (Table 3). Nanophanerophyte perennial shrubs and fruticose lichens were the predominant lifeform in the heath and wood savannah. They are characterized by multi-stemmed above ground and rhizomatous below ground growth. Adventitious roots from the underground rhizomes were also characterized by ericoid mycorrhiza colonization. In the forest community the dominant lifeforms were characterized by perennial trees, herbs and pleurocarpous mosses, which have many different growth forms (single stem, stoloniferous, creeping and foliose) and perennating structures (mesophanero-, chamae-, geo-, and epiphyte). Fine roots of forest species (mainly perennial trees) were also colonized by both endo and ecto-mycorrhizae.

The plant communities also varied greatly in their successional status and regeneration characteristics. In the heath and wood savannah, communities were characterized by obligate initial colonizers that regenerate primarily through vegetative structures and had low seed production. The forest community supported both early and late successional species that were primarily seed regenerating with moderate seed abundance. Communities also differed in terms of species‟ habitat tolerances, mainly in that forest species had significantly lower fire tolerance and higher fertility requirements.

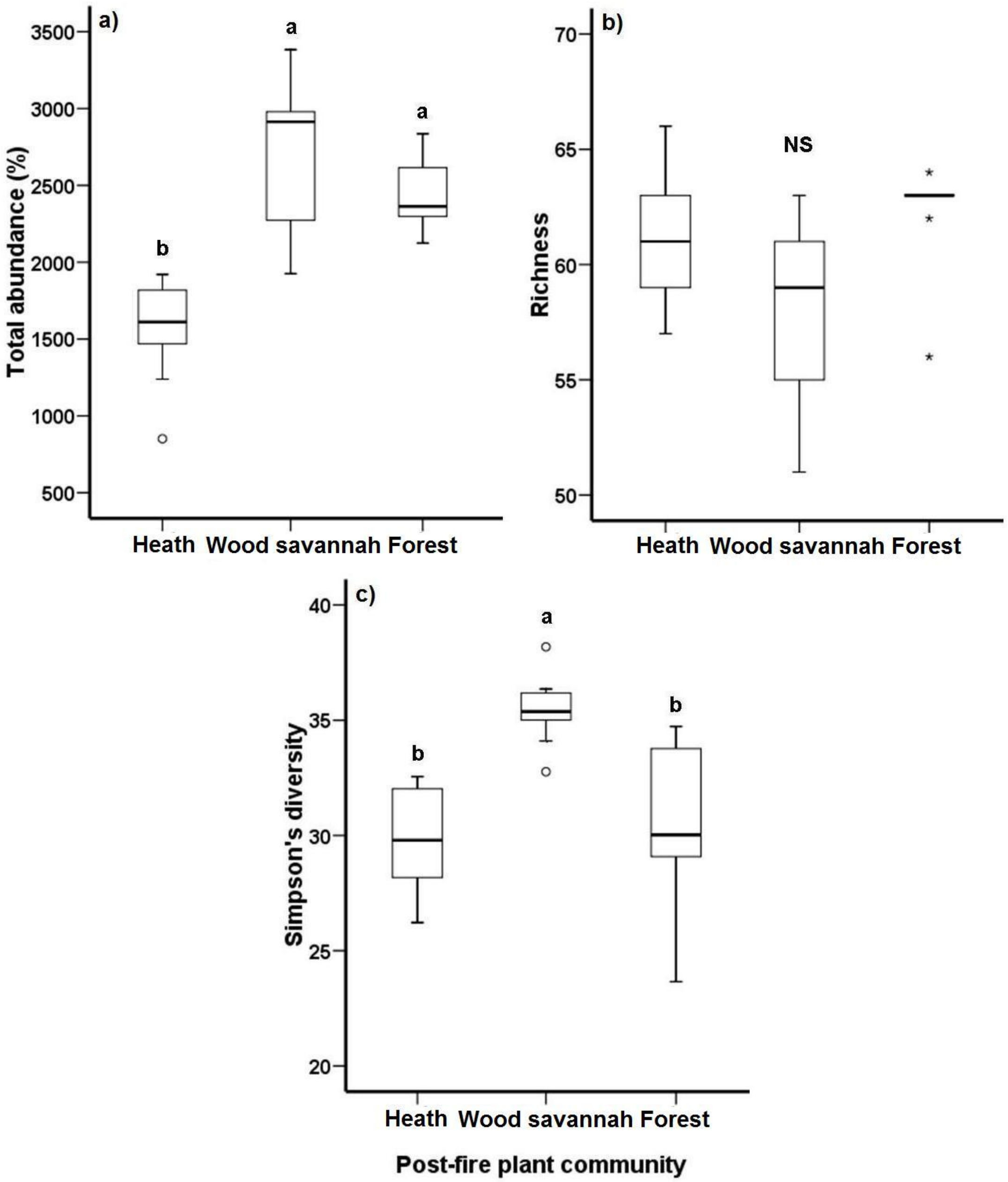

Figure 7. Post-fire ANOVA and Tukey post-hoc multiple comparison test comparing total mean (a) abundance ($F_{2,26}$=20.568, p<0.001), (b) richness ($F_{2,26}$=3.299, p=0.054) and (c) diversity ($F_{2,26}$=12.602, p<0.001) of traits among heath, wood savannah and forest communities. Error bars represent 95% confidence intervals, and the solid lines in each box depict the sample median. Different letters above each box represent significant differences among communities.

Table 3. Indicator traits and importance values (IV) of total mean trait representation for (a) heath vs. forest and (b) wood savannah vs. forest plant communities. Importance values (IV) represent the faithfulness of species to each community and are supported by the significance value *p*. *P*-values <0.05 indicate significant indicator species among plant communities.

Trait Category	Heath$_{a}^{*}$ and Wood savannah$_{b}^{*}$			Forest		
Lifeform	Trait	IV	*P*-value	Trait	IV	*P*-value
	Perennial shrub	65.1_{a}	0.010_{a}	Perennial tree	99.4_{a}	$<0.001_{a}$
		69.6_{b}	$<0.001_{b}$		62.9_{b}	$<0.001_{b}$
	Lichen	74.0_{a}	$<0.001_{a}$	Perennial herb	74.8_{b}	0.023_{b}
		80.2_{b}	$<0.001_{b}$			
				Bryophyte	81.1_{a}	$<0.001_{a}$
					65.9_{b}	0.045_{b}
Architecture	Multi stem	84.7_{a}	$<0.001_{a}$	Single stem	99.4_{a}	$<0.001_{a}$
		86.3_{b}	$<0.001_{b}$		62.9_{b}	$<0.001_{b}$
	Rhizomatous	58.9_{a}	0.037_{a}	Stoloniferous	66.6_{a}	0.016_{a}
		62.6_{b}	0.005_{b}		65.6_{b}	0.038_{b}
	Fruticose	85.7_{a}	$<0.001_{a}$	Creeping	55.6_{a}	0.030_{a}
		88.2_{b}	$<0.001_{b}$		55.6_{b}	0.029_{b}
				Pleurocarpous	92.4_{a}	$<0.001_{a}$
				Foliose	84.5_{a}	$<0.001_{a}$
Raunkiaer lifeform	Nanophanerophyte	69.4_{a}	0.001_{a}	Mesophanerophyte	99.4_{a}	$<0.001_{a}$
		72.8_{b}	$<0.001_{b}$		62.9_{b}	$<0.001_{b}$
				Chamaephyte	73.0_{a}	0.017_{a}
					57.3_{b}	0.041_{b}
				Epiphyte	87.3_{a}	$<0.001_{a}$
				Geophyte	74.8_{b}	0.023_{b}
Mycorrhizal Symbiont	Ericoid	66.3_{a}	0.005_{a}	Ecto	99.2_{a}	$<0.001_{a}$
		69.0_{b}	$<0.001_{b}$		63.2_{b}	$<0.001_{b}$
				Endo	93.0_{a}	$<0.001_{a}$
Root concentration				Organic	59.3_{a}	$<0.001_{a}$

Table 3 continued.

Successional status	Obligate initial colonizer	65.1_{a}	0.020_{a}	Climax-obligate climax	99.4_{a}	$<0.001_{a}$
		68.8_{b}	0.001_{b}		65.1_{b}	$<0.001_{b}$
				Pioneer	70.4_{a}	0.007_{a}
					78.9_{b}	$<0.001_{b}$
				Seral-mid seral	76.7_{a}	0.006_{a}
				Facultative seral	71.2_{a}	0.021_{a}
Regeneration	Vegetative	65.4_{a}	0.002_{a}	Seed	97.8_{a}	$<0.001_{a}$
		68.5_{b}	$<0.001_{b}$		62.5_{b}	$<0.001_{b}$
	Low seed abundance	65.5_{a}	0.004_{a}	Medium seed abundance	95.2_{a}	$<0.001_{a}$
		65.9_{b}	0.042_{b}		60.8_{b}	0.001_{b}
	High seed abundance	64.2_{b}	0.014_{b}	Serotiny	99.5_{a}	$<0.001_{a}$
					62.8_{b}	$<0.001_{b}$
	Animal dispersed	60.7_{a}	0.032_{a}	Wind dispersed	93.8_{a}	$<0.001_{a}$
					61.6_{b}	0.001_{b}
				Resprout ability	59.7_{a}	$<0.001_{a}$
Shade tolerance	Low-intolerant	68.0_{a}	0.007_{a}	Medium	66.7_{a}	$<0.001_{a}$
		65.5_{b}	0.023_{b}			
Fire tolerance	Medium	69.6_{a}	0.009_{a}	Low	70.2_{a}	0.003_{a}
		73.8_{b}	0.007_{b}			
	High	61.2_{b}	0.006_{b}			
Fertility requirements	Low	70.2_{a}	0.003_{a}	High	87.4_{a}	0.008_{a}
		75.1_{b}	$<0.001_{b}$		82.0_{b}	0.007_{b}
				Medium	80.7_{a}	$<0.001_{a}$
					60.4_{b}	$<0.001_{b}$
Drought tolerance	Medium	66.6_{a}	0.004_{a}			
		69.4_{b}	$<0.001_{b}$			
Growth rate	Moderate	67.9_{a}	0.018_{a}	Slow	88.4_{a}	$<0.001_{a}$
		72.3_{b}	0.010_{b}		60.9_{b}	0.003_{b}
	Rapid	63.7_{a}	0.030_{a}			
		68.2_{b}	0.002_{b}			

Table 3 continued.

C:N ratio	Medium	72.5_a 67.7_b	0.002_a 0.026_b	High	64.3_a	$<0.001_a$
Allelopathic	Yes	69.9_a 74.7_b	0.003_a $<0.001_b$			

$^{*}{}_{a}$=Heath vs. forest, $_{b}$=Wood savannah vs. forest.

The 95% confidence intervals for black spruce and *Kalmia* biomass reflect their highly variable productivity among communities (Figure 8). Nonetheless, black spruce biomass was negligible in the heath and more than 40 times higher in the wood savannah and forest ($F_{2,26}$=4.984; p=0.015). *Kalmia* productivity was 1.5 times lower in the heath than the wood savannah and forest ($F_{2,26}$=3.680; p=0.040) (Figure 8). *Kalmia* and other ericaceous shrubs maintain dominance in a low productivity condition. Although total biomass of *Kalmia* was high in the forest understory, significantly lower estimates of standing dead biomass in the forest ($F_{2,26}$=23.301; p<0.001) indicate that ericaceous species cover was suppressed by black spruce canopy cover (Figure 8). Thus, the results provide evidence that black spruce and *Kalmia* perform differently among the plant communities when in dominant vs. subordinate roles.

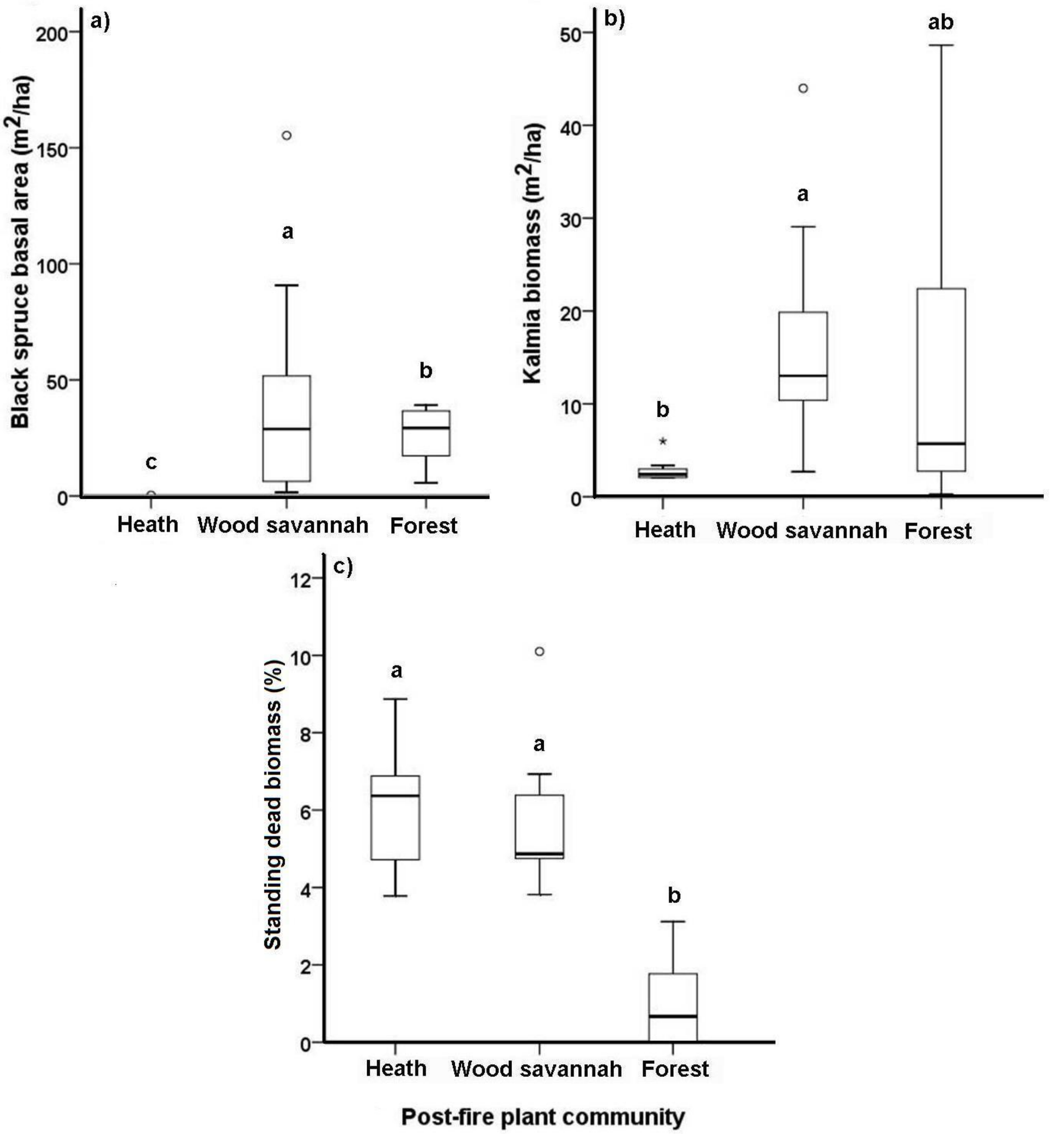

Figure 8. Post-fire ANOVA and Tukey post-hoc multiple comparisons of mean (a) black spruce ($F_{2,26}$=4.984; p=0.015) and (b) *Kalmia* ($F_{2,26}$=3.680; p=0.040) productivity, and (c) standing dead biomass ($F_{2,26}$=23.301; p<0.001) in heath, wood savannah and forest communities. Equal variances were not assumed for black spruce and *Kalmia* productivity. Error bars represent 95% confidence intervals, and the solid lines in each box depict the sample median. Different letters above each box represent significant differences among communities.

3.3 Fire severity and current substrate conditions

Fire weather records were available for 5 out of the 9 sites, and the data indicate that the most recent fires at all three heath sites were lower in severity (SI = 200-412) than at one wood savannah (SI = 3948) and one forest site (SI = 3948) (Table 4). Mean ROM depth was approximately two times deeper in the heath than the wood savannah and six times deeper in the heath than the forest (Figure 9a; $F_{2,26}$=26.578; p<0.001). When ROM was separated by its location in the wood savannah (outside vs. inside black spruce islands), ROM among heath and outside black spruce islands were similar, and nearly four times deeper than ROM depths in the forest and under black spruce islands respectively (Figure 9b; $F_{2,26}$=11.444; p<0.001). Also, mean rank RAB of charcoal was 1.5 times lower in the heath than wood savannah and forest (Figure 9c; $F_{2,26}$=7.861; p=0.002) and most abundance under black spruce islands (Figure 9d: $F_{2,26}$=6.954; p<0.001) . The results provide strong evidence that areas characterized by *Kalmia* dominance have experienced lower fire severity than areas dominated by black spruce.

Profiles of ROM along each belt transect illustrate that the pattern of ROM is different among plant communities (Figure 10). In the heath, there was a continuous distribution of ROM above 2 cm, indicating low fire severity. The opposite was true for forest plots, which had a continuous distribution of ROM below 2 cm indicating high fire severity. ROM was discontinuous in the wood savannah with lower ROM inside black spruce islands, suggesting patchiness in fire severity. Also, there were differences in charcoal content of the organic horizon among plant communities, suggesting differences in organic matter consumption (Figure 11). Heath sites had low charcoal content in the upper organic horizon, ranging from 2-50% abundance. In the forest, charcoal content ranged from 50-100% near the organic-mineral soil horizon interface. Charcoal was also high outside the black spruce islands, particularly in Gambo

South site (Figure 11), but it was more abundant inside than outside of the black spruce islands indicating patchiness in organic matter consumption.

DOM did not differ among plant communities (Figure 12a, $F_{2,26}$=0.959; p=0.397) or microsites (Figure 12b, $F_{2,26}$=1.375; p=0.268). When heath and island microsite measurements were considered separately, SM was significantly lower within the black spruce islands than in the surrounding heath (Figure 12d, $F_{2,26}$=4.488; p=0.010).

Table 4. Fire weather records of study sites located in the greater Terra Nova ecosystem. NA represents information that was not available through FRI data or personal correspondence.

Plant community	Site name	Time since fire (yrs)	Burn duration (days)	Drought code (DC)	Moisture code (MC)	Severity index (SI)
Heath	Thorburn	12	2	100	275	200
	Charlottetown	25	2	206	210	412
	Terra Nova Rd.	31	2	206	210	412
Wood Savannah	Gambo South	28	14	282	180	3948
	Spracklin Rd.	>100	NA	NA	NA	NA
	Ochre Hill	>100	NA	NA	NA	NA
Forest	Gambo North	28	14	282	180	3948
	Arnold"s Pond	>100	NA	NA	NA	NA
	Southwest Arm	>100	NA	NA	NA	NA

(Information was obtained through personal communication documented in Bloom, 2001)

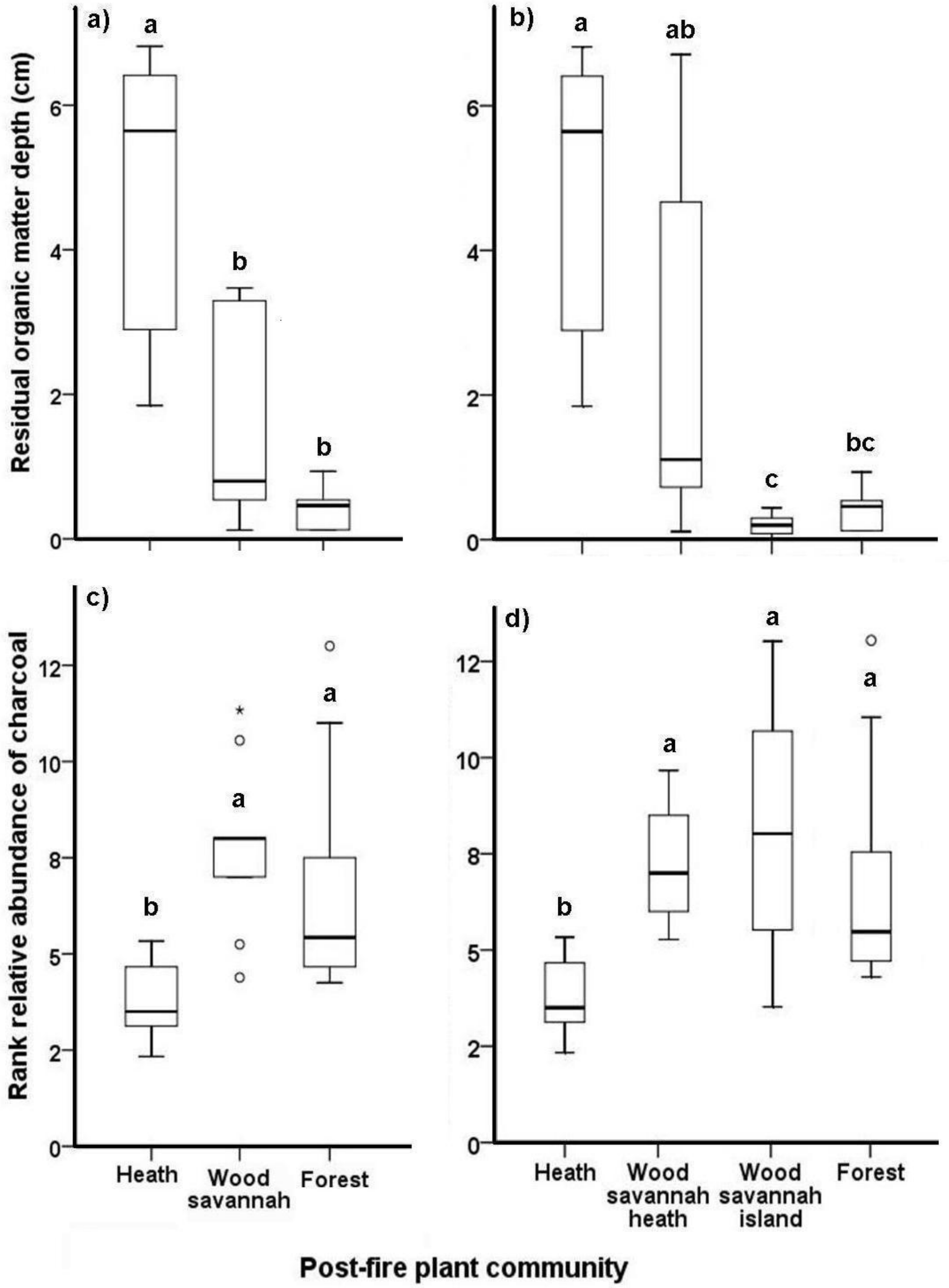

Figure 9. Post-fire ANOVA and Tukey post-hoc multiple comparison of residual organic matter depth (cm) among (a) communities ($F_{2,26}$=26.578; p<0.001) and (b) microsites ($F_{2,26}$=11.444; p<0.001), and rank relative abundance of charcoal among (c) communities ($F_{2,26}$=7.861; p=0.002) and (d) microsites ($F_{2,26}$=6.954; p<0.001). Error bars represent 95% confidence intervals, and solid lines in each box depict the sample median. Different letters above each box represent significant differences among communities.

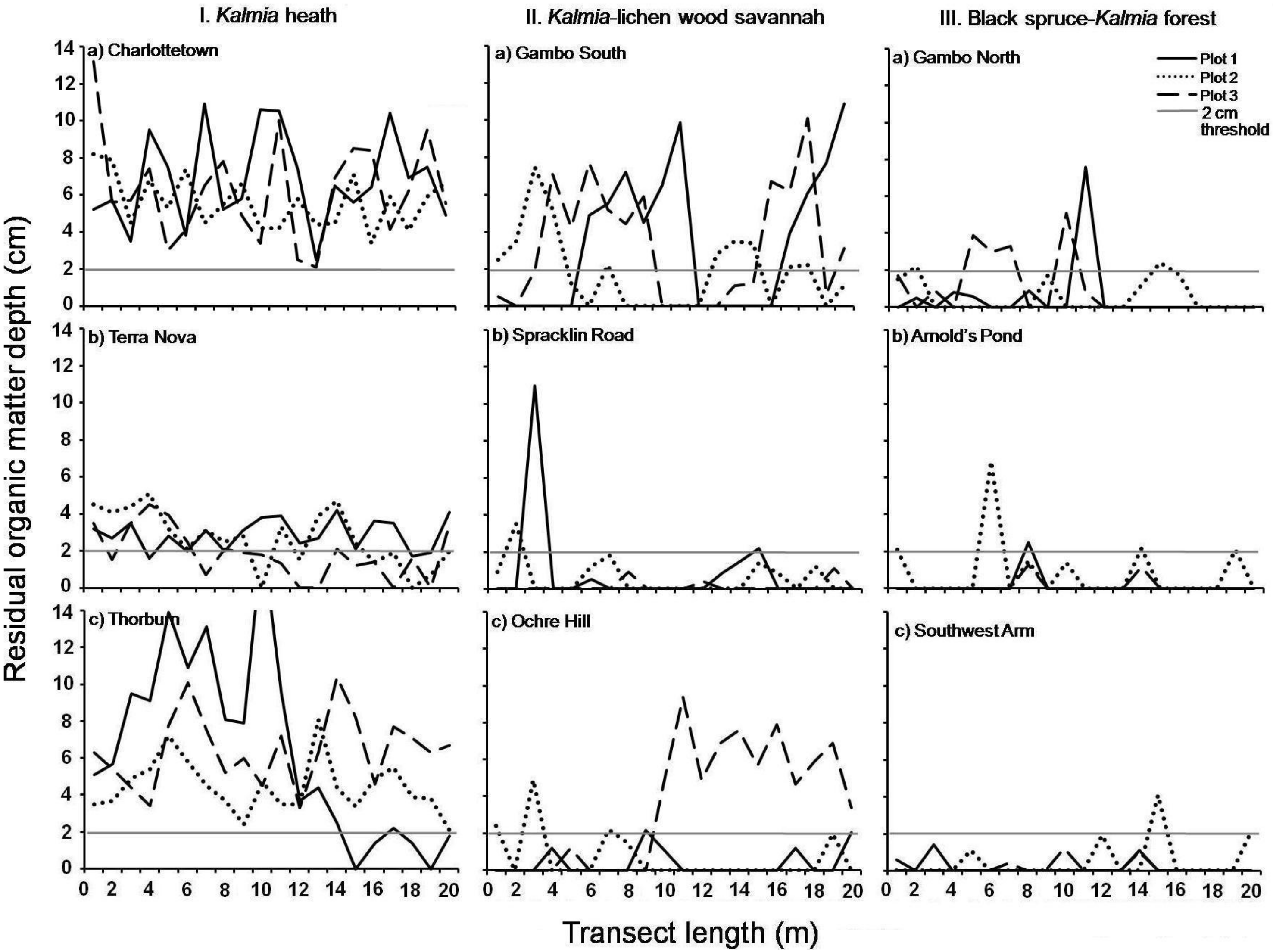

Figure 10. Residual organic matter (ROM) distributions along each 20 x 1 m belt transect in I) *Kalmia* heath, II) *Kalmia*-lichen wood savannah and III) black spruce forests. Lines drawn at 2 cm indicate the critical depth differentiating high and low severity fire.

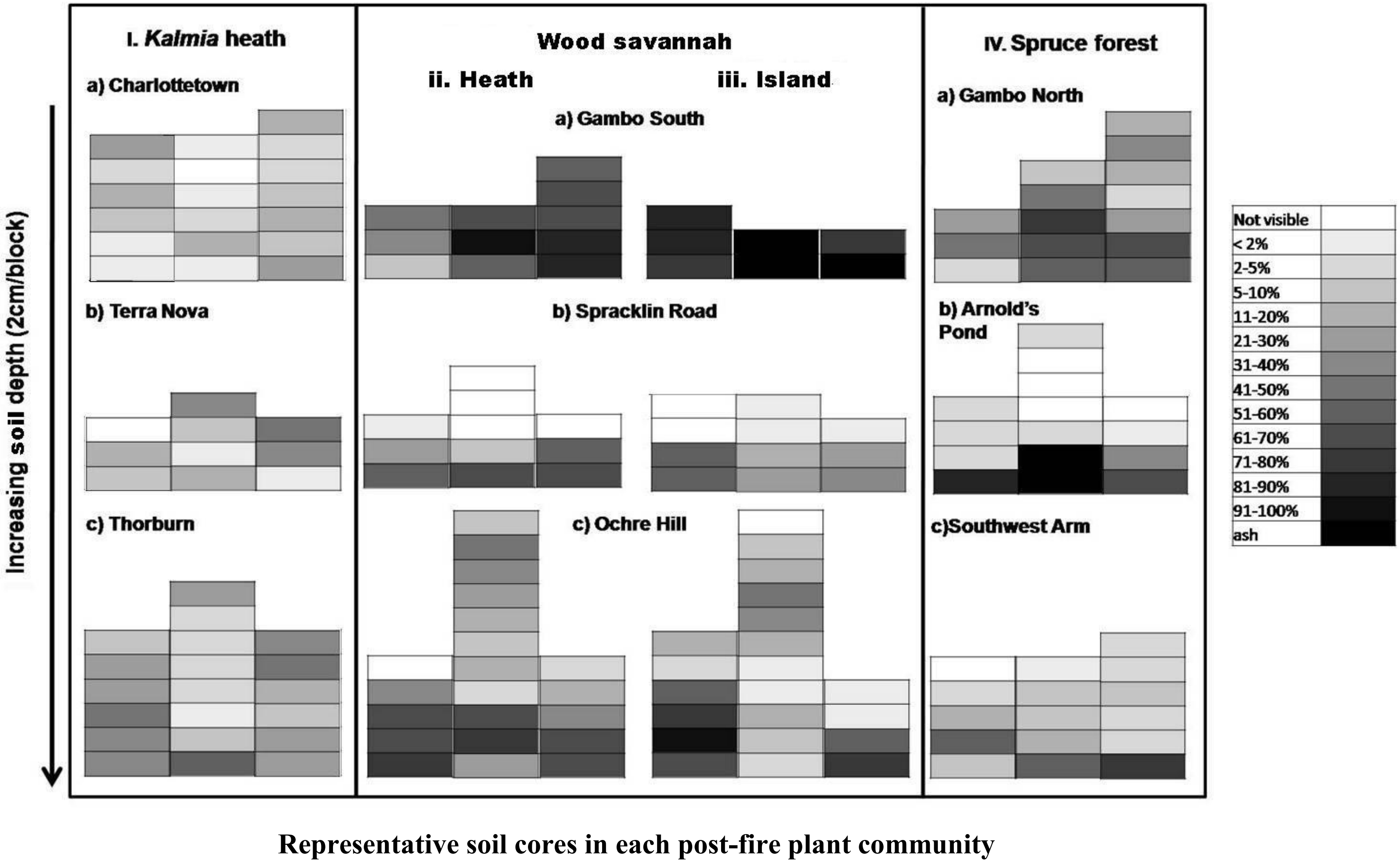

Figure 11. Thematic profiles of soil cores depicting the change in charcoal concentration with depth in each post-fire plant community. The three profiles per site represent the three representative soils cores, and the rectangular blocks in each profile represents a 2 cm soil section.

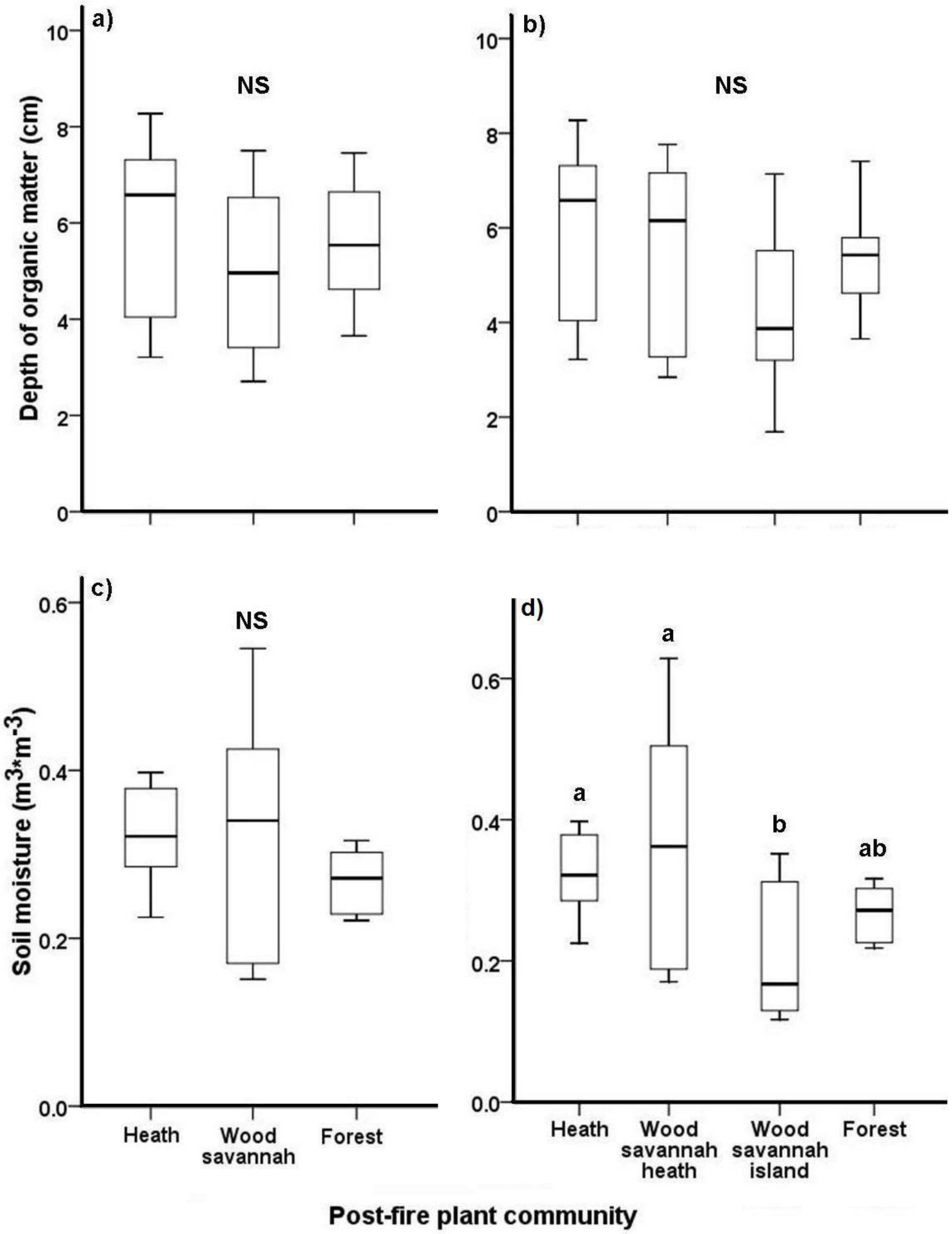

Figure 12. Post-fire ANOVA and Tukey post-hoc multiple comparison of total organic matter depth (cm) among (a) communities ($F_{2,26}$=0.959; p=0.397) and (b) microsites ($F_{2,26}$=1.375; p=0.268), and relative soil moisture among (c) communities ($F_{2,26}$=0.703; p=0.505) and (d) microsites ($F_{2,26}$=4.488; p=0.010). Error bars represent 95% confidence intervals, and the solid lines in each box depict the sample median. Different letters above each box represent significant differences among plant communities. NS represents no significant differences among groups.

3.4 Effect of fire severity on the post-fire plant community

3.4.1 Species response to ROM depth

Among the significant differences in post-fire species response described in 3.2.1, ROM was only a significant predictor of the increase in species richness (adj. $R^2 = 80.6\%$, $p<0.001$) and diversity (adj. $R^2 = 26.8\%$, $p<0.001$) between the heath and forest (Appendix 3a; Figure 13).

From the CCA, we predicted that 47.0 % of the cumulative variation in species composition among communities could be explained by differences in substrate conditions (Table 5). The variation was mainly accounted for by ROM (r=0.881) and charcoal content (r=-0.377) along axis 1, and to a lesser extent SM along axis 2 (r=0.686) (Table 6). Species correlation coefficients along axis 1 demonstrated that ericaceous shrubs, acrocarpous mosses and fruticose lichens were strongly associated with high ROM and low charcoal content, and that trees (black spruce), herbaceous ground cover, pleurocarpous mosses and some lichen species were strongly associated with low ROM and high charcoal content (Table 7; Figure 14). The results support the primary hypothesis that early post-fire ROM strongly filters post-fire community assembly.

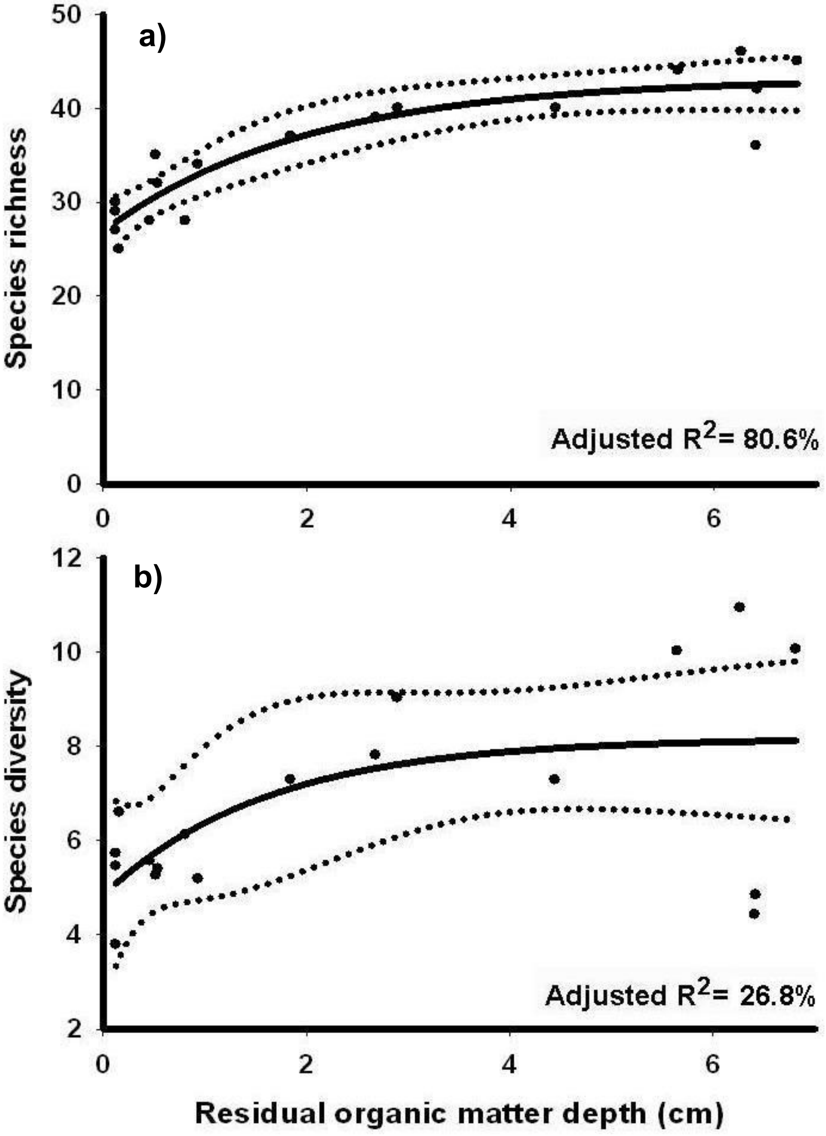

Figure 13. Exponential rise of (a) species richness (N=18, $F_{2, 15}$=36.45, p<0.001) and (b) species diversity (N=18, $F_{2, 15}$=4.12, p=0.037) to increasing residual organic matter between forest and heath plant communities. Dotted lines represent upper and lower 95% confidence intervals.

Table 5. Summary statistics of CCA on species abundance and environmental data. *P*-values <0.05 for axis 1 and 2 indicate that environmental conditions significantly influence species composition among plant communities.

Axis	Eigenvalue	*P*-value	Variance in species data	R - squared	Species-environment correlation	*P*-value
1	0.337	0.001	25.0	0.658	0.873	0.001
2	0.133	0.01	9.8	0.099	0.847	0.01

Table 6. Correlation coefficients of substrate variables along axis 1 and 2 of the CCA ordination.

Variable	Axis 1	Axis 2
Residual organic matter	0.881	-0.167
Charcoal content (%)	-0.414	-0.092
Total organic horizon	0.106	-0.035
Soil moisture	0.026	0.686

Table 7. Correlation coefficients of species abundance data along axis 1 of the CCA ordination.

Lifeform	Species	-ve	Species	+ve
Trees	*Picea mariana*	-0.932	_ _ _	_ _ _
Shrub	*Gaultheria hispidula*	-0.545	*Vaccinium angustifolium*	0.669
	Vaccinium vitis-idaea	-0.376	*Kalmia angustifolia*	0.461
	_ _ _	_ _ _	*Rhododendron canadense*	0.349
	_ _ _	_ _ _	*Chamaedaphne calyculata*	0.349
	_ _ _	_ _ _	*Rhododendron groenlandicum*	0.258
Herbs	*Linnaea borealis*	-0.551	_ _ _	_ _ _
	Clintonia borealis	-0.465	_ _ _	_ _ _
	Cornus canadensis	-0.399	_ _ _	_ _ _
Sedge	_ _ _	_ _ _	*Carex trisperma*	0.414
Bryophytes	*Pleurozium schreberi*	-0.838	*Dicranum acutifolium*	0.540
	Hylocomium splendens	-0.740	*Ceratodon purpurea*	0.483
	Ptilium crista-castrensis	-0.690	*Polytrichum juniperinum*	0.465
	Dicranum scoparium	-0.496	_ _ _	_ _ _
Lichens	*Parmelia sulcata*	-0.713	*Cladonia crispata*	0.856
	Usnea spp.	-0.558	*Cladonia sulphurina*	0.743
	Bryoria spp.	-0.512	*Cladonia cornuta*	0.724
	Cladonia coniocrea	-0.497	*Cladina mitis*	0.709
	Hypogymnia physodes	-0.417	*Cladina rangiferina*	0.630
	_ _ _	_ _ _	*Cladonia gracilis*	0.608
	_ _ _	_ _ _	*Cladonia borealis/cristatella*	0.509
			Cladonia cenotea	0.357

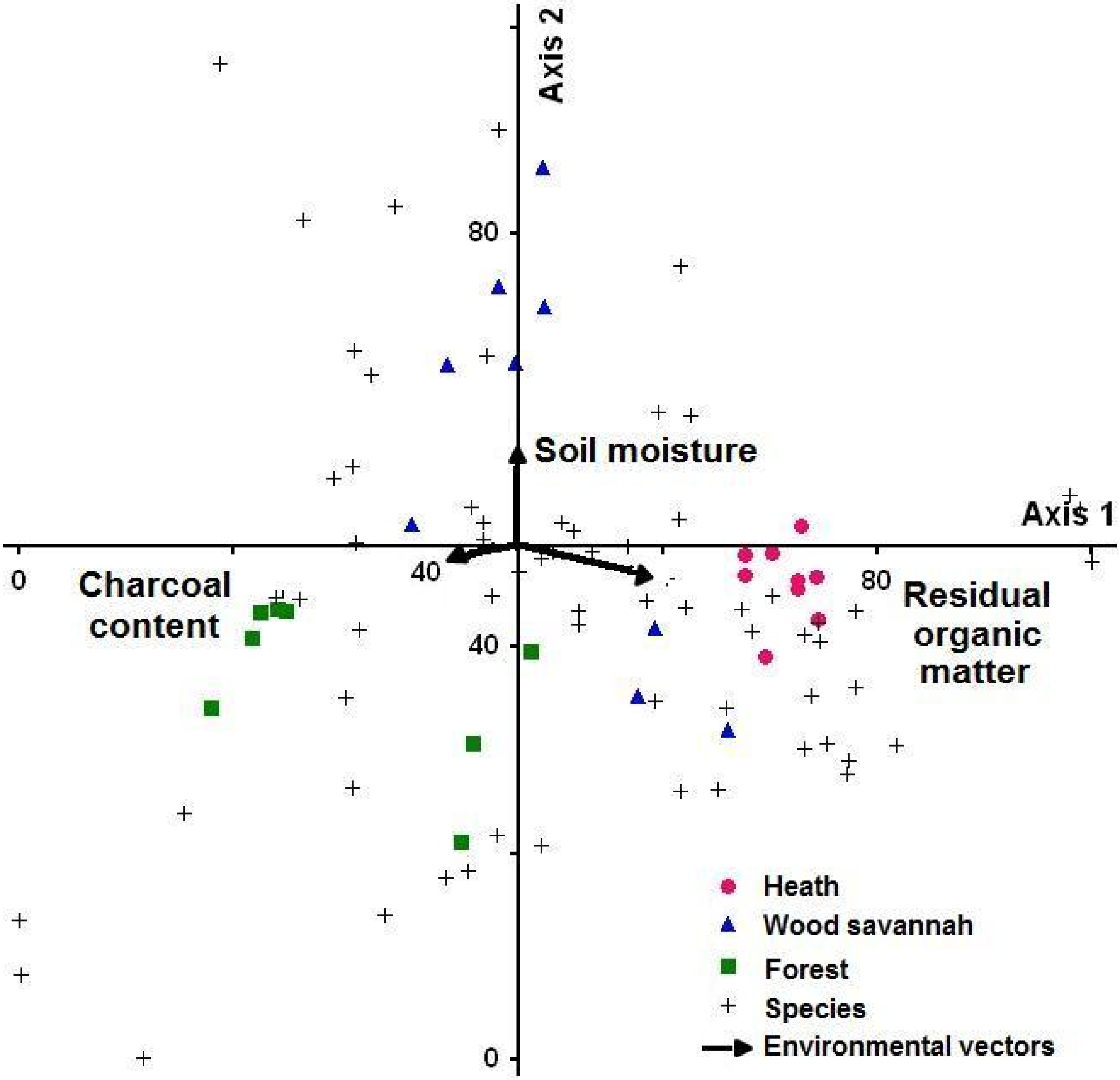

Figure 14. CCA vector bi-plot of residual organic matter, charcoal content and soil moisture effect on species (+) and sample locations among heath (●), wood savannah (▲) and forest (■) communities.

3.4.2 Trait response to ROM depth

Significant differences in total trait response (abundance, richness and diversity) described in 3.2.2 were not a function of ROM among communities (Appendix 3b), yet ROM strongly predicted all of the significant principal components (11) summarized by PCA (Appendix 4a) and two out of three performance traits in comparisons between the heath and forest (Appendix 5a). However, ROM was not a significant predictor for any of the significant principal components (9) (Appendix 4b) nor any of the performance traits in comparisons between the wood savannah and forest (Appendix 5b).

Among the traits most strongly predicted by ROM (Figure 15a-h), the following differences are significant as ROM increases above 2 cm depth: black spruce biomass declines (adj. $R^2 = 83.0\%$, $p<0.001$), standing dead biomass increases (adj. $R^2 = 83.0\%$, $p<0.001$), species architecture changes from single to multi-stem (adj. $R^2 = 80.6\%$, $p<0.001$), growth rate increases from slow to moderate (adj. $R^2 = 76.6\%$, $p<0.001$), fire tolerance increases from low to high (adj. $R^2 = 74.5\%$, $p<0.001$), regeneration strategy changes from seed to vegetative (adj. $R^2 = 74.1.0\%$, $p<0.001$), and species (adj. $R^2 = 77.1\%$, $p<0.001$) and Raunkiaer lifeform (adj. $R^2 = 75.7\%$, $p<0.001$) changes from tree, herb and pleurocarpous mosses to shrub, fruticose lichen and acrocarpous mosses. Thus, the results provide strong evidence that the differences in species composition and functional traits between the heath and forest are a function of fire severity decline, which is filtering the dominant species mode of regeneration and performance through high ROM.

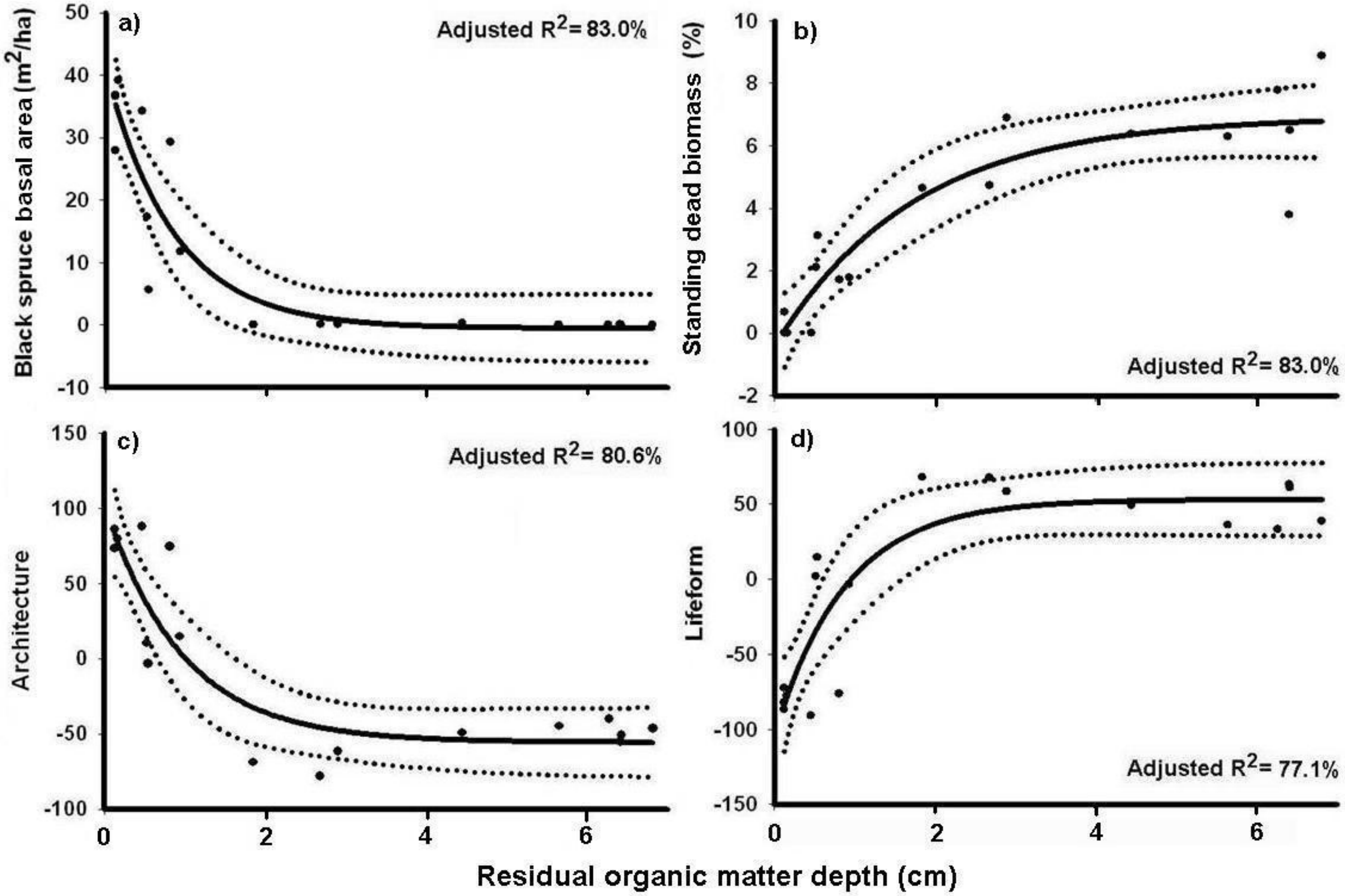

Figure 15. Exponential response of (a) black spruce basal area (N=18, $F_{2,15}$=39.78, p<0.001), (b) standing dead biomass (N=18, $F_{2,15}$=42.42, p<0.001), (c) architecture (N=18, $F_{2,15}$=36.31, p<0.001), and (d) lifeform (N=18, $F_{2,15}$=29.59, p<0.001) to ROM increase between forest and heath communities. Dotted lines represent upper and lower 95% confidence intervals.

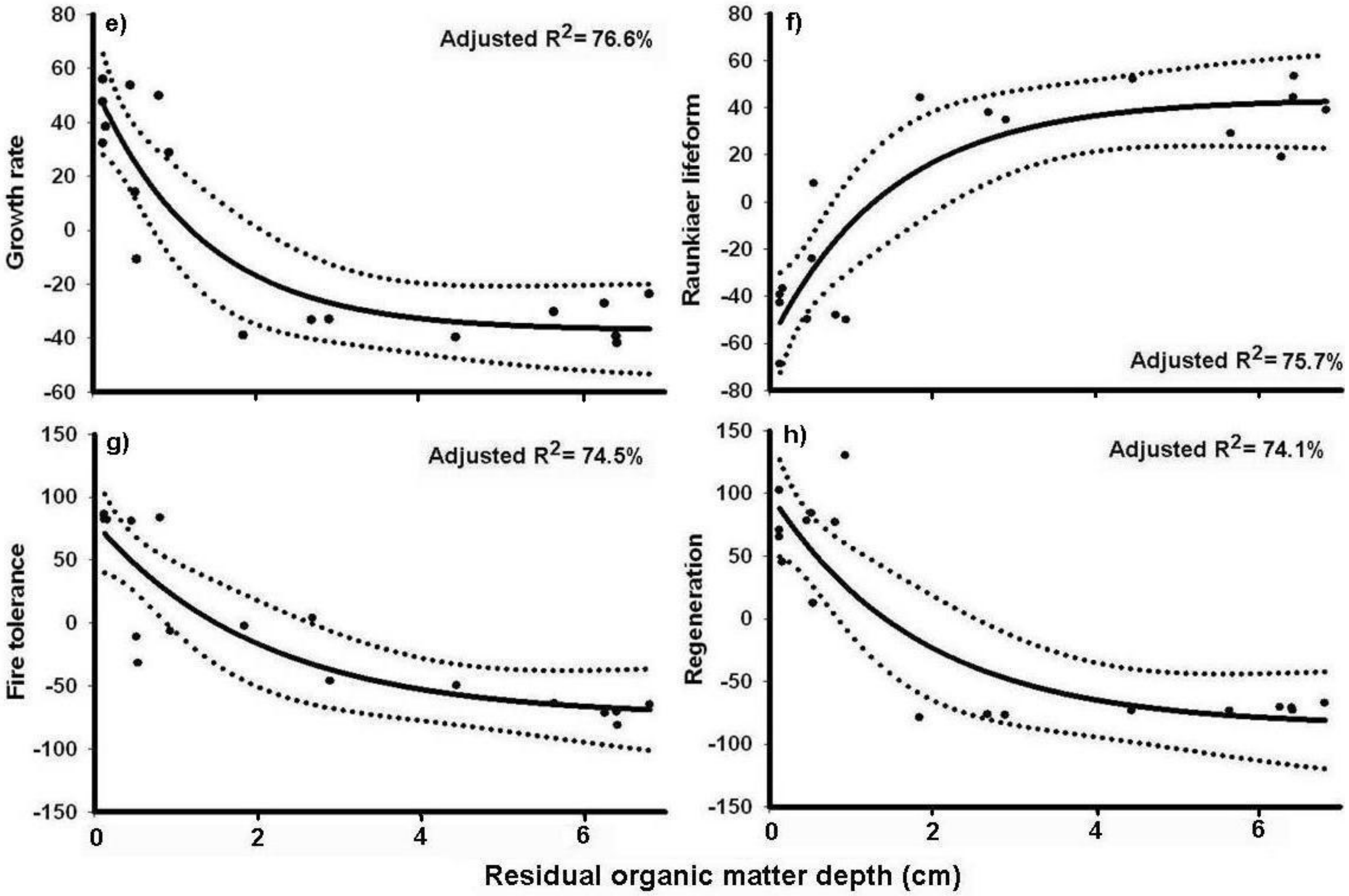

Figure 15 continued. Exponential response of (e) growth rate (N=18, $F_{2,\,15}$=28.92, p<0.001), (f) Raunkiaer lifeform (N=18, $F_{2,\,15}$=27.54, p=0.001), (g) fire tolerance (N=18, $F_{2,\,15}$=25.79, p<0.001) and (h) regeneration (N=18, $F_{2,\,15}$=25.32, p<0.001) to ROM increase between forest and heath communities. Dotted lines represent upper and lower 95% confidence intervals.

3.5 Seed availability and seedbed condition

Kalmia produced 488.8 ± 96.3 (std. error) fruits/m^2 and each fruit contained 32.2 ± 3.4 seeds/fruit. Seed production was therefore equivalent to 15, 730 seeds/m^2 and approximately 1.6 × 10^8 seeds/ha. Although black spruce seed traps did not capture any seed, Power (2005) predicted that three years after fire black spruce dispersed 16,539 seeds/ha in this site, which is sufficient for restocking black spruce at pre-fire density. Therefore, seed availability does not seem to be a limiting factor on post-fire recovery of black spruce or *Kalmia*.

As described in section 2.2.4, there was 0% germination of black spruce and *Kalmia* in both high and low severity microsites in the field. However, in the laboratory 42% and 25% of all black spruce seeds germinated on high and low severity substrates respectively, yet the differences among substrate types were not significant (t=-1.45, p=0.165).

4. Discussion

The concept that fire severity influences post-fire succession through its effects on forest floor properties is not new, however this study has advanced the understanding of post-fire community assembly by showing that i) the relative importance of abiotic and biotic filtering in post-fire community assembly depends in part on ROM, ii) when ROM is shallow (< 2 cm), abiotic filtering enables the establishment of black spruce and other seed regenerating species, favoring black spruce forests, iii) when abiotic filtering is the predominant habitat constraint, it controls species composition and functional traits directly by filtering species mode of regeneration, and indirectly through its effects on the dominant species‟ performance, and iv) priority effects play an important part in determining the relative importance of abiotic vs. biotic filtering when ROM depth is around a threshold value (~2 cm). Therefore, in eastern Newfoundland, *Kalmia* heath and to a lesser extent the *Kalmia*-lichen wood savannah seem to represent divergent communities of black spruce-*Kalmia* forest as a result of differences in species‟ responses to the depth and distribution of ROM.

4.1 Community assembly of *Kalmia* heath

The dominant characteristics of species assemblages are considered to be a combination of abiotic and biotic constraints on species colonization and establishment. But the results of this research and related studies show that the relative role of abiotic constraints on community assembly is strongly linked to disturbance severity, supporting our primary hypothesis (Schimmel and Granstrom, 1996; Bloom, 2001; Charron and Greene, 2002; Rydgren et al., 2004; Bonnet et al., 2005; Johnstone and Kasischke, 2005; Johnstone and Chapin, 2006).

In black spruce-*Kalmia* plant communities, recovery of spruce and other seed regenerating species depends on low (<2cm) ROM created by high severity fire. In its absence, high (>2cm) ROM no longer favours seed regeneration of conifers, causing shifts in species composition and functional traits that can lead to *Kalmia* heath formation. Johnstone and Chapin (2006) reported similar findings that there is a dramatic decline in conifer regeneration on post-fire soils >2.5 cm due to seedling establishment constraints. But why does high ROM select against seed regeneration? Both Duchesne and Sirois (1995) and Johnstone and Chapin (2006) attribute seed regeneration failure to seedling desiccation caused by diurnal heat fluctuations and rapid drying of incompletely burned substrates. These effects generally fall most strongly on small seeded species, whose seedlings are not as well provisioned with large carbohydrate stores in cotyledons, unlike those of large-seeded species (Fenner and Thompson, 2004). Therefore, the smaller the seed, the lower its threshold tolerance is to residual organic matter increase. High ROM can also inhibit black spruce recovery by increasing the "after-life" effects of partially decomposed humus containing secondary compounds that inhibit growth of understory vegetation (Wardle et al., 1997). Physiochemical filtering can maintain *Kalmia* and ericaceous dominance by locking up soil nutrients in the organic horizon, limiting resource availability to black spruce seedlings (Mallik, 2003; Bloom and Mallik, 2005).

While high ROM selects against seed regenerating species, shifts in species composition and functional traits are also due to positive selection of vegetatively regenerating species. In non-severe fires, vegetative buds on underground rhizomes and stem bases of *Kalmia* and other ericaceous plants remain protected under residual humus (Whittle et al., 1997). The protection afforded by unburned humus enables ericaceous plants to re-sprout quickly in the early post-fire habitat (Mallik, 1993; 1994). Early establishment is a critical component of *Kalmia* success because through species interactions (competition and allelopathy) it is able to suppress dominance of its neighbours. However, if its underground rhizomes are consumed by high severity fire, then the early establishment of later successional species is sufficient to check *Kalmia* growth, shifting its priority in the habitat from dominant to subordinate (Bloom and Mallik, 2004).

Although the results of this study area consistent with the direct filtering of species by mode of regeneration through ROM, filtering also indirectly affects species composition and functional traits, marked by shifts in lifeform, architecture and growth characteristics of species as ROM increases to 2cm (Figure 12). Indirect filtering is most likely to be a function of differences in black spruce and *Kalmia* architecture and performance, which determine available light at the forest floor. Lack of canopy species in the heath and dominance of *Kalmia* in a low biomass state (Figure 8) allows direct sunlight to penetrate the post-fire substrate. High light exposure creates ideal habitat conditions for many shade intolerant fruticose lichens (*Cladonia* and *Cladina* spp.) and acrocarpous mosses (*Dicranum* spp.) (Foster, 1985; Bonan and Shugart, 1989), resulting in higher species richness in the heath (Figure 13). Under black spruce canopy, shade tolerant epiphytic and fruticose lichens (*Parmelia sulcata, Bryoria* spp., *Hypogymnia physodes* and *Cladonia coniocrea*) as well as pleurocarpous mosses (*Hylocomium splendens, Pleurozium schreberi,* and *Ptilium crista-castrensis*) thrive in the shade at the forest floor.

Fruticose lichen beds also approximate the substrate condition of burned duff because their surfaces are highly susceptible to extreme moisture fluctuations and are water repellent (Foster, 1985). Seeds often have difficulty penetrating through the lichen thalli to reach moist soil, contributing to the abiotic constraints on seedling establishment (Cornellissen et al., 2007).

Thus, the negative filtering effects of high ROM on seed regenerating species is compounded by the habitat characteristics and species associations of the early dominant species, increasing the potential for community divergence from forest to heath.

4.2 Community assembly of *Kalmia*-lichen wood savannah

The primary hypothesis predicts that species composition and functional traits in *Kalmia*-lichen wood savannah are a function of variability in abiotic filtering by ROM. Thus, patchiness in ROM distribution should be associated with a mosaic of black spruce and *Kalmia*-dominated patches. This holds true in the wood savannah, but black spruce islands occur only where substrate conditions indicate the highest severity of burning (<1 cm ROM). But if the community was black spruce-*Kalmia* forest prior to disturbance, then what are the mechanisms responsible for patchiness in ROM depth and distribution? Greene et al. (2007) suggests that patchiness in ROM can occur through smoldering combustion around the base of mature trees, even when pre-fire species composition and organic matter distribution is uniform. Greene et al. (2007) attribute patchiness in ROM to higher heat absorption around tree boles, resulting in higher localized combustion and thus fire severity.

Community composition and functional traits did not correspond with ROM depth outside the black spruce islands, providing evidence to support the alternative hypothesis. In this case, species interactions between black spruce and *Kalmia* rather than post-fire ROM depth seem to be the predominant constraint on black spruce establishment. Moreover, ROM depth outside black spruce islands was statistically similar to ROM in the heath and forest. Based on our predictions of community assembly under abiotic habitat constraints, substrate conditions in ROM should have been suitable to support establishment of seed regenerating species. It is probable that filtering effects of ROM fluctuating around 2cm were sufficient to protect *Kalmia* and other rhizomatous species concentrated at the interface of the organic-mineral soil horizon (Whittle et al., 1997). These species would have competitive advantage over dispersed banked seeds. Even if the rhizomes of ericaceous species were completely consumed by fire, if black spruce did not disperse within the first four years, *Kalmia* could quickly become dominant by vegetatively spreading into the low ROM substrate areas (Mallik et al., 2008) or to a much lesser extent by seed (Mallik, 2003). Thus, hysteresis in the threshold of ROM and priority effects seems to play an important role in determining the relative importance of abiotic vs. biotic filtering on community assembly of the wood savannah.

4.3 Limitations and future direction

The study highlights some important limitations to using ROM as a proxy for fire severity, and determining pre-fire origin of plant communities using FRI and survey data. There is very little if any literature describing the temporal changes in charcoal position in the organic horizon through time. Deluca and Aplet (2008) recently reviewed the literature on charcoal formation and deposition after wildfire and described that freeze-thaw action causes mixing of charcoal in the organic layer into the upper mineral soil horizon. Thus, it is possible that charcoal movement could have confounded estimates of ROM in this study.

FRI data and surveying adjacent unburned stands did provide sufficient evidence to suggest that plant communities were similar black spruce-*Kalmia* forests prior to fire, however these estimates can only date back to the most recent fire event (≈100 yrs). Therefore, connecting the legacy effects of variation in fire severity to current conditions by viewing them as abiotic and biotic filters of species and functional traits depends, in part, on untested assumptions. Much could be learned by reconstructing vegetation dynamics and fire history using paleoecological methods, such as dating plant macrofossils, charcoal, soil, and pollen in co-occurring heath, wood savannah and forest communities. Also, paleoecological methods would allow us to determine if *Kalmia* dominance is truly a recent phenomenon, and would shed light on the persistence of *Kalmia* as a dominant species and the stability of *Kalmia* heath over time.

What remains to be determined in the context of conifer-ericaceous plant communities is just how long ericaceous species persist as the dominant cover. In *Kalmia* heath, Bloom (2001) determined that *Kalmia* can remain dominant up to 40 yrs after non-severe fire. This apparent persistence, coupled with the fact that variability in fire severity mediates successional divergence, suggests that *Kalmia* heath and *Kalmia*-lichen wood savannah may represent alternate persistent states (APS) (Damman, 1971; Noy-Meir, 1975; May, 1977; Augustine et al., 1998; Latham, 2003; Jasinski and Payette, 2005). APS predicts that succession can lead to divergent communities in situations where colonizing species (ie. seed vs. vegetatively regenerating) respond differently to differences in habitat starting conditions (ie. high vs. low ROM) (Holling, 1973; Sutherland, 1974; 1990; Noy-Meir, 1975; May, 1977; Connell and Sousa, 1983; Sousa and Connell, 1985; Knowlton, 1992; Petraitis and Latham, 1999; Scheffer and Carpenter, 2003; Groffman et al., 2006). Community persistence is then enabled by the positive feedbacks involving the dominant species, which alter the physical and chemical nature of the post-disturbance environment (Petraitis and Latham, 1999; Latham, 2003). On the other hand, at least some *Kalmia*-dominated communities may simply be in a state of arrested succession, whereby *Kalmia* remains dominant for a period of time due to strong neighbourhood effects, until a critical shift in *Kalmia* growth and soil feedbacks gives way to black spruce establishment (Inderjit and Mallik, 1999; Bloom and Mallik, 2006; Mallik et al., 2008).

Understanding the persistence of *Kalmia* after non-severe fire is critical to predicting the long-term implications of its dominance, and will shed further light on whether fire severity difference creates divergent plant communities in black spruce-*Kalmia* forests of eastern Canada.

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Appendix 1. Mean abundance of all species among heath, wood savannah and forest communities.

		Heath			Wood savannah			Forest		
	Species	Charlotte-town	Terra Nova	Thorburn	Gambo South	Spracklin Road	Ochre Hill	Gambo North	Arnold's Pond	Southwest Arm
Tree	*Abies balsamea*	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.02
	Betula papyrifera	0.00	0.00	0.08	0.08	0.00	0.00	0.00	0.83	0.00
	Larix laricinia	0.00	0.00	0.00	0.00	0.00	1.21	0.00	0.00	0.00
	Picea mariana	0.04	0.06	0.91	34.32	38.84	42.72	59.36	72.82	63.61
	Populus tremuloides	0.00	0.00	0.00	0.02	0.00	0.00	2.07	0.00	0.00
Shrub	*Acer rubrum*	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.02	0.00
	Alnus viridis var. crispa	0.00	0.00	0.64	9.87	0.00	0.00	19.43	0.00	0.00
	Amelanchier spp.	1.41	0.14	0.87	0.00	0.84	2.22	0.00	0.07	0.04
	Chameadaphne calyculata	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Gaultheria hispidula	0.01	0.00	0.00	0.12	0.00	0.06	0.00	1.24	8.43
	Kalmia angustifolia	28.08	39.14	60.94	45.27	48.87	60.93	41.97	17.31	10.82
	Nemopanthus mucronata	1.138	0.86	0.85	0.00	0.06	3.73	1.61	1.22	0.52
	Rhododendron canadense	9.22	11.08	12.74	5.61	28.14	13.59	2.53	0.00	0.00
	Rhododendron groenlandicum	3.64	1.10	3.89	1.13	6.69	4.65	0.29	0.00	0.00
	Salix spp.	0.01	0.11	0.00	0.04	0.14	0.33	0.43	0.00	0.00
	Vaccinium angustifolium	10.59	18.77	11.03	6.86	16.15	9.24	7.06	0.55	1.22
	Vaccinium vitis-idaea	0.00	0.21	0.00	0.00	0.00	1.15	0.02	0.29	1.10
	Viburnum cassinoides	0.34	0.00	0.07	0.13	0.12	0.23	0.00	0.11	0.19
Herbs	*Clintonia borealis*	0.04	0.00	0.01	0.00	0.00	0.00	0.00	1.74	1.91
	Coptis trifolia	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Cornus canadensis	6.85	7.33	5.04	0.00	0.00	15.56	1.27	9.88	16.28
	Linnaea borealis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.52	0.29
	Maianthemum canadense	0.16	0.00	0.43	0.07	0.00	0.06	0.00	0.02	0.96
	Trientalis borealis	0.06	0.09	0.00	0.00	0.00	0.06	0.03	0.00	0.00
Fern	*Pteridium aquilinum*	0.19	0.38	0.00	0.00	0.00	2.13	0.00	0.00	0.46

Sedge	*Carex* spp.	0.20	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00
Mosses	Copperwire moss	0.00	0.00	0.00	0.12	0.00	0.00	0.00	0.00	0.00
	Dicranum acutifolium	0.06	3.48	2.03	1.66	2.04	0.00	0.00	0.00	0.00
	Dicranum fuscescens	0.11	0.00	0.00	0.00	1.03	0.16	0.84	0.00	0.00
	Dicranum polysetum	5.44	4.13	5.06	0.29	3.02	9.03	3.92	5.53	5.29
	Dicranum scoparium	0.03	0.00	0.29	0.01	0.00	0.61	0.00	6.51	0.96
	Dicranum undulatum	4.78	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Drepanocladus uncilialus	0.00	0.00	0.00	0.00	0.00	0.00	0.79	0.00	0.00
	Hylocomium splendens	0.13	0.00	0.27	0.00	0.00	2.02	0.04	9.50	14.67
	Oncophorus wahlenbergii	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Pleurozium schreberi	5.67	6.83	6.11	4.48	33.44	70.50	16.99	70.64	57.76
	Polytrichum juniperinum	5.10	4.14	3.24	4.03	0.02	0.00	6.97	0.00	0.00
	Polytrichum piliferum	0.00	0.11	0.04	0.01	0.02	0.00	0.00	0.00	0.00
	Ptilium crista-castrensis	0.01	0.00	0.13	0.07	0.01	1.08	0.19	17.28	44.43
	Rhytadelphus triquestris	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.00	0.00
	Sphagnum spp.	0.67	0.00	0.03	0.00	0.00	0.01	0.32	0.14	0.07
	Hypogymnia physodes	2.59	0.72	0.71	4.92	8.17	8.43	10.40	3.80	3.88
	Icmadophila ericetorum	0.19	0.04	0.17	0.22	0.00	0.00	0.00	0.00	0.83
	Leafy Liverwort	0.02	0.13	0.00	0.14	2.13	1.40	1.04	1.45	0.20
Lichens	*Bryoria spp.*	0.06	0.18	0.03	0.02	7.44	3.51	0.12	5.10	2.33
	Buellia punctata	0.65	0.51	0.03	0.17	1.13	0.01	0.00	0.09	0.01
	Ceratadon purpurea	2.84	0.20	0.61	0.66	0.00	0.00	0.66	0.00	0.00
	Cetraria spp.	0.27	0.37	0.19	3.02	2.94	0.63	1.12	0.04	0.43
	Cladina mitis	4.91	22.64	8.67	14.38	3.37	0.38	0.49	0.00	0.00
	Cladina rangiferina	8.48	39.91	11.24	28.61	13.62	5.86	3.73	0.23	0.04
	Cladina stellaris	0.73	10.00	0.93	4.00	54.47	31.31	0.14	0.00	0.00
	Cladonia cristatella/ borealis	1.01	1.93	8.34	0.81	0.21	0.05	0.42	0.01	0.00
	Cladonia cenotea	0.11	0.11	0.47	0.18	0.35	0.00	0.24	0.05	0.02
	Cladonia chlorophea	0.04	0.08	0.43	0.04	0.19	0.21	0.40	0.11	0.09
	Cladonia	0.01	0.02	0.16	0.04	0.22	0.16	0.67	0.43	0.22

coniocrea									
Cladonia cornuta	1.82	2.65	0.84	0.89	0.00	0.03	0.02	0.00	0.00
Cladonia crispata	6.99	9.47	7.07	4.86	0.01	0.01	0.34	0.00	0.03
Cladonia deformis	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.02
Cladonia fimbriata	0.00	0.00	0.01	0.11	0.00	0.00	0.00	0.00	0.12
Cladonia gracilis	2.47	0.82	1.07	0.72	0.25	0.00	0.42	0.00	0.00
C.gracilis var gracilis	0.09	0.11	0.08	0.14	0.37	0.14	0.28	0.00	0.02
Cladonia multiformis	0.00	0.01	0.04	0.00	0.00	0.00	0.02	0.00	0.00
Cladonia pyxidata	0.01	0.01	0.00	0.02	0.00	0.00	0.00	0.00	0.00
Cladonia sulphurina	1.15	3.14	1.20	1.52	0.04	0.12	0.37	0.00	0.00
Cladonia verticillata	0.01	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Cladonia spp.	0.00	0.00	0.00	0.40	0.09	0.00	0.00	0.00	0.03
Parmelia sulcata	0.04	0.14	0.03	0.03	2.49	8.64	0.06	6.54	6.13
Parmeliopsis ambigua	0.09	0.25	0.19	1.57	0.79	1.15	0.15	0.00	0.08
Peltigeria neopolydactyla	0.92	0.00	0.00	0.23	0.00	0.01	0.00	0.00	0.07
Stereocaulon tomentosa	0.00	0.03	0.00	0.53	0.06	0.03	0.04	0.00	0.00
Usnea spp.	0.04	0.04	0.00	0.02	4.19	10.25	0.01	5.85	2.77

Appendix 2. Mean abundance of all traits among heath, wood savannah and forest communities.

	Community	Heath			Wood savannah			Forest		
Category	Trait	Charlotte-town	Terra Nova	Thorburn	Gambo South	Spracklin Road	Ochre Hill	Gambo North	Arnold's Pond	Southwest Arm
MPP traits	**Lifeform**									
	Perennial tree	0.04	0.06	1.00	34.42	38.84	43.94	61.42	73.68	63.62
	Perennial shrub	54.76	71.41	91.04	69.03	101.01	96.12	73.35	20.78	22.32
	Perennial subshrub	6.99	7.33	5.04	0.00	0.00	15.56	1.27	11.40	16.58
	Perennial herb	0.26	0.09	0.44	0.07	0.00	0.12	0.03	1.76	2.87
	Perennial forb	0.19	0.38	0.00	0.00	0.00	2.13	0.00	0.00	0.46
	Perennial sedge	0.20	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00
	Bryophyte	24.91	19.20	17.83	11.45	41.71	84.82	31.89	111.05	123.38
	Lichen	32.67	93.16	41.90	67.46	100.41	70.92	19.44	22.25	17.11
	Raunkiaer lifeform									
	Mesophanero-phyte	0.04	0.06	1.00	34.42	38.84	43.94	61.42	73.68	63.62
	Microphanero-phyte	0.01	0.11	0.64	9.91	0.14	0.33	19.86	0.00	0.00
	Nanophanero-phyte	54.75	71.09	90.41	59.12	100.87	94.63	53.47	20.49	21.22
	Chamaephyte	0.00	0.21	0.00	0.00	0.00	1.15	0.02	1.81	1.39
	Protohemicrypto-phyte	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Hemicrypto-phyte	7.19	7.72	5.04	0.00	0.00	17.68	1.27	9.88	16.74
	Geophyte	0.26	0.09	0.44	0.07	0.00	0.12	0.03	1.76	2.87
	Epiphyte	3.74	2.20	1.18	9.76	27.17	32.62	11.86	21.42	15.63
	Successional status									
	Pioneer	5.43	4.74	3.65	4.16	0.18	4.48	7.44	10.35	15.12
	Obligate initial	30.92	39.34	61.56	45.93	48.87	60.93	42.63	17.31	10.82
	Early seral	1.61	0.36	0.87	0.03	0.84	4.57	0.02	0.36	1.14
	Seral-mid seral	23.40	25.77	24.91	10.17	62.43	105.07	23.06	99.64	120.89
	Facultative seral	15.99	41.41	20.77	31.18	19.52	9.69	26.98	2.08	2.48
	Late seral	5.08	1.96	5.18	1.31	6.74	8.50	1.91	2.47	9.91
	Climax-obligate climax	0.17	0.06	1.18	34.32	38.84	44.76	59.39	82.32	78.29
	Architechture									
	Single Stem	0.04	0.06	1.00	34.42	38.84	43.94	61.42	73.68	63.62
	Multi-Stem	26.34	32.06	29.46	13.77	52.14	33.98	11.93	1.94	1.97
	Thicket	0.00	0.00	0.64	9.87	0.00	0.00	19.43	0.00	0.00
	Rhizomateous	35.85	47.16	66.43	45.34	48.87	79.88	43.29	29.24	31.53
	Stoloniferous	0.01	0.00	0.00	0.12	0.00	0.06	0.00	1.24	8.43
	Creeping	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.52	0.29
	Bunch	0.20	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00

	Parasitic	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Pleurocarpus	5.81	6.83	6.51	4.54	33.44	73.61	17.34	97.42	116.86
	Acrocarpus	19.08	12.24	11.32	6.77	6.14	9.81	13.50	12.18	6.32
	Fruticose	28.19	91.48	40.78	59.79	87.76	52.65	8.79	11.83	6.10
	Foliose	3.64	1.13	0.93	7.28	11.51	18.25	10.66	10.33	10.16
	Crustose	12.43	29.07	48.95	61.57	53.69	51.79	65.34	43.96	21.23
	Reproductive									
	Primarily seed	1.80	0.53	2.58	44.46	39.94	47.87	81.30	74.14	64.96
	Primarily vegetative	59.28	77.80	94.09	59.09	99.86	106.21	53.13	30.51	38.47
	Persistent seed	10.84	8.64	9.09	1.46	6.81	22.84	1.59	12.38	26.00
	SeedBank	10.83	8.64	9.09	1.34	6.81	21.58	1.59	11.14	17.57
	Low seed abundance	27.36	37.18	29.25	12.69	44.29	38.50	10.87	11.69	26.89
	Medium seed abundance	4.06	1.16	4.89	35.58	45.65	47.61	59.65	74.68	65.72
	High seed abundance	29.48	39.28	62.54	55.24	49.71	64.35	63.46	19.75	11.16
	Resprout ability	59.70	78.19	95.81	103.55	138.96	151.86	134.43	106.34	105.29
	Wind dispersed	7.27	1.86	6.14	46.27	45.67	51.11	82.24	74.92	72.51
	Water dispersed	0.00	0.00	0.64	9.87	0.00	0.00	19.43	0.00	0.00
	Animal dispersed	19.34	26.46	17.44	7.06	17.11	28.45	8.36	12.44	20.09
	Serotinous	0.04	0.06	0.91	34.32	38.84	42.72	59.36	72.82	63.61
	Mycorrhizal status									
	Ecto-	0.04	0.06	1.63	44.29	38.84	43.94	80.85	73.66	63.62
	Endo-l	0.59	0.47	1.08	9.96	0.00	2.26	21.52	3.28	3.64
	Arbutoid	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Ericoid	42.65	59.22	75.87	53.38	71.71	76.02	49.34	19.38	21.57
	Lacking	0.20	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00
Performance	**Growth rate**									
	Slow	10.69	8.49	10.28	35.52	45.53	63.00	60.92	82.72	80.87
	Moderate	21.99	30.70	25.29	22.42	45.27	28.66	29.48	2.65	4.73
	Rapid	28.08	39.14	61.03	45.37	48.87	62.13	44.03	18.16	10.82
	C:N ratio									
	High	38.77	50.53	76.12	95.23	116.83	121.06	123.71	91.46	82.92
	Medium	11.50	18.77	11.19	7.12	16.27	9.47	9.13	3.24	3.32
	Low C:N	6.85	7.54	5.04	0.00	0.00	16.71	1.29	10.17	17.38
	Drought tolerance									
	Intolerant	0.21	0.11	0.64	9.94	0.14	0.33	19.86	0.00	0.00
	Low	17.71	19.48	18.92	5.61	28.20	36.05	5.48	22.63	34.48
	Medium	44.41	59.54	77.24	53.57	72.67	79.51	49.32	19.29	22.12
	Fertility requirement									
	Low	43.08	51.85	78.45	52.04	84.54	84.72	44.79	17.37	11.32

	Moderate	19.17	27.35	19.08	51.51	55.31	73.08	91.25	88.73	94.23
	High	0.13	0.00	0.27	0.00	0.00	2.02	0.04	9.50	14.67
	Fire tolerance									
	Low-none	57.11	112.41	61.05	113.30	180.95	199.72	110.36	207.54	205.30
	Moderate	26.24	31.30	29.37	23.68	51.95	31.09	29.66	3.73	4.54
	High	35.34	46.97	65.98	45.48	49.01	79.00	45.74	28.43	35.99
	Shade tolerance									
	Tolerant	18.16	18.94	19.37	5.71	28.98	35.59	3.84	19.48	32.43
	Moderate	35.27	40.50	67.07	91.38	94.52	108.52	121.71	90.24	74.62
	Low-intolerant	11.77	19.95	11.97	7.00	16.34	15.66	11.19	4.63	4.75
Effect trait	**Known allelopath**									
	Yes	41.14	51.70	77.58	52.01	83.71	81.29	44.79	17.31	11.28
Attribute	**Root concentration**									
	Mineral	1.98	0.59	2.49	44.29	39.68	47.06	80.85	73.72	64.11
	Organic	60.72	78.33	96.59	103.42	139.79	154.07	132.36	105.55	105.33

Sources of soft trait data:

1. USDA Plants Database http://plants.usda.gov/index.html
2. Fire Effects Database http://www.fs.fed.us/database/feis/
3. http://www.evergreen.ca/nativeplants/search/view-plant.php?ID=00826
4. Malloch, D. and Malloch, B. 1981. The mycorrhizal status of boreal plants: species from northeastern Ontario. Canadian Journal of Botany. 59: 2167-2172.
5. Malloch, D. and Malloch, B. 1982. The mycorrhizal status of boreal plants: additional species from northeastern Ontario. Canadian Journal of Botany. 60: 1035-1040
6. Brodo, M.I., Sharnoff, S.D., Sharnoff, S. 2001. Lichens of North America. Yale University Press, New Haven.

Appendix 3a. Exponential regression diagnostics for species response to residual organic matter depth for heath vs. forest and wood savannah vs. forest plant communities.

			Model Summary						Parameter estimates		
Comparison	Response	Model	Adj. R^2 %	*F*	df1	df2*	Prob. Constant	Prob. ROM	B_0	B_1	B_2
Heath vs. forest	Abundance	Decay	66.8	18.10	2	15	0.980	<0.001	-13.75	248.29	0.08
	Richness	Rise to max	80.6	36.45	2	15	<0.001	<0.001	26.87	16.27	0.50
	Diversity	Rise to max	26.8	4.12	2	15	<0.001	0.037	4.83	3.33	0.62
Wood savannah vs. forest	Diversity	Rise to max	0.0	<-0.001	2	15	<0.001	1.00	7.07	-0.57	873.74

*Degrees of freedom (df) are corrected for the mean of observations (N=18).

Appendix 3b. Exponential regression diagnostics for trait response to residual organic matter depth for heath vs. forest and wood savannah vs. forest plant communities.

			Model Summary						Parameter estimates		
Comparison	Response	Model	Adj. R^2 %	*F*	df1	df2*	Prob. Constant	Prob. ROM	B_0	B_1	B_2
Heath vs. forest	Abundance	Decay	59.2	13.31	2	15	0.198	<0.001	1112.07	1387.18	0.23
Wood savannah vs. forest	Diversity	Rise to max	0.0	<-0.001	2	15	<0.001	1.00	34.83	-1.72	337.03

*Degrees of freedom (df) are corrected for the mean of observations (N=18).

Appendix 4a. Summary statistics of PCA on 14 categories of soft traits between heath and forest plant communities. Principal components were only significant along axis 1 for each trait category, and when $p < 0.05$.

Trait category	Eigenvalue	% Variance Explained	*P*-value
Lifeform	66541.77	77.87	0.001
Architecture	66551.68	68.23	0.001
Raunkiaer lifeform	32281.20	85.78	0.001
Mycorrhizal Symbiont	32161.85	86.22	0.002
Root concentration	33463.13	90.42	0.002
Successional status	56500.97	83.33	0.001
Regeneration	106460.64	82.57	0.001
Shade tolerance	16995.71	88.34	0.131
Fire tolerance	72545.69	94.78	0.001
Fertility requirements	31804.86	88.05	0.004
Drought tolerance	9448.10	73.60	0.410
Growth rate	25205.45	84.82	0.002
C:N ratio	15148.58	92.76	0.104
Allelopathic	10337.07	99.91	0.003

Appendix 4b. Summary statistics of principal component analysis on 14 categories of soft traits between wood savannah and forest plant communities. Principal components were only significant along axis 1 for each trait category, and when $p < 0.05$.

Trait category	Eigenvalue (axis 1)	% Variance explained	*P*-value
Lifeform	57882.83	72.85	0.001
Architecture	49890.23	62.35	0.002
Raunkiaer lifeform	23040.00	77.68	0.001
Mycorrhizal Symbiont	15666.62	79.84	0.001
Root concentration	8852.23	55.12	0.803
Successional status	42379.05	77.92	0.002
Regeneration	40779.57	59.67	0.001
Shade tolerance	6395.80	64.22	0.200
Fire tolerance	35119.59	76.48	0.518
Fertility requirements	21136.47	82.78	0.003
Drought tolerance	10920.81	66.33	0.908
Growth rate	13597.81	75.28	0.001
C:N ratio	6668.90	78.56	0.265
Allelopathic	15404.39	99.99	0.001

Appendix 5a. Exponential regression diagnostics for trait composition (PC +performance) response to residual organic matter depth between heath and forest plant communities.

Response	Model	Model Summary Adj. R^2 %	F	df1	df2	Prob. Constant	Prob. ROM	Parameter estimates B_0	B_1	B_2
Lifeform	Decay	77.1	29.59	2	15	<0.001	<0.001	53.26	-157.32	1.13
Architecture	Rise to max	80.6	36.31	2	15	<0.001	<0.001	102.17	-158.01	1.03
Raunkiaer lifeform	Decay	75.7	27.54	2	15	0.001	<0.001	43.60	-103.11	0.68
Mycorrhizal symbiont	Decay	67.2	18.41	2	15	0.012	<0.001	46.34	-98.29	0.51
Root concentration	Decay	63.4	15.69	2	15	0.048	<0.001	52.01	-100.54	0.41
Successional status	Decay	72.4	23.31	2	15	0.001	<0.001	49.70	-138.40	0.99
Regeneration	Rise to max	74.1	25.32	2	15	<0.001	<0.001	100.29	-185.72	0.55
Fire tolerance	Rise to max	74.5	25.79	2	15	<0.001	<0.001	80.41	-154.68	0.49
Fertility requirements	Decay	73.3	24.34	2	15	0.010	<0.001	51.17	-102.73	0.44
Growth rate	Rise to max	76.6	28.92	2	15	<0.001	<0.001	54.93	-92.09	0.75
Allelopathic	Rise to max	44.1	7.72	2	15	0.028	0.005	-30.79	48.32	0.97
Black spruce basal area (m^2/ha)	Decay	83.0	39.78	2	15	<0.001	<0.001	40.97	-41.46	1.18
Kalmia biomass (m^2/ha)	Decay	1.6	1.14	2	15	0.946	0.345	-6.81	20.75	0.13
Standing dead biomass (%)	Decay	83.0	42.42	2	15	<0.001	<0.001	6.92	-7.34	0.57

*Degrees of freedom (df) are corrected for the mean of observations (N=18)
PC=principal component

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Appendix 5b. Exponential regression diagnostics for trait composition (PC + performance) response to residual organic matter depth between wood savannah and forest plant communities.

		Model Summary						Parameter estimates		
Response	Model	Adj. R^2 %	*F*	df1	df2*	Prob. Constant	Prob. ROM	B_0	B_1	B_2
Lifeform	Decay	14.2	2.41	2	15	0.236	0.124	34.22	-99.78	2.21
Architecture	Decay	14.2	2.40	2	15	0.234	0.124	-32.17	92.12	2.15
Raunkiaer lifeform	Decay	4.4	1.39	2	15	0.474	0.279	10.15	-76.05	6.48
Mycorrhizal symbiont	Decay	0.0	0.619	2	15	0.631	0.551	5.82	-44.28	6.57
Successional status	Rise to max	13.9	2.38	2	15	0.203	0.126	-42.71	80.89	1.27
Regeneration	Decay	5.2	1.47	2	15	0.420	0.262	-12.20	175.23	10.85
Fertility requirements	Decay	2.1	1.18	2	15	0.505	0.333	9.77	-60.09	5.36
Growth rate	Rise to max	20.9	3.25	2	15	0.167	0.067	-41.99	57.47	3.06
Allelopathic	Rise to max	0.0	<0.001	2	15	<0.001	1.0	29.23	-29.23	2923091.67
Black spruce basal area (m^2/ha)	Decay	0.0	0.276	2	15	0.281	0.762	25.23	22.97	1.45
Kalmia biomass (m^2/ha)	Decay	16.7	2.71	2	15	0.946	0.099	-31.86	52.56	9.07
Standing dead biomass (%)	Rise to max	26.1	3.99	2	15	0.958	0.041	0.09	5.60	1.61

*Degrees of freedom (df) are corrected for the mean of observations (N=18)

PC=principal component