

Article

# Burn Severity Dominates Understory Plant Community Response to Fire in Xeric Jack Pine Forests

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**Abstract:** Fire is the most common disturbance in northern boreal forests, and large fires are often associated with highly variable burn severities across the burnt area. We studied the understory plant community response to a range of burn severities and pre-fire stand age four growing seasons after the 2011 Richardson Fire in xeric jack pine forests of northern Alberta, Canada. Burn severity had the greatest impact on post-fire plant communities, while pre-fire stand age did not have a significant impact. Total plant species richness and cover decreased with disturbance severity, such that the greatest richness was in low severity burns (average 28 species per 1-m<sup>2</sup> quadrat) and plant cover was lowest in the high severity burns (average 16%). However, the response of individual plant groups differed. Lichens and bryophytes were most common in low severity burns and were effectively eliminated from the regenerating plant community at higher burn severities. In contrast, graminoid cover and richness were positively related to burn severity, while forbs did not respond significantly to burn severity, but were impacted by changes in soil chemistry with increased cover at pH >4.9. Our results indicate the importance of non-vascular plants to the overall plant community in this harsh environment and that the plant community is environmentally limited rather than recruitment or competition limited, as is often the case in more mesic forest types. If fire frequency and severity increase as predicted, we may see a shift in plant communities from stress-tolerant species, such as lichens and ericaceous shrubs, to more colonizing species, such as certain graminoids.

**Keywords:** *Pinus banksiana*; burn severity; composite burn index; revegetation; forest regeneration; lichen

## 1. Introduction

Large fires are expected to become more common in northern boreal forests in the future with a changing climate [1], and these fire events are often characterized by highly variable burn severity [2–4]. Many studies have examined tree regeneration after variable severity burns in the boreal forest [5,6], but in terms of overall plant diversity, understory species are most important, especially in the tree species-poor, xeric jack pine (*Pinus banksiana*) forests of the northern boreal [7]. Understory plant communities also play critical roles in maintaining key ecosystem processes, such as nutrient cycling, habitat for wildlife and overstory succession [8,9].

The regeneration mechanism of understory plants differs from that of the jack pine canopy trees, *i.e.*, an aerial seedbank of serotinous cones that releases seeds immediately after burning [10,11]. In contrast, after fire in the northern boreal forest, understory plants may resprout from roots or rhizomes [7,12,13], germinate from seeds in the soil seed bank [14,15], germinate from seeds carried in from off-site [16] or encroach from surrounding areas [17]. The relative importance of these different regeneration mechanisms differs by species and will likely be impacted by disturbance severity, stand

age and soil properties. Previous work on jack pine regeneration after the same fire as this current study showed that stand age and burn severity were the main drivers of tree regeneration [2], but it is not clear if these same drivers are controlling understory plant community re-establishment.

The regeneration of understory plants may be impacted by high burn severities by altering seed bed availability, with most species requiring exposed mineral soil to germinate. High burn severities can also change the composition of surviving vegetation from which resprouting is possible by reducing or eliminating stored seedbanks in the organic material where most seeds are found and by eliminating competition [18]. Stand age has a clear impact on species composition related to the successional stage of forest development with more shade-tolerant species being found in older forests and species that are more adapted to the specific soil and site conditions rather than to disturbance [19]. This influences the species present on site and capable of vegetative reproduction, but may not influence regeneration from seed. Soil properties may also impact understory plant regeneration after disturbance to a greater degree than tree regeneration, as understory plant species are more sensitive to changes in soil chemical and physical properties than are tree species growing on the same sites. However, how these factors interact with each other and with environmental conditions to influence plant community establishment in boreal jack pine forests in the years following fire is not clear.

Most studies on forest understory plant community response to disturbance focus on vascular plants [20–22], which are the dominant plant groups in most mesic boreal forests and are more responsive to disturbance than non-vascular species [8]. However, in harsh environments within the boreal forest, such as the xeric jack pine-dominated forests that are the focus of this study, non-vascular lichens and bryophytes are a more significant component [7]. This also holds true for other harsh environments, such as bogs at the other end of the moisture gradient within the boreal forest, where the understory community is also dominated by non-vascular plant species, such as *Sphagnum* mosses. Less is known about the regeneration ecology of these non-vascular species when compared to herbaceous and shrub vegetation, and the response of the non-vascular community to varying levels of disturbance severity is not well understood [23,24].

We studied understory plant communities in response to a range of natural burn severities and pre-fire stand ages in the xeric jack pine boreal forest of north-eastern Alberta, Canada. This forest area is not currently being developed for timber, but will likely be impacted, at least in part, in the future by expanding oil sands developments. Therefore, it is important to gain a better understanding of how the plant communities in this area respond to varying levels of disturbance severity and identify any potential risks to ecosystem sustainability in a post-disturbance landscape. The specific questions we asked are: (1) How do burn severity and pre-fire stand age impact understory plant community development post-fire in these xeric, pure jack pine boreal forests? (2) Do all plant groups respond in a similar manner to these drivers?

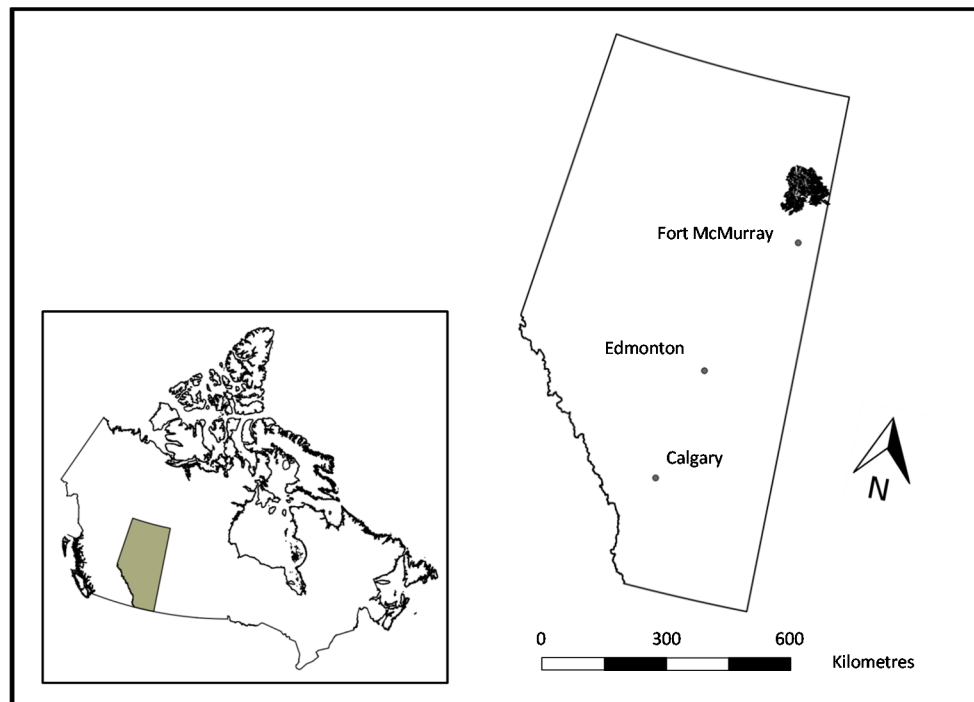
## 2. Methods

### 2.1. Study Area and Fire Description

We examined plant community development four growing seasons after the Richardson Fire, a 576,000-ha fire in north-eastern Alberta, Canada (Figure 1). This fire resulted from human ignition, burned from May until August 2011 and was the second largest documented fire in western Canadian history. During periods of extreme fire weather, there were spread rates of over 30 km per day with modelled head fire intensities in excess of  $10,000 \text{ kW} \cdot \text{m}^{-1}$ .

The dominant forest type in the region is jack pine growing on sandy dystric Brunisol soils on aeolian parent material with common understory vegetation consisting of *Arctostaphylos uva-ursi*, *Vaccinium myrtilloides* and *Cladonia arbusculata* subsp. *mitis*. The local site type is referred to as the xeric “a” eco-site in the Canadian Shield and Boreal Mixedwood Ecological Areas [25]. The southern and western portions of the Richardson Burn also contain stands of more mesic trembling aspen

(*Populus tremuloides*) and white spruce (*Picea glauca*) forest types, but this work focused on the jack pine-dominated portion of the burn, which accounts for 65% of the total burned area. The climate in the area is continental with long, cold winters (average January temperature  $-19^{\circ}\text{C}$ ) and short, cool summers (average July temperature  $17^{\circ}\text{C}$ ) (based on Fort McMurray climate normal from Environment Canada). Median annual precipitation is 455 mm, which is less than the average annual potential evaporation of 480 mm [26]. The xeric site type and moisture-limiting climate indicate that these forests are very challenging environments for many types of plants to grow, and this is supported by the low basal area (average  $16.3\text{ m}^2\cdot\text{ha}^{-1}$ ) and short canopy height (average 11.8 m) for mature jack pine stands [2].



**Figure 1.** Location of the 2011 Richardson Fire in northeastern Alberta, Canada.

## 2.2. Field Sampling

The sampling design was based on a previous project [2], which examined jack pine regeneration after the Richardson Burn in stands of different pre-fire age and burn severity. For the current study, we used this matrix of three burn severities (low, moderate and high) and two pre-fire stand ages (young and old) and measured understory plant community composition in six or seven stands within each of the six categories for a total of 38 stands. Selected stands had pure jack pine overstories with the pre-fire stand age and burn severity determined in the year immediately following the fire as part of the pine regeneration study. Burn severity was determined using the Composite Burn Index (CBI), which incorporates measures of forest floor, understory and overstory burn severity [27], and was then categorized as low, moderate or high. High burn severity stands had complete overstory mortality and greater than 50% forest floor consumption; moderate burn severity stands had on average 75% overstory mortality and 25%–50% forest floor consumption; and low burn severity stands had <25% overstory mortality and only light charring of the forest floor. Pre-fire stand ages were determined from cores taken at breast height of representative canopy trees. Stands were sampled according to pre-fire stand age, with stands less than 30 years old considered “young” and stands greater than 60 years old considered “old”. Soil samples were taken from the upper 15 cm of mineral

soil and were analyzed for texture, percent carbon, electrical conductivity (EC) and pH, none of which were significantly different among burn severity or pre-fire stand age classes.

Plot centres were established at a random point within each selected stand, and then, four 1 m × 1 m quadrats were located 10 m from the plot centre along cardinal bearings. This size of quadrat was used, as it is the standard in the region and will allow for comparison with other studies. At each quadrat, all vascular and non-vascular plants, including lichens, were identified to the species level, and cover was visually estimated to the nearest percent with cover values of 0.5% and + (present but at lower than 0.5% cover) also recorded. A complete stand level species list was also developed for the area enclosed by the four quadrats, an area of approximately 300 m<sup>2</sup>, by completing a walkaround survey. For quantitative analyses, the average cover at the stand level was used with + assigned a value of 0.05% and presence in the area enclosed by the quadrats, but not in the quadrats themselves, assigned a cover value of 0.005%. Total species richness (the total number of understory species per stand) and average percent cover of vegetation (the average of the four quadrats) were determined for each stand. Richness and cover by species group, *i.e.*, lichen, bryophyte, graminoid, forb, shrub, were also determined. Species nomenclature was standardized for vascular plants [28], bryophytes [29] and lichens [30].

### 2.3. Statistical Analyses

Non-metric multidimensional scaling (NMDS) ordinations were used to identify patterns of understory species composition with the Sorensen (Bray–Curtis) distance used as a measure of ecological dissimilarity in the NMDS ordinations conducted using PC-ORD [31]. To quantify the multi-variate differences between groups, we used the multi-response permutation procedure (MRPP) in PC-ORD with Bonferroni correction of *post hoc* pairwise comparisons conducted in R [32]. These ordinations were completed for all plant species together and then for the vascular plants and non-vascular plants (lichens and bryophytes) separately. Indicator species analysis [33], conducted in PC-ORD, was used to identify characteristic species for each burn severity class. This method combines the relative abundance of a species with its relative frequency of occurrence within each burn severity type, producing a maximum value (100%) when all individuals of a species are found in a single burn severity type and when the species occurs in all samples within that type. Significance of each species as an indicator was tested for the burn severity type in which it reached its maximum value using a randomization procedure.

Two-way ANOVA followed by Tukey *post hoc* tests were used to compare species richness and cover among burn severity and pre-fire stand age groups. Regression analysis was used to determine the specific relationship between species groups' richness and cover and continuous site and environmental variables, including burn severity and soil pH. Regression tree analysis was used to quantify distinct thresholds in the response variables. These analyses were conducted using Systat13 (Systat Software Inc., Chicago, IL, USA).

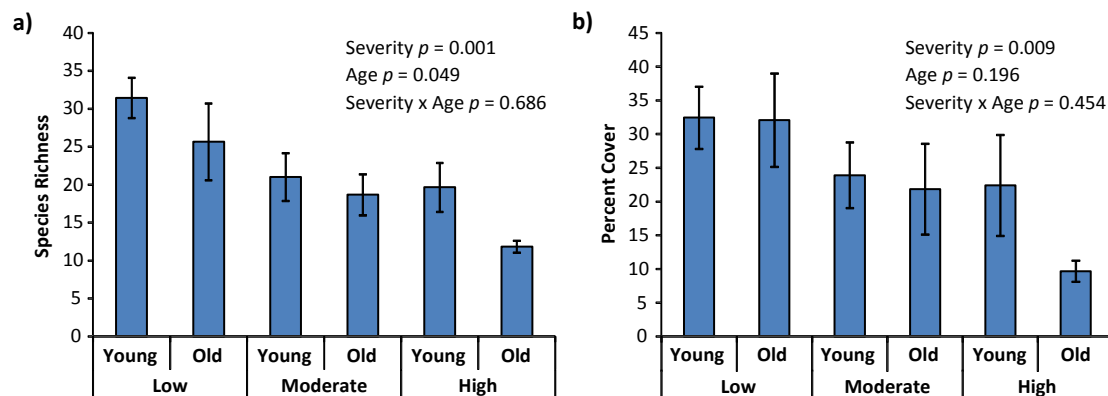
## 3. Results

There was a total of 95 plant (including lichen) species (Appendix A) found across all stands with the most numerous species group being lichens with 32 different species found followed by forbs with 31 species found. Stand-level species richness decreased with burn severity and pre-fire stand age (Figure 2a), such that the greatest richness was found in young stands with low burn severity, and the lowest richness was found in old stands with high burn severity. Vascular plant richness, when considered separately, showed no significant differences among burn severity ( $p = 0.885$ ) or age classes ( $p = 0.537$ ). Average stand level total plant cover ranged from 4%–63% and also decreased with burn severity, but was not affected by pre-fire stand age (Figure 2b).

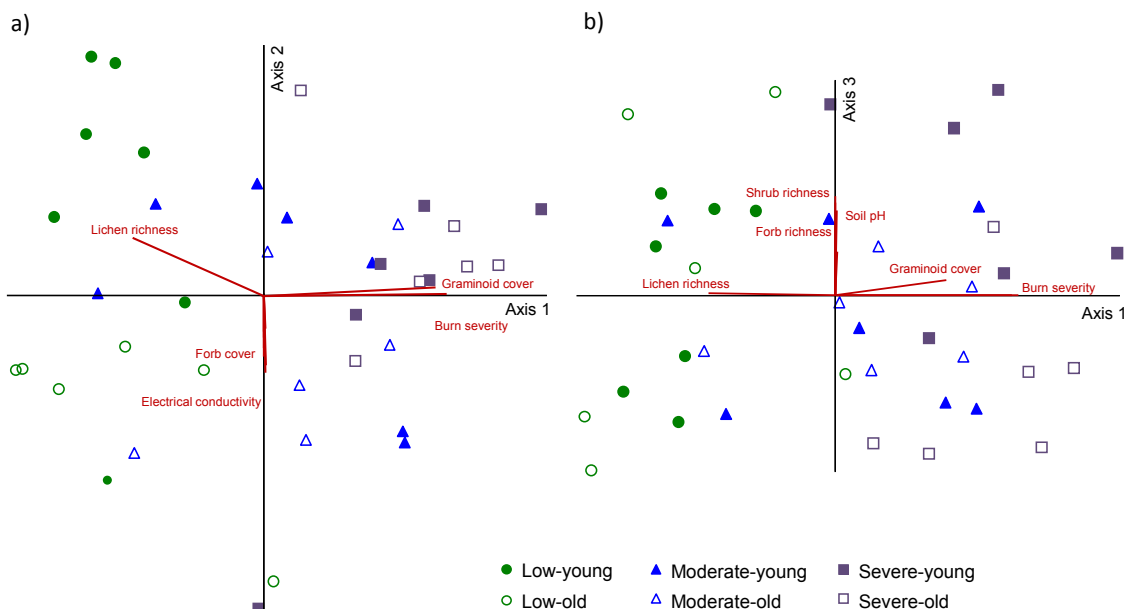
The ordination including all vegetation (Figure 3) and supported by MRPP clearly shows differing plant communities among burn severity classes ( $A = 0.072$ ,  $p < 0.001$ ), but there were no significant differences among pre-fire age classes ( $A = 0.010$ ,  $p = 0.083$ ). Axis 1 is positively correlated with burn

severity and graminoid cover, while lichen richness and cover were negatively correlated (Figure 3a). Axes 2 and 3 function mostly as a soil chemistry gradient with pH and EC positively related to forb and shrub richness (Figure 3a,b).

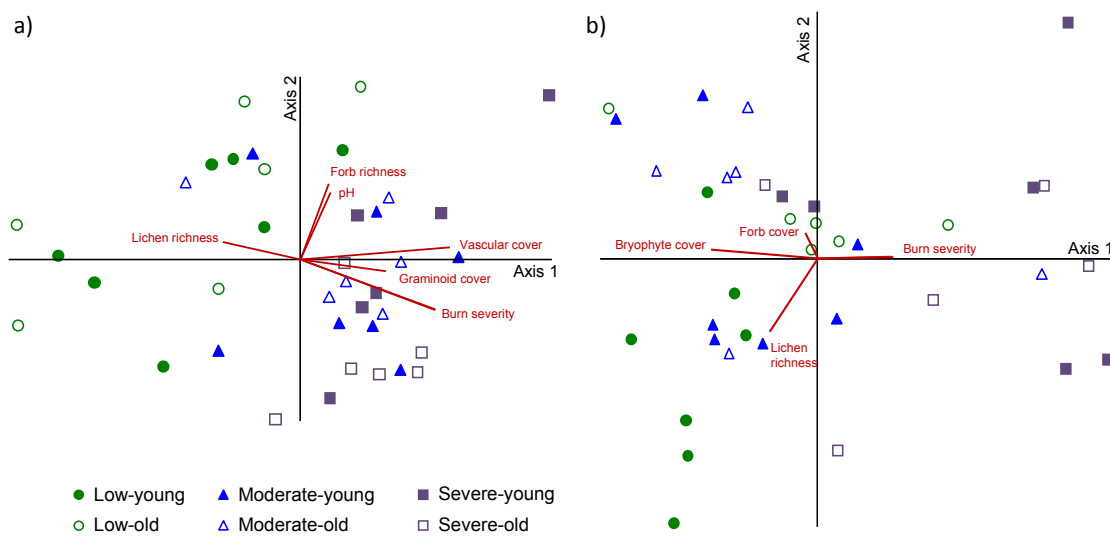
Including only vascular vegetation in the ordination clearly separates the stand replacing moderate and high severity burns from the low severity burns and results in a main gradient defined by burn severity ( $A = 0.068, p < 0.001$ ) and a secondary gradient associated with soil variables, but there was no difference among pre-fire stand age classes ( $A = -0.004, p = 0.645$ ) (Figure 4a). When only non-vascular species are included in the ordination, high severity burns are clearly separated with burn severity again being the primary factor along Axis 1 ( $A = 0.045, p = 0.003$ ), but there is no difference among pre-fire stand age classes ( $A = -0.003, p = 0.302$ ) (Figure 4b). In this ordination, the secondary gradient is negatively correlated with greater lichen richness and positively with forb cover.



**Figure 2.** (a) Species richness (total number of plant species found in each stand) and (b) percent cover (total cover of all species averaged from four 1 m × 1 m quadrats per stand), in relation to burn severity (as measured by the Composite Burn Index) and pre-fire stand age.



**Figure 3.** Non-metric multidimensional scaling ordination of all plant community data: (a) Axes 1 and 2; (b) Axes 1 and 3. The environmental overlays present the most significant relationships for each species group, burn severity and soil chemistry with  $r > 0.5$ .



**Figure 4.** Non-metric multidimensional scaling ordination including only (a) vascular plants or (b) non-vascular plants. The environmental overlays present the most significant relationships for each species group, burn severity and soil chemistry with  $r > 0.5$ .

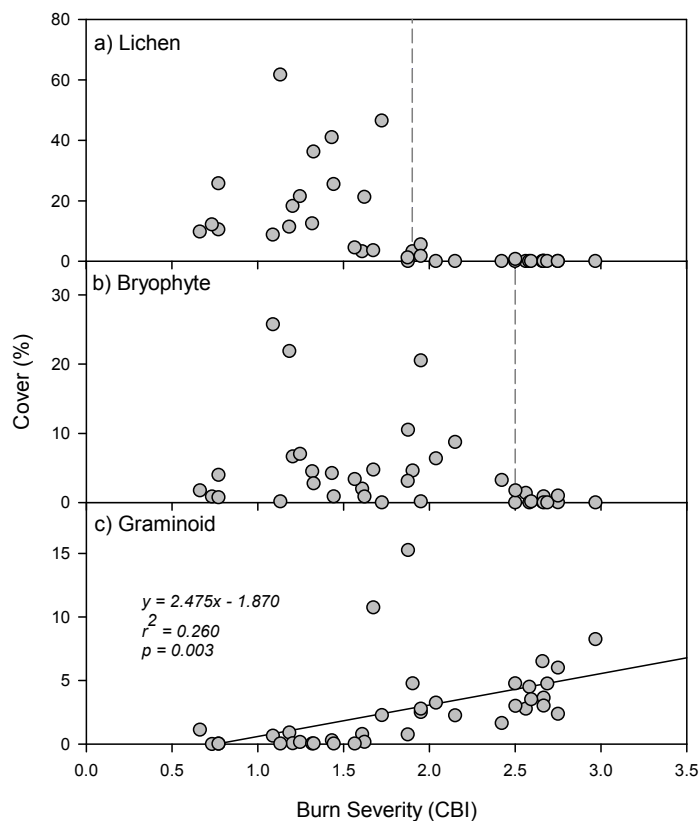
Lichen species, mainly from the genus *Cladonia* with the most common species being *Cladonia arbusculata* subsp. *mitis* and *Cladonia gracilis* subsp. *turbinata*, which were found in 16 out of 38 stands each, accounted for 70% of total cover and 38% of the total species richness in low severity burns where they were most common. Lichen cover showed a negative relationship to burn severity with a significant threshold at CBI 1.9, with lichens being effectively eliminated from the plant community beyond this point (Figure 5a). Bryophyte cover showed a similar pattern to lichens with a negative relationship to burn severity, but with an elimination threshold at a higher burn severity of 2.5 CBI (Figure 5b). The most common bryophytes were *Ceratodon purpureus* and *Polytrichum piliferum*, which were found in 37 and 30 of 38 stands, respectively. *P. piliferum* along with the two lichen species *C. arbusculata* subsp. *mitis* and *C. gracilis* subsp. *turbinata* were the strongest indicators of low severity burns (Table 1), but *C. purpureus*, a ubiquitous species associated with disturbance and open sandy soils, was not a significant indicator of burn severity (Table 1).

Graminoid cover, on the other hand, was quite low (average 2.1% across all burn severities), but was positively related to burn severity (Figure 5c). Graminoid species richness was also positively correlated to burn severity ( $r = 0.468$ ,  $p = 0.003$ ) with the rhizomatous, quickly colonizing *Carex siccata* indicative of moderate and high severity burns (Table 1).

Forb cover was low overall (average 1.2%) and was not related to burn severity ( $p = 0.802$ ) or pre-fire stand age ( $p = 0.409$ ), but it was related to soil pH with significantly higher ( $p < 0.05$ ) forb cover on soils with  $pH > 4.9$  (average 4.1 %) compared to soils with  $pH < 4.9$  (average 0.8%). The most common forbs were *Solidago simplex*, *Campanula rotundifolia* and *Apocynum androsaemifolia*, which were found in 24, 20 and 15 of 38 plots, respectively, across the range of soil pH. On the higher pH soils, however, *Maianthemum canadense* and *Cornus canadensis* became dominant, with the highest forb cover values found in any stands associated with these two species. Colonizing species with small windblown seeds, such as *Chamerion angustifolium* and *Symphyotrichum laeve*, were each only found in nine of 38 stands. Although not as ubiquitous, the annual forbs *Erigeron canadensis* and *Leucophysalis grandiflora* were both significant indicators of high severity burns (Table 1).

Shrub cover averaged 3.8% and was not related to burn severity ( $p = 0.520$ ), pre-fire stand age ( $p = 0.189$ ) nor measured soil properties ( $pH$ ,  $p = 0.272$ ). The most common species were all low shrubs, mainly ericaceous, with *Arctostaphylos uva-ursi*, *Hudsonia tomentosa* and *Vaccinium myrtilloides* being found in 38, 24 and 22 of 38 stands, respectively, and there were no significant shrub indicators of burn severity.





**Figure 5.** Relationships between the cover of plant groups and burn severity as measured by the Composite Burn Index (CBI) for (a) lichens, (b) bryophytes and (c) graminoids. The thresholds for lichen cover at 1.9 CBI and bryophyte cover at 2.5 CBI were determined from regression tree analysis at a significance level of  $p < 0.05$ .

**Table 1.** Significant indicator species with an indicator value >25 for each burn severity class as determined by the method of Dufrêne and Legendre [33]. Each species was only tested for significance in the group for which it had its maximum indicator value.

Severity	Indicator Species	Indicator Value	$p$	Growth Form	Life Strategy
Low	<i>Cladonia arbusculata</i> subsp. <i>mitis</i>	82.1	0.0002	lichen	perennial
	<i>Cladonia gracilis</i> subsp. <i>turbinata</i>	76	0.0008	lichen	perennial
	<i>Polytrichum piliferum</i>	75.4	0.0034	moss	perennial
	<i>Pyrola chlorantha</i>	64.7	0.001	forb	perennial
	<i>Cladonia pyxidata</i>	59.1	0.0002	lichen	perennial
	<i>Cladonia deformis</i>	54.3	0.0008	lichen	perennial
	<i>Trapeliopsis granulosa</i>	50.1	0.011	lichen	perennial
	<i>Cladonia sulphurina</i>	47.7	0.0012	lichen	perennial
	<i>Cladonia subulata</i>	45.7	0.003	lichen	perennial
	<i>Cetraria ericetorum</i>	44.7	0.0042	lichen	perennial
	<i>Cladonia uncialis</i>	43.6	0.0432	lichen	perennial
	<i>Cladonia botrytes</i>	41.7	0.0056	lichen	perennial
	<i>Parmeliopsis ambigua</i>	38.5	0.0074	lichen	perennial
	<i>Cladonia cristatella</i>	38	0.0124	lichen	perennial
	<i>Peltigera malacea</i>	37	0.0184	lichen	perennial
	<i>Cladonia cornuta</i>	36.6	0.0334	lichen	perennial
	<i>Dicranum polysetum</i>	35.3	0.0238	moss	perennial
	<i>Vulpicida pinastri</i>	30.8	0.0284	lichen	perennial
	<i>Cladonia borealis</i>	28	0.0498	lichen	perennial
	Moderate	<i>Carex siccata</i>	29	-	graminoid
High	<i>Carex siccata</i>	69.6	0.0252	graminoid	perennial
	<i>Erigeron canadensis</i>	31.9	0.0338	forb	annual
	<i>Leucophysalis grandiflora</i>	25	0.0272	forb	annual

#### 4. Discussion

There are distinct plant communities developing four years after burns of differing severity, and three out of five main species groups (lichens, bryophytes and graminoids) responded significantly to burn severity. Low severity burns favour the persistence of lichens and bryophytes and have higher overall species richness than high severity burns. In contrast, the vegetation community after high severity burns is comprised mainly of annual forbs and colonizer-type graminoids seeding in from off site along with resprouting forbs and shrubs, resulting in lower overall species diversity and cover. Species richness did not increase with moderate levels of disturbance, as has been suggested by other studies [34,35], but instead, species richness declined with burn severity in our study. While peaks in species richness at intermediate levels of disturbance are actually the exception rather than the rule in published studies [36], the intermediate disturbance hypothesis and underlying mechanisms are fundamental concepts in community ecology, and it is important to understand under what situations these mechanisms function. In our study, in a climatically marginal forest area and on a xeric site type, the number of species capable of surviving there is much less than are available to a more mesic site type, indicating that the plant community developing here may be environmentally limited rather than recruitment or competition limited. Certainly, it is the trade-off between early successional species adapted for colonization (colonizers) *versus* later successional species better able to compete for resources (competitors) that is thought to be one of the primary mechanisms responsible for the peak in species richness at intermediate levels of disturbance [35,37]. While no peak in richness at moderate burn severity was observed in our study, differential species responses to disturbance were observed.

High severity burns, which result in a loss of more than 50% of the total forest floor, result in greatly reduced species richness, as much of the seedbank and resprouting organs are found in the forest floor [12,15]. The new forest plant community must therefore rely mainly on colonizing species from outside, of which there appear to be few other than select graminoids and forbs, capable of surviving in this harsh environment. It also appears that competition between plants is not a major component in determining community composition in this forest given the low overall vegetation cover ( $16\% \pm 4\%$  (mean  $\pm$  SE) in high severity burns) and the corresponding high level of bare ground, again indicating that environmental and not internal controls (*i.e.*, competition) are mainly responsible for controlling plant community development. In contrast, after the same fire event, mesic boreal mixedwood sites had much greater vegetation cover and species richness [22] indicative of higher competition levels among plants and suggesting that this xeric jack pine forest responds differently to fire than do nearby mesic forests.

Lichens and bryophytes were completely eliminated from the plant community at high burn severity, a response frequently evident in non-vascular plants following high severity burns [38]. Although generally considered to be dispersal limited [39], lichens are expected to begin initial recolonization one to three years following the fire, with pioneer lichen species, such as *Cladonia coccifera* (likely equivalent to our *C. borealis*) and *C. gracilis* [7]. Both of these pioneer species were found in our study, although they were confined to low and moderate severity burns and likely represent relict populations from pre-fire communities. Four years post-fire, lichens are only just beginning to recolonize the most severely-burnt sites, with *Cladonia* species present in seven of the twelve stands, but in early stages of regeneration (basal scales only). This is consistent with a generalized successional sequence found throughout lichen-dominated forests of the northern taiga and tundra regions [40]. The bryophytes *Polytrichum piliferum* and *P. juniperinum* were both detected in all age and burn severity classes, along with the ubiquitous *Ceratodon purpureus*. The presence of these species is typical of post-fire succession in northern boreal forests and indicates that these moss species are not dispersal limited, as is hypothesized for lichens. Increased bryophyte diversity in the low and moderate severity burns is also typical of later successional sequences and indicates persistence after low severity burns rather than recolonization. While this general successional sequence of non-vascular plants has been documented in black spruce (*Picea mariana*) [41], lodgepole pine (*Pinus contorta* var. *latifolia*) [42] and jack pine/lichen forests [7], xeric jack pine lichen forests in northern Alberta may follow an alternate



successional trajectory leading to a final park-like pine/lichen stage, instead of the more closed canopy pine/feathermoss stage [7].

Unlike bryophytes and lichens, graminoid cover increased with burn severity. Most of these species are thought to seed in from outside areas, but they may have been a component of the seedbank. Other studies from more southern, climatically-favourable jack pine forests have described the rapid expansion of graminoids, particularly *Carex*, after disturbance with possible negative implications for tree regeneration [43], but the low cover values for graminoids in our study (average 4.4% in high severity) indicate that is not a concern in this forest area. The lack of graminoids in low severity burns with little disturbance to the forest floor also indicates that these species are transient members of the plant community and are likely not a substantial part of the mature forest understory.

Forb cover and richness were not related to burn severity, but were related to soil chemistry with increased cover above pH 4.9. This is comparable to more forb-rich aspen stands of the region, which were found to have pH ( $\pm$  SE) values of  $5.28 \pm 0.33$  and  $4.77 \pm 0.19$  for mature and post-fire stands, respectively [22]. The lack of response to burn severity may reflect the vegetative regeneration strategy of many common perennial forb species, including the species most abundant on high pH soils, *Maianthemum canadense* and *Cornus canadensis* [44,45]. Even on sites with very low competition levels and correspondingly high suitable seedbeds in the form of exposed mineral soil, forb richness did not increase, suggesting that colonizing forb species with widely-dispersed seed rain, such as *Chamerion angustifolium* and *Symphytotrichum laeve* [46,47], were not able to thrive in this harsh environment. Instead, the sites with the most abundant forb cover relied on resprouting of existing forbs.

Shrub cover and richness were not related to burn severity, pre-fire stand age or any measured environmental variable. Most shrubs can regenerate vegetatively, and this appears to be the case here with similar shrub species found across the range of site types and burn severities. The low shrub cover (average 3.8% across all sites) may therefore be more indicative of the slow growth rates of the dominant ericaceous shrubs, rather than a limitation in recruitment to the site given that *Arctostaphylos uva-ursi* was found in every sampled stand.

## 5. Conclusions

In conclusion, we demonstrate the relatively large range of potential plant communities developing following a large, spring fire in xeric, boreal jack pine forests. Although there are indications that soil chemical factors play a secondary role in structuring the forb community, four years post-fire, the variation in plant communities is primarily due to burn severity and is evident in both the vascular and non-vascular components of the flora. If fire frequency and severity continue to increase as predicted [1], these results indicate that we may see a shift in plant communities from stress-tolerant, slower growing species, such as lichens and ericaceous shrubs, to more colonizing species, such as select graminoids and forbs, which appear to be able to tolerate the harsh environmental conditions of this forest. The implications of this potential shift in understory plant communities on wildlife habitat, particularly for the woodland caribou, which rely on lichen for much of their diet, is not known. As this study was based on only a single, albeit massive, fire event, caution is needed in extrapolating these results to other areas. The clear message from this study, however, is that the potential range of post-disturbance plant communities is dependent on burn severity at the site level.

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**Author Contributions:** Bradley D. Pinno and Ruth C. Errington both contributed to all aspects of the work, including designing the experiment, analyzing the data and writing the paper.

**Conflicts of Interest:** The authors declare no conflict of interest.

## Appendix A

Table A1. Complete species list with the number of stands the species was found in grouped according to burn severity and pre-fire age class.

Burn Severity			Low		Moderate		High	
Age Class			Old	Young	Old	Young	Old	Young
Number of plots per stand type			N = 6	N = 7	N = 6	N = 7	N = 6	N = 6
Species	Layer	Life Strategy						
<i>Achillea millefolium</i> Linnaeus	herb	perennial	0	2	0	0	0	0
<i>Agrostis scabra</i> Willdenow	herb	perennial	5	6	5	7	6	5
<i>Alnus viridis</i> (Chaix) de Candolle subsp. <i>crispa</i> (Aiton) Turrill	shrub	perennial	0	0	0	1	0	1
<i>Amelanchier alnifolia</i> (Nuttall) Nuttall ex M. Roemer	shrub	perennial	1	1	1	0	0	2
<i>Anemone multifida</i> Poiret	herb	perennial	2	1	1	0	0	2
<i>Apocynum androsaemifolium</i> Linnaeus	herb	perennial	3	3	2	3	1	4
<i>Aralia nudicaulis</i> Linnaeus	herb	perennial	0	0	0	0	0	1
<i>Arctostaphylos uva-ursi</i> (Linnaeus) Sprengel	shrub	perennial	6	7	6	7	6	6
<i>Bryoria simplicior</i> (Vainio) Brodo & D. Hawksw.	lichen	perennial	0	1	0	0	0	0
<i>Calamagrostis stricta</i> subsp. <i>inexpansa</i> (A. Gray) Greene	herb	perennial	1	1	1	0	0	2
<i>Campanula rotundifolia</i> Linnaeus	herb	perennial	3	5	3	3	1	4
<i>Capnoides sempervirens</i> (Linnaeus) Borkhausen	herb	biennial	0	0	0	0	1	0
<i>Carex foenea</i> Willdenow	herb	perennial	0	1	2	4	2	4
<i>Carex praticola</i> Rydberg	herb	perennial	0	0	1	0	0	0
<i>Carex c.f. richardsonii</i> R. Brown	herb	perennial	1	0	1	0	0	1
<i>Carex siccata</i> Dewey	herb	perennial	4	5	6	7	6	6
<i>Carex tonsa</i> (Fernald) E.P. Bicknell	herb	perennial	5	7	5	7	5	6
<i>Carex umbellata</i> Schkuhr ex Willdenow	herb	perennial	0	0	1	0	1	0
<i>Ceratodon purpureus</i> (Hedwig) Bridel	bryophyte	perennial	6	7	6	7	6	5
<i>Cetraria ericetorum</i> Opiz	lichen	perennial	2	5	0	2	0	0
<i>Chamerion angustifolium</i> (Linnaeus) Holub subsp. <i>angustifolium</i>	herb	perennial	0	1	3	1	1	3
<i>Cladonia amaurocraea</i> (Flörke) Schaerer	lichen	perennial	0	1	0	0	0	0
<i>Cladonia borealis</i> S. Stenroos	lichen	perennial	0	5	0	2	0	0
<i>Cladonia botrytes</i> (K.G. Hagen) Willd.	lichen	perennial	1	5	0	2	0	0
<i>Cladonia cariosa</i> (Ach.) Sprengel	lichen	perennial	0	1	0	0	0	0
<i>Cladonia cornuta</i> (L.) Hoffm.	lichen	perennial	0	5	0	3	0	0
<i>Cladonia crispata</i> (Ach.) Flotow	lichen	perennial	0	4	1	2	0	0

Table A1. Cont.

Burn Severity			Low	Moderate	High			
<i>Cladonia cristatella</i> Tuck.	lichen	perennial	1	5	0	2	0	0
<i>Cladonia deformis</i> (L.) Hoffm.	lichen	perennial	2	7	0	3	0	0
<i>Cladonia</i> c.f. <i>fimbriata</i> (L.) Fr.	lichen	perennial	2	1	0	0	0	0
<i>Cladonia gracilis</i> (L.) Willd. subsp. <i>turbinata</i> (Ach.) Ahti	lichen	perennial	3	7	2	3	0	0
<i>Cladonia macilentata</i> Hoffm.	lichen	perennial	1	0	0	0	0	0
<i>Cladonia macrophylla</i> (Schaerer) Stenh.	lichen	perennial	0	0	0	1	0	0
<i>Cladonia arbusculata</i> (Wallr.) Flotow subsp. <i>mitis</i> (Sandst.) Ruoss	lichen	perennial	4	7	1	3	0	0
<i>Cladonia multiformis</i> G. Merr.	lichen	perennial	1	1	0	0	0	0
<i>Cladonia pyxidata</i> (L.) Hoffm.	lichen	perennial	2	6	0	1	0	0
<i>Cladonia rangiferina</i> (L.) F.H. Wigg.	lichen	perennial	1	0	0	0	0	0
<i>Cladonia</i> sp. P. Browne	lichen	perennial	6	6	5	5	4	3
<i>Cladonia stygia</i> (Fr.) Ruoss	lichen	perennial	1	0	0	0	0	0
<i>Cladonia subulata</i> (L.) F.H. Wigg.	lichen	perennial	1	5	0	1	0	0
<i>Cladonia sulphurina</i> (Michaux) Fr.	lichen	perennial	2	5	0	2	0	0
<i>Cladonia uncialis</i> (L.) Weber ex F.H. Wigg.	lichen	perennial	4	5	1	3	0	0
<i>Cladonia verticillata</i> (Hoffm) Schaerer	lichen	perennial	0	4	0	2	0	0
<i>Collomia linearis</i> Nuttall	herb	annual	2	0	0	0	0	0
<i>Comandra umbellata</i> (Linnaeus) Nuttall	herb	perennial	1	0	1	0	0	0
<i>Cornus canadensis</i> Linnaeus	herb	perennial	1	0	0	0	0	1
<i>Crepis tectorum</i> Linnaeus	herb	annual	0	0	3	0	0	1
<i>Dichanthelium acuminatum</i> (Swartz) Gould & C.A. Clarke subsp. <i>fasciculatum</i> (Torrey) Freckmann & Lelong	herb	perennial	0	0	0	1	1	0
<i>Dicranum polysetum</i> Swartz	bryophyte	perennial	4	1	1	0	0	0
<i>Diphasiastrum complanatum</i> (Linnaeus) Holub	herb	perennial	1	1	0	0	0	1
<i>Erigeron canadensis</i> Linnaeus	herb	annual	0	0	3	0	2	3
<i>Evernia mesomorpha</i> Nyl.	lichen	perennial	0	1	0	0	0	0
<i>Festuca saximontana</i> Rydberg	herb	perennial	1	0	0	0	0	0
<i>Flavocetraria nivalis</i> (L.) Kärnefelt & A. Thell	lichen	perennial	0	2	0	0	0	0
<i>Fragaria virginiana</i> Miller	herb	perennial	2	1	1	0	0	1
<i>Galium boreale</i> Linnaeus	herb	perennial	2	2	1	0	0	1
<i>Geocaulon lividum</i> (Richardson) Fernald	herb	perennial	0	0	0	0	0	1
<i>Geranium bicknellii</i> Britton	herb	annual or biennial	0	0	1	1	0	2
<i>Hieracium umbellatum</i> Linnaeus	herb	perennial	2	1	0	0	1	1
<i>Hudsonia tomentosa</i> Nuttall	herb	perennial	2	3	4	6	5	4
<i>Hylocomium splendens</i> (Hedwig) Shimper in P. Bruch and W.P. Shimper	bryophyte	perennial	1	0	0	0	0	0

Table A1. Cont.

Burn Severity			Low	Moderate	High			
<i>Leucophysalis grandiflora</i> (Hooker) Rydberg	herb	annual	0	0	0	1	0	3
<i>Leymus innovatus</i> (Beal) Pilger subsp. <i>innovatus</i>	herb	perennial	0	0	0	0	0	1
<i>Linnaea borealis</i> Linnaeus	herb	perennial	3	1	1	0	0	1
<i>Maianthemum canadense</i> Desfontaines	herb	perennial	3	3	2	2	1	3
<i>Melampyrum lineare</i> Desrousseaux	herb	annual	1	0	0	0	0	0
<i>Oryzopsis asperifolia</i> Michaux	herb	perennial	1	2	1	0	0	1
<i>Packera paupercula</i> (Michaux) Á. Löve & D. Löve	herb	perennial	1	1	0	0	0	1
<i>Parmeliopsis ambigua</i> (Wulfen) Nyl.	lichen	perennial	2	3	0	0	0	0
<i>Peltigera malacea</i> (Ach.) Funck	lichen	perennial	2	3	0	1	0	0
<i>Peltigera rufescens</i> (Weiss) Humb.	lichen	perennial	0	2	0	0	0	0
<i>Pinus banksiana</i> Lambert	tree	perennial	4	7	6	7	6	6
<i>Piptatheropsis pungens</i> (Torrey ex Sprengel) Romaschenko, P.M. Peterson & Soreng	herb	perennial	4	4	2	5	4	5
<i>Pleurozium schreberi</i> (Wildenow ex Bridel) Mitten	bryophyte	perennial	2	1	1	0	0	0
<i>Polytrichum juniperinum</i> Hedwig	bryophyte	perennial	5	6	5	3	2	2
<i>Polytrichum piliferum</i> Hedwig	bryophyte	perennial	6	7	5	6	2	2
<i>Populus tremuloides</i> Michaux	tree	perennial	1	1	0	2	0	1
<i>Prunus pennsylvanica</i> Linnaeus f.	tree, shrub	perennial	3	1	2	2	1	3
<i>Ptilidium ciliare</i> (L.) Hampe	bryophyte	perennial	2	1	1	0	0	0
<i>Ptilium crista-castrensis</i> (Hedwig) De Notaris	bryophyte	perennial	1	0	0	0	0	0
<i>Pyrola chlorantha</i> Swartz	herb	perennial	4	5	1	2	0	1
<i>Rosa acicularis</i> Lindley	shrub	perennial	1	1	1	0	0	1
<i>Salix bebbiana</i> Sargent	shrub	perennial	0	2	0	0	0	0
<i>Selaginella densa</i> Rydb.	herb	perennial	0	0	0	0	1	0
<i>Sibbaldia tridentata</i> (Aiton) Paule & Soják	herb	perennial	1	2	0	0	0	2
<i>Solidago simplex</i> Kunth var. <i>simplex</i>	herb	perennial	3	4	5	4	4	3
<i>Stereocaulon alpinum</i> Laurer ex Funck	lichen	perennial	0	1	0	0	0	0
<i>Symphotrichum ciliolatum</i> (Lindley) Á. Löve & D. Löve	herb	perennial	0	1	0	1	0	0
<i>Symphotrichum laeve</i> (Linnaeus) Á. Löve & D. Löve var. <i>laeve</i>	herb	perennial	3	1	2	0	0	3
<i>Trapeliopsis granulosa</i> (Hoffm.) Lumbsch	lichen	perennial	2	5	0	3	0	0
unknown seedling		#N/A	0	1	1	0	0	0
<i>Vaccinium myrtilloides</i> Michaux	shrub	perennial	4	4	4	4	1	4
<i>Vaccinium vitis-idaea</i> Linnaeus	shrub	perennial	3	1	2	1	0	2
<i>Viola adunca</i> Smith	herb	perennial	1	1	1	0	0	2
<i>Vulpicida pinastri</i> (Scop.) J.-E. Mattsson & M.J. Lai	lichen	perennial	1	3	0	0	0	0

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