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Paludification in black spruce (*Picea mariana*) forests of eastern Canada: Potential factors and management implications

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Abstract

Over time boreal black spruce forests on fine-textured soils in western Quebec, Canada develop very thick forest floors composed of poorly decomposed litter created by the tree and understory layers. These paludified soils are typically waterlogged and cold, and in this fire-mediated landscape, are at least partially consumed by stand replacing fires, which facilitates the establishment of the next generation of trees. Within a context of ecosystem-based management, forest harvest should mimic the dual effects of high severity fire on tree and forest floor biomass. This study was designed to investigate potential factors of forest floor thickness in order to determine the impact of removing only a tree layer, and to suggest strategies to limit paludification in this important forestry region. Forest floor thickness, fire severity, basal area, canopy closure, cover of *Sphagnum* spp. and ericaceous spp. were measured in black spruce stands across a chronosequence from 50 to 350 years after fire. Fire severity was determined to be a key factor in determining forest floor thickness by path analysis. After high severity fires forest floor thickness was primarily dependant on stand age, but was also positively influenced by *Sphagnum* spp. cover and negatively influenced by the presence of trembling aspen (*Populus tremuloides*). These results suggest that forest interventions that do no remove the organic layer may be mimicking low severity fires and promoting poor tree growth and regeneration. Forest floor thickness may be limited by avoiding interventions that open the canopy and may promote the presence of *Sphagnum* spp. and ericaceous spp., and or by practicing mixed silviculture of trembling aspen and black spruce. However, a balance needs to be maintained between the application of these techniques and the preservation of paludified forests in the landscape.

Keywords: Forest floor; Boreal; Fire severity; *Sphagnum*; Ericaceous; Paludification

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1. Introduction

Boreal black spruce (*Picea mariana* Lamb.) forests develop thick forest floors composed of partially decomposed and undecomposed plant matter that is a product of the understory and tree layers. The thickest forest floors occur in regions prone to paludification, such as the interior of Alaska (Viereck et al., 1993), old glacial Lake Agassiz (Heinselman, 1963), the Clay Belt of Québec and Ontario (Taylor et al., 1987), and Labrador (Foster, 1985). In these regions, decom-

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position is considerably slower than litter production, due to low temperatures, and the presence of poor decomposition substrates in the litter (Prescott et al., 2000). As a result, very thick forest floors accumulate, and forests may develop into peatlands (Crawford et al., 2003).

While paludification is frequently discussed, the local mechanisms that result in reduced decomposition are not clear. Cited causes include *Sphagnum* spp. invasion (Lawrence, 1958), thick-feather moss cover (Viereck et al., 1993), the presence of ericaceous species (DeLuca et al., 2002), and water table rise due to a variety of causes (Taylor et al., 1987; Bonan and Shugart, 1989). Regardless of the cause, the accumulation of deep forest floors has a profound negative effect on forest productivity (Glebov and Korzukhin, 1992; Bonan and Shugart, 1989), as paludified soils tend to be waterlogged, cold and have a significant proportion of nutrients locked up in the poorly decomposed organic matter that makes up the forest floor (Glebov and Korzukhin, 1992; Bonan and Shugart, 1989; Van Cleve and Viereck, 1981; Heinselman, 1963). These changes are believed to cause a drop in the growth rate of trees (Van Cleve and Viereck, 1981), and inhibit the development of seedlings (Greene et al., 1999; Bonan and Shugart, 1989). As a result, regeneration is decreased without a stand replacing fire that burns through the forest floor.

Ecosystem-based management includes the concept that diversity (biological and structural) can be conserved when forestry interventions are modelled after natural disturbances (McRae et al., 2001). Therefore, in a landscape where forestry is applied, it is important to understand how the disturbance regime affects ecosystem processes in order to accurately mimic them. Within the boreal forest, it is frequently assumed that clearcuts mimic the stand replacing fires that are the dominant disturbance factor. However, it has been suggested that without site preparation to disturb the accumulated forest floor, clearcuts do not resemble fires (Bergeron et al., 1999). Ultimately, without a better understanding of how forest floor biomass is accumulated after fire, and how this process is affected by fire characteristics (e.g. severity or depth of burn in forest floor) the potential impacts of a lack of forest floor disturbance can only be speculated.

The objectives of this study are to examine some of the factors that are believed to influence the accumulation of thick forest floors in boreal black spruce stands on fine-textured soils on the Clay Belt of Québec and Ontario. Factors included in the analyses are fire severity, stand density, degree of crown closure, density of trembling aspen, and cover of *Sphagnum* spp. and ericaceous spp. cover. High fire severity, stand density and trembling aspen presence are expected to decrease forest floor thickness, while low canopy closure, and high cover of ericaceous and *Sphagnum* spp. are expected to increase forest floor thickness. With a better understanding of these factors, it may then be possible to suggest silvicultural solutions to either better mimic high severity, stand replacing fires or to limit forest floor accumulation.

1.1. Study area

The study was conducted in the western boreal forest of Québec, within the black spruce (*P. mariana*)-feather moss (*Pleurozium schreberi*) forest type (Grondin, 1996). Specifically, the study took place within the Clay Belt of Québec and Ontario, a major physiographic region created by the deposits left by Lakes Barlow and Ojibway after their maximum extension during the Wisconsonian (Vincent and Hardy, 1977). The Clay Belt is an excellent area in which to study forest floor accumulation, because it is prone to paludification (Boudreault et al., 2002) and supports a large forestry industry. Average annual temperature is 0.8 °C with an average of 856.8 mm of precipitation annually, recorded at the closest weather station, La Sarre, Québec (Environment Canada, 1993). The dominant disturbance types are large fires that kill all above ground vegetation. Between 1850 and 1920, the fire cycle was ca. 135 years, and it has since increased to ca. 398 years; mean stand age is 148 years (Bergeron et al., 2004).

2. Materials and methods

2.1. Data collection

During the summer of 2003, 18 black spruce dominated sites ranging from 50 to 350 years since fire (see Appendix 1 for a full description) were sampled. A stand initiation map (Bergeron et al., 2004) and an ecoforestry map (Harper et al., 2002) were used to choose sites on a slight incline with fine-textured deposits. Slope and soil texture were both verified at the site, and time since fire was established by either dating dominant trees or verification of fire map dates by dating a few dominant trees. The severity of the last fire on the forest floor was established by determining the position of the uppermost charcoal layer within numerous forest floor profiles. While strictly speaking, more fuel may have been consumed in the low severity fires, severity of fire on the forest floor may be most accurately measured by the amount of forest floor not consumed by fire (Nguyen-Xuan et al., 2000; Alexander, 1982). If the charcoal was situated at the interface between the forest floor and the mineral soil, the last fire was designated as high severity. If, however, the charcoal layer was within the forest floor layer, the last fire was designated as low severity. For further details on the methods used, see Lecomte et al. (submitted for publication). Among the stands sampled, 13 sites were established after high severity fire and 5 sites after low severity fire.

Within each site, five quadrats of 100 m^2 were installed, with four nested quadrats of 25 m^2. Within each 25 m^2 quadrat, forest floor thickness was determined by measuring the depth to mineral soil in a randomly chosen location, including therefore the entire organic layer. The clay A horizon provided a clear end point to forest floor depth. A densiometer reading was taken (a concave mirror scored with a grid to allow estimation of canopy cover), and the diameter at breast height (dbh) of all trees greater than 8 cm was measured. Basal area per hectare was calculated for all species together, and for trembling aspen alone. Both stand density and canopy openness were included as variables, as stand density also includes the effect of the trees on the soil. Covers (%) of *Sphagnum* spp. and ericaceous spp. (primarily *Ledum groenlandicum* and *Kalmia angustifolia*) were estimated. The 25 m^2 quadrats were assumed to be independent, as soil processes tend to vary on the scale of a few meters, therefore analyses were performed on the values for the 25 m^2 quadrats.

2.2. Statistical analyses

Forest floor thickness was natural log transformed in all analyses for normality. All other variables were normally distributed.

Pearson correlations were calculated between transformed forest floor thickness and potential explanatory variables [basal area, open canopy, trembling aspen (PET) basal area, *Sphagnum* spp. and ericaceous spp. cover] for all sites and high severity sites separately. Spearman's correlation coefficient was used for fire severity. Because many of the potential explanatory factors examined were auto-correlated, partial correlation and path analysis, rather than multiple regression, were used to determine the potential structure (including direction) of the relationships among the variables. A d-sep test (Shipley, 2000) was used to determine the likelihood that an a-priori structure was correct. Partial correlation coefficients (or path coefficients) among the variables allowed the determination of the magnitude of direct and indirect effects among variables. The variables included in each path analysis were selected from the list of potential variables based on strong partial correlation with forest floor thickness, indicating they were related when the other variables were held constant. The percent of variation in forest floor thickness explained by the selected explanatory variables was calculated with linear regression using SPSS 10.0. A $p = 0.05$ was used in all analyses, except the Pearson correlations, where a $p = 0.01$ was used, due to the large number of correlations calculated.

3. Results

Forest floor thickness was negatively correlated with fire severity (i.e. thinner forest floors after high severity fires), total basal area, and trembling aspen (PET) basal area, and positively correlated with cover of ericaceous spp. and *Sphagnum* spp., canopy openness, and time since fire (TSF) (Table 1). The importance of fire severity is visible in the different curves for sites after high and low severity fires (Fig. 1). After a high severity fire, a 50-year-old site had only approximately 17 cm of forest floor on average, while in a neighbouring site, 50 years after a fire of low severity; there was approximately 40 cm of forest floor.

As most of the potential factors were auto-correlated, partial correlations were calculated to determine which would be retained for path analysis.

Table 1
Pearson correlation coefficients (Spearman for severity) among factors influencing forest floor thickness, in all sites, and after high severity fires

All sites	Severity	Basal area	Open canopy	*Sphagnum* cover	Ericaceous cover	PET basal area	TSF
Forest floor thickness	**−0.358**	**−0.547**	**0.573**	**0.584**	**0.640**	**−0.169**	**0.738**
	Severity	**0.309**	**−0.260**	**−0.201**	**−0.341**	0.093	0.000
		Basal area	**−0.577**	**−0.451**	**−0.607**	**0.249**	**−0.506**
			Open canopy	**0.414**	**0.561**	−0.108	**0.580**
				Sphagnum cover	**0.557**	**0.147**	**0.526**
					Ericaceous cover	**−0.145**	**0.605**
						PET basal area	−0.099

High severity	Basal area	Open canopy	*Sphagnum* cover	Ericaceous cover	PET basal area	TSF
Forest floor thickness	**−0.489**	**0.565**	**0.661**	**0.634**	**−0.177**	**0.802**
	Basal area	**−0.551**	**−0.501**	**−0.585**	**0.261**	**−0.618**
		Open canopy	**0.449**	**0.591**	−0.103	**0.685**
			Sphagnum cover	**0.644**	**−0.150**	**0.724**
				Ericaceous cover	−0.139	**0.770**
					PET basal area	−0.122

Values in bold are significant at $p = 0.01$.

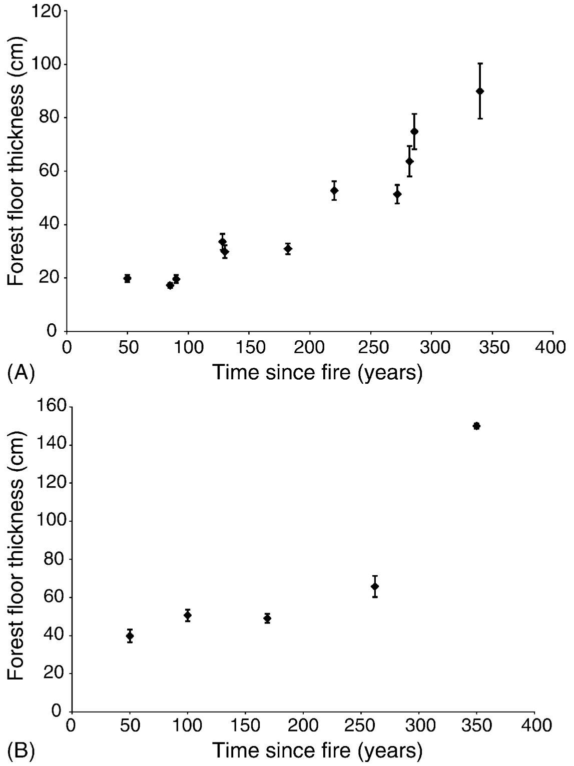

Fig. 1. Development of forest floor with time since (A) high and (B) low severity fires as mean thickness with standard error. Each point represents the mean of 20 values for each site.

TSF, fire severity, cover of *Sphagnum* spp. and ericaceous spp. were retained, as they had a significant partial correlation, even when the other factors were taken into consideration (Table 2). The structure determined by path analysis (Fig. 2), which was not rejected by d-sep analysis ($p = 0.2989$; Shipley, 2000), indicated that TSF and fire severity were the two dominant factors on forest floor thickness, with the largest direct effects 0.606 and −0.295, respectively. The cover of *Sphagnum* spp. and ericaceous

Table 2
Direct effect, indirect effect and error terms for path analysis of forest floor thickness in all sites, and after high severity fires

Variable	Direct	Indirect	Error	Total
All sites				
Time since fire	0.606	0.307	0.0711	0.738
Severity	−0.295	−0.123	0.047	0.371
Sphagnum cover	0.164	0.324	0.0960	0.584
Ericaceous cover	0.079	0.513	0.0481	0.640
High severity				
Time since fire	0.489	0.284	0.0273	0.800
Sphagnum cover	0.198	0.288	0.174	0.659
PET basal area	−0.116	0.0235	−0.0845	−0.177
Ericaceous cover	0	0.621	0.0100	0.631
Open canopy	0	0.519	0.0460	0.565

Total value represents the Pearson correlation coefficient (R^2).

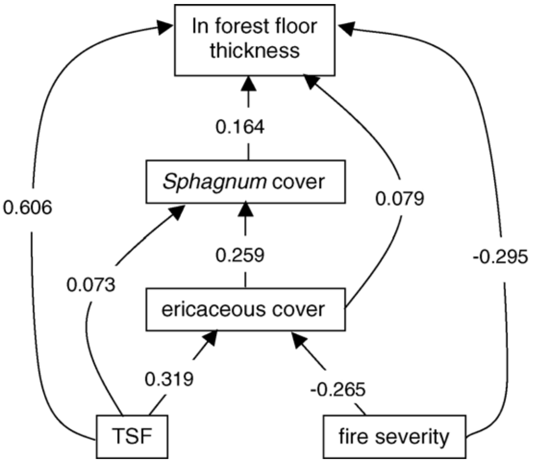

Fig. 2. Path analysis of factors affecting forest floor thickness after high and low severity fires combined. The structure was not rejected by d-sep analysis (Shipley, 2000; $p = 0.2989$). Multiple regression indicated that 70% of the variability was explained by the included variables. Arrows and numbers indicate the direction of causality and the path coefficient between two variables.

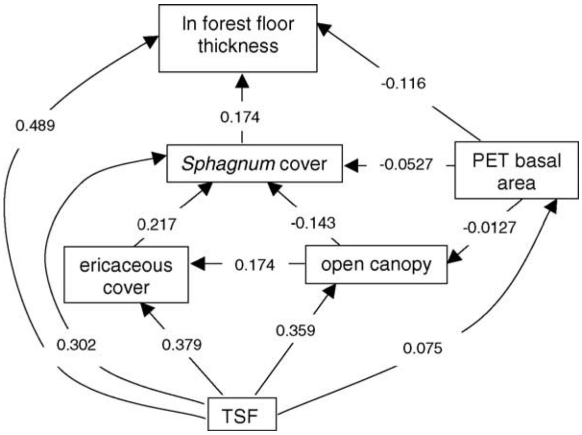

Fig. 3. Path analysis of factors affecting forest floor thickness after high severity fires. The structure was not rejected by d-sep analysis (Shipley, 2000; $p = 0.725$). Multiple regression indicated that 65% of the variability was explained by the included variables. Arrows and numbers indicate the direction of causality and the path coefficient between two variables.

spp. also had statistically significant direct effects, although with less influence than TSF and fire severity. In fact, the majority of the correlation between forest floor thickness and *Sphagnum* spp. and ericaceous spp. cover is due to shared correlation with TSF and fire severity. In turn, *Sphagnum* spp. cover was positively influenced by cover of ericaceous spp. and TSF. Cover of ericaceous species was influenced negatively by fire severity and positively by TSF.

As fire severity was a dominant factor, the severe sites were analysed separately. After severe fires, forest floor thickness was highly correlated with the amount of open canopy, cover of *Sphagnum* spp., cover of ericaceous spp., amount of trembling aspen, and TSF, which were all also auto-correlated (Table 1).

TSF, amount of trembling aspen, cover of *Sphagnum* spp. and ericaceous spp., and canopy openness all had significant partial correlations when the other factors were accounted for. The structure suggested by path analysis, indicated that only TSF, *Sphagnum* spp. cover, and amount of trembling aspen had direct effects on forest floor thickness (Table 2; Fig. 3). The cover of ericaceous spp. and the amount of open canopy had an indirect effect via *Sphagnum* spp. cover. The presented model explains 65% of the variability ($p < 0.0001$), as indicated by multiple regression and the structure was not rejected by a d-sep test (Shipley, 2000) with a $p = 0.725$.

4. Discussion

4.1. Time since fire and fire severity

Time since fire was the most important factor influencing forest floor thickness within the both the entire data set and the analyses restricted to the high severity fire sites. This is only logical, as the organic matter within the forest floor takes time to accumulate. However, the linear relationship with TSF also indicates that on fine-textured soils on the Clay Belt, no additional initiative process is required. This is in contrast to other geographical areas, where a non-linear relationship exists, and thick forest floors are developed after the creation of an impermeable layer by an external factor such as the development of permafrost, a chemical change in the soil or the expansion of neighbouring peatlands (Viereck et al., 1993; Bonan and Shugart, 1989; Glebov and Korzukhin, 1992).

From TSF, it is possible to calculate the rate of accumulation of forest floor matter. However, the true rate of accumulation in the oldest stands cannot yet be accurately determined, as these sites may be older than indicated by dendrochronological age alone. Carbon 14 tests on similar stands in the same region have indicated that the oldest trees currently found were actually established a long time after the last fire (Cyr et al., 2005), resulting in an underestimation of stand age. While a change in stand age would affect the rate of forest floor accumulation and potentially the relative importance of each mechanism, it would not affect the mechanisms investigated here.

After TSF, fire severity was the most important factor in explaining variation in forest floor thickness in the complete data set. This is reflected in the very different forest floor thickness in young stands after high and low severity fires, and in the relationship between forest floor thickness and time (Fig. 1). This may be due to two causes. The intuitive cause is that residual matter left by a low severity fire gives the forest floor a head start. However, the presence of residual matter may also accelerate the rate of accumulation by affecting the function of factors suggested here, primarily *Sphagnum* spp. and ericaceous spp. For example, the residual layers of the forest floor left after non-severe fires may facilitate *Sphagnum* spp. establishment, and growth (Purdon et al., 2004; Dyrness and Norum, 1983). For this reason, a separate analysis was completed for the high severity fire sites. A similar detailed analysis of the low severity sites was not possible with the data from this study, as too few low severity fires were sampled. Therefore, future studies should focus on understanding the influence of low fire severity and residual matter on the factors influencing the development of forest floors proposed here. This may be of particular importance, as the long fire cycles found in the eastern boreal forests permit the accumulation of a significant forest floor. This may cause a self-perpetuating cycle as forests with a thicker forest floor are moister and lose less organic matter during subsequent fires (Kasischke et al., 2000; Foster, 1985).

4.2. *Forest floor thickness after high severity fires*

While TSF was overwhelmingly the most important factor influencing forest floor thickness, there was variation in the thickness of the forest floor within and among sites, particularly at later stages in the chronosequence (Fig. 1). Within this analysis, the factors explaining this variation were the cover of *Sphagnum* spp., the amount of trembling aspen, the openness of the canopy, and the cover of ericaceous spp.

The presence of *Sphagnum* spp. in the understory has frequently been implicated as a key factor in the development of thick forest floors. They are believed to have a negative effect on decomposition through the development of a cold, wet, and acidic environment for decomposers (Turetsky, 2003). In addition, they also affect decomposition rates through their rapid production of biomass, which has a high C:N ratio, and is resistant to decomposition (Turetsky, 2003; Hobbie, 1996). However, while our results indicate that they are a direct factor in determining forest floor thickness, the magnitude of effect is comparatively weak.

The direct negative effect of the presence of trembling aspen on forest floor thickness is due to the presence of a high quality litter on the forest floor, which results in higher decomposition rates overall. Légaré et al. (in press) found increasing decomposition rates of popsicle sticks, in the forest floor with increasing presence of trembling aspen in the forest composition. In addition to this direct effect, the presence of trembling aspen diminished the cover of *Sphagnum* spp. This effect is particularly interesting when canopy openness is accounted for and implies that there is a relationship that is not directly related to shade. It has been suggested that deciduous leaves have a negative effect on the growth of forest floor mosses, either through a chemical interaction or through smothering (Saetre et al., 1997; Frego and Carelton, 1995).

Canopy openness had only an indirect effect on forest floor depth, via *Sphagnum* spp. cover. The negative interaction between these two factors is surprising, as *Sphagnum* spp. is generally considered to be shade intolerant, and dependent on full sunlight for maximum growth (Bisbee et al., 2001; Ohlson et al., 2001). However, *Sphagnum capillifolium*, a highly shade tolerant species (Hayward and Clymo, 1983), dominates in young stands (Fenton, unpublished data). As a result, total *Sphagnum* cover does not display the expected relationship with canopy openness. The negative relationship may be due to improved growth of *Sphagnum* spp. in the less illuminated sites, which allows them to avoid desiccation and photoinhibition.

The cover of ericaceous species had only an indirect effect on forest floor depth, via *Sphagnum* spp. However, in Europe *Empetrum nigrum,* has been shown to have a strong direct impact on ecosystemic processes (Wardle et al., 2003, 1997) through the production of phenols that retard decomposition (DeLuca et al., 2002). In this study, while *Kalmia angustilofolia* and *Ledum groenlandicum* litter have been shown to produce phenols (Inderjit and Mallik, 2002, 1997), their effect on forest floor thickness after high severity fires was solely through their effect on the abundance of *Sphagnum* spp., and probably not a direct effect on decomposition rate. Ericaceous species and vascular plants in general, may stimulate *Sphagnum* spp. growth through a ‘‘scaffolding’’ effect, where the *Sphagnum* spp. use vascular plants to physically support fast vertical growth (Malmer et al., 2003). The high level of variability in forest floor depth within sites, particularly in the older sites (Fig. 1), indicates the importance of very local factors, such as small canopy openings, and *Sphagnum* spp. and ericaceous spp. cover.

4.3. Management implications

Ecosystem-based management requires an understanding of regional disturbance and stand dynamics in order to be successfully applied. The development of thick forest floors on the Clay Belt of Québec and Ontario is an excellent example. Because on the Clay Belt black spruce stands on fine-textured soils accumulate thick forest floors over time, which have a negative effect on tree growth (Heinselman, 1981; Glebov and Korzukhin, 1992), any management technique that wishes to emulate a stand replacing fire must also remove at least a part of the forest floor. The very thick forest floors, and low stand density of stands established after low severity fires illustrate potential consequences of failing to do so. Further research is required in order to determine which method is most efficient at removing forest floor and creating favourable sites for black spruce.

The factors affecting forest floor thickness determined in this study suggest several potential solutions for limiting the development of the forest floor within a stand, which should be further tested. The importance of *Sphagnum* spp. and ericaceous spp. in forest floor depth suggest that stands with these mostly shade intolerant species in the understory should be opened up only with caution, to prevent an acceleration of forest floor accumulation. Furthermore, to limit their establishment, stands should be re-established at high density to limit light. The influence of trembling aspen on forest floor thickness, and the more detailed analyses completed by Légaré et al. (in press) suggest that the inclusion of a moderate component of trembling aspen may limit the development of a thick forest floor. However, further research is required to determine optimal densities.

4.4. Conclusions

While within managed stands the accumulation of thick forest floor needs to be mitigated for continued sustainability of harvests, these stands are an important part of the natural forest mosaic. As such, they are important for conserving the diversity of a variety of taxonomic groups. Therefore, rather than suggesting that all these stands should be harvested, scarified, and planted, we suggest that fire be more accurately mimicked within the component of the landscape that is managed for timber.

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Appendix A

See Table A1.

Table A1
Description of high and low fire severity sites used in analyses

Severity	Site	TSF[a]	Forest floor thickness (cm)	Basal area[c]	PET basal area[c]	Open canopy	*Sphagnum* cover	Ericaceous cover
High	D2	56	19.9 ± 1.4	45.82 ± 0.022	0.00 ± 0.00	35.85 ± 0.87	9.5 ± 2.4	1.1 ± 0.58
	N23	88	16.6 ± 1.3	44.08 ± 0.031	0.00 ± 0.00	43.67 ± 2.48	9.7 ± 4.9	5.74 ± 3.79
	S1	90	19.7 ± 1.5	41.94 ± 0.057	0.0050 ± 0.0035	29.07 ± 2.0	21.8 ± 4.4	7.87 ± 1.73
	N12	99	20.9 ± 1.2	47.41 ± 0.039	0.0073 ± 0.0052	52.68 ± 1.71	7.4 ± 2.6	6.05 ± 2.55
	N18	130	33.6 ± 3.0	27.23 ± 0.042	0.00 ± 0.00	55.59 ± 2.73	15.4 ± 5.2	32.26 ± 5.42
	W1	130	29.9 ± 2.4	43.74 ± 0.057	0.0030 ± 0.0030	53.75 ± 1.38	11.0 ± 3.2	30.26 ± 4.31
	D1	187	31.0 ± 2.0	21.17 ± 0.017	0.0012 ± 0.0012	57.36 ± 3.27	23.7 ± 5.9	57.85 ± 4.74
	S74	220	55.2 ± 4.0	30.38 ± 3.73	0.00 ± 0.00	54.71 ± 2.43	35.0 ± 3.6	60.50 ± 5.04
	N50	224	50.4 ± 6.0	20.67 ± 0.020	0.00 ± 0.00	67.40 ± 2.74	68.5 ± 4.6	74.25 ± 3.27
	L22	272	51.4 ± 3.5	22.89 ± 0.032	0.00 ± 0.00	68.75 ± 2.97	55.0 ± 4.1	67.25 ± 4.22
	N16	290	74.9 ± 6.7	15.19 ± 0.021	0.00 ± 0.00	73.49 ± 4.03	67.3 ± 3.4	63.25 ± 4.16
	N6	290	60.9 ± 6.5	21.31 ± 0.028	0.00 ± 0.00	67.40 ± 2.74	62.7 ± 2.9	49.25 ± 5.22
	N20	357	90.0 ± 10.3	7.19 ± 0.017	0.00 ± 0.00	74.83 ± 3.29	62.0 ± 4.2	76.00 ± 1.84
Low	D3	56	39.9 ± 3.4	16.33 ± 0.027	0.00 ± 0.00	59.08 ± 3.07	31.4 ± 6.6	60.0 ± 4.14
	N3	97	50.7 ± 3.0	17.14 ± 0.020	0.00 ± 0.00	65.83 ± 2.85	56.3 ± 3.8	69.5 ± 3.68
	N5	173	49 ± 2.4	30.41 ± 0.057	0.00 ± 0.00	62.72 ± 2.60	67.5 ± 3.9	41.90 ± 5.00
	L9724	262	65.8 ± 5.5	20.14 ± 0.027	0.00 ± 0.00	69.11 ± 2.60	31.8 ± 3.3	71.75 ± 4.33
	H1	350	150 ± 0[b]	2.70 ± 0.0027	0.00 ± 0.00	78.32 ± 3.87	51.5 ± 3.3	79.25 ± 2.95

Values are means and standard errors.

[a] Time since fire.

[b] Estimation only, no mineral soil was reached.

[c] Value in m^2/ha.

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