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Effects of fire severity and initial tree composition on understorey vegetation dynamics in a boreal landscape inferred from chronosequence and paleoecological data

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Abstract

Question and Location: How does soil burn severity and early post-fire tree composition affect long-term understorey vegetation dynamics in the coniferous forests of eastern Canada?

Method: Vegetation dynamics were assessed using paleoecological methods and a chronosequence analysis of extant stands. The relation between environmental factors and succession was evaluated using ordination techniques on the chronosequence data. Understorey succession was studied by regression analysis on the chronosequence data and through within-site Markovian transition probabilities between successive 1-cm layers of plant macroremains from soil organic matter profiles.

Results: Initial tree composition (*Picea mariana* and *Pinus banksiana*) had little effect on understorey composition. Soil burn severity (measured as the thickness of the residual forest floor humus) significantly affected temporal changes in understorey species. Following fires of high severity, stands underwent a gradual paludification with a net increase in *Sphagnum* and ericaceous shrubs (*Ledum groenlandicum*), and a decrease in feathermosses. Paludification was accelerated after low severity fires, which led to the dominance of *Sphagnum* less than 200 years after fire, and of *L. groenlandicum* shortly after fire. *In situ* paleo-ecological work confirmed results obtained with the chronosequence analysis.

Conclusions: One vegetation gradient related to time after disturbance is insufficient to account for the full complexity of long-term changes in understorey composition following fire. Current forestry practices that protect the forest floor humus may induce a premature paludification.

Keywords: Chronosequence; Disturbance; Ericaceous shrub; Macrofossil; Paleo-ecology; Paludification; *Picea mariana*; *Pinus banksiana*; Organic matter; *Sphagnum*; Succession.

Abbreviations: AMS = Accelerated mass spectrometry; GCC = Global climate change; HS = High severity; LS = Low severity; TSF = Time since last fire.

Nomenclature: Marie-Victorin (1995) and Montgomery (1977) for vascular plants; Anderson et al. (1990) for bryophytes and Lévesque et al. (1988) for macrofossils.

Introduction

Although boreal forest understorey species represent a small fraction of the above-ground living biomass, they often make up a significant portion of stand net primary production and may even out produce overstorey tree species (Chapin 1983; O'Connell et al. 2003). The continuous ground cover of non-vascular species that characterizes boreal forests (Oechel & Van Cleve 1986) affects soil thermal regimes, nutrient availability and tree productivity (Heinselman 1963; Van Cleve & Viereck 1981). Ericaceous shrubs can influence ecosystem processes such as nutrient cycling and have a detrimental effect on tree growth (e.g. Nilsson et al. 1993; Inderjit & Mallik 1997). Given the importance of understorey species to the functioning of boreal ecosystems, it is important to understand how environmental gradients determine the distribution of these species within landscapes.

Even under similar abiotic conditions, multiple successional trajectories in overstorey tree composition and structure can co-occur within boreal forest landscapes (e.g. Payette et al. 2000; Lesieur et al. 2002; Lecomte et al. in press). This co-occurrence can be strongly linked to site specific historical fire regimes (Larocque et al. 2000; Johnstone & Chapin in press). Short fire intervals tend to favour tree species that reach sexual maturity quickly – e.g. *Pinus banksiana* in eastern North America – while longer fire cycles will tend to favour longer lived species or species that are able to regenerate in the absence of fire – e.g. *Picea mariana*. Long fire cycles that characterize eastern Canadian boreal landscapes (Foster 1985; Bergeron et al. 2004a) cause a high proportion of low severity fires that do not fully consume the thick forest floor that has accumulated during fire-free intervals (Foster 1985; Simon & Schwab in press). Fire severity affects tree regeneration and, hence, stand structural development (Foster 1985; Lecomte et al. in press). Global climate change (GCC) will undoubtedly affect fire regimes (Flannigan et al. 2001; Bergeron et al. 2004a) and in turn the frequency of overstorey successional trajectories and fire severity types. Hence, understanding how GCC may influence the distribution of understorey species necessitates the comprehension of how the abundance of these species varies along multiple overstorey successional series co-occurring within a landscape under similar topo-edaphic conditions.

To circumvent the problem of long time spans in studying boreal forest vegetation dynamics, the chronosequence approach has often been used to study changes in understorey composition (e.g. Taylor et al. 1987; Wang et al. 2003). The major drawback of this approach resides in the uncertainty that the selected stands have experienced the same history, perhaps due to differences in fire behaviour, pre-burn composition and/or initial understorey composition. The use of paleo-ecological methods to determine past vegetation and fire severity in individual stands forming the chronosequence addresses some of the shortcomings associated with time-series analyses. In boreal forests, under moist, cool and acidic conditions unfavourable to decomposition processes, plant remains are gradually incorporated in the organic soil layer as stands age. The stratigraphic analysis of partially or undecomposed plant detritus (macroremains) within forest floor profiles can reveal temporal changes in understorey composition since the last fire as well as the fire's severity (Foster 1985; Ohlson et al. 2001).

In this study, we investigated how the initial tree composition and the severity of the last fire influenced long-term changes in understorey species composition of coniferous boreal stands. Here, we refer to fire severity exclusively as the effects of fire on the accumulated soil organic matter (quantity of duff burned / quantity of duff unburned *sensu* Miyanishi & Johnson 2002) as opposed to the effects of fire on the canopy (% trees killed; *sensu* Greene et al. 2004). Temporal changes were analysed along three chronosequences of stands that showed contrasting fire history and initial post-fire tree composition: *Pinus*-dominated stands after high severity fires, *Picea*-dominated stands after high severity fires, and *Picea*-dominated stands after low severity fires. While temporal changes in understorey composition have been documented along boreal stand chronosequences (e.g. Foster 1985; Taylor et al. 1987; De Grandpré et al. 1993; Wang et al. 2003) few, if any, studies have compared changes in understorey vegetation composition along multiple overstorey successional series. Also, while the short-term influences of fire severity on understorey species composition have been studied (e.g. Schimmel & Granström 1996; Nguyen-Xuan et al. 2000; Rydgren et al. 2004), to our knowledge no study has compared long-term successional changes occurring after high and low severity fires. Temporal trends observed with time series analysis were compared to those observed with macrofossil analyses of forest floor profiles from all study sites.

Pinus-dominated stands transmit more light to the understorey (Messier et al. 1998; Légaré et al. 2001) and produce litter with higher N-content (Preston et al. 2000) than *Picea*-dominated stands; therefore, we hypothesize that the initial post-fire dominance of *Pinus* favours shade intolerant and nutrient demanding understorey species. As low severity fires favour species that were present in the preburn stand (Schimmel & Granström 1996; Nguyen-Xuan et al. 2000; Rydgren et al. 2004), we hypothesize that a low severity fire accelerates the rate of successional change in understorey composition compared to high severity fires.

Methods

Study area

The study area (49° - 51°20' N; 78°30' - 79° 50' W) is located in the Clay Belt of northeastern Ontario and northwestern Quebec, Canada and is within the *Picea mariana*-feathermoss bioclimatic domain (Robitaille & Saucier 1998). The Clay Belt is a physiographic unit composed mostly of clay deposits left by pro-glacial Lake Ojibway (Veillette 1994). Although a few rocky outcrops are present, the topography is generally flat. Mean annual temperature (1971-2000) at the closest weather station to the north (Matagami, 49°46' N, 77°49' W) and south (La Sarre, 48°46' N, 79°13' W) of the study area are –0.7°C and +0.7°C with mean annual precipitation of 906 mm and 890 mm, respectively (Anon. 2005). Most of the area is covered by structurally diverse coniferous forests dominated either by *Picea mariana* or *Pinus banksiana* (Lecomte & Bergeron 2005) with a forest floor dominated either by *Sphagnum* spp. or *Pleurozium schreberi* (Boudreault et al. 2002). Occasional deciduous stands are dispersed across the landscape. Although agricultural settlement south of the study area began in the middle of the 1930s, intensive logging of this area commenced in the late 1970s. Fire is the main disturbance that terminates and initiates secondary successions. Fire cycle length has increased from 101 years before 1850, to 398 years since 1920; with a mean stand age of 148 years at present (Bergeron et al. 2004b).

Field and laboratory analyses

In this study we sampled 48 stands which differed with respect to the severity of the last fire, the time since the last fire and the initial tree composition after fire, but had similar mineral soil texture and slope (App. 1). Initial tree composition was evaluated based on current composition of live and dead stems (including buried stems). Stand age (fire year) was determined by carefully dating cross-sections taken at the base of live and dead dominant trees. In stands where the oldest tree exceeded 200 years, and no fire scars or pioneer species (*Pinus banksiana*) were present, samples of carbonized plant remains found in soils were AMS (Accelerated mass spectrometry) radiocarbon dated. The severity of the last fire for each stand was qualified as high (HS) or low (LS) based on the mean thickness of the residual organic matter present in the stand (i.e. the soil organic matter that was not burned by the last fire). At each stand, understorey vegetation was assessed in $10 \times 1\text{-m}^2$ square plots. *In situ* temporal changes in understorey composition was evaluated by determining the abundance of plant macroremains found in forest floor humus monoliths taken at each stand (two to three monoliths per stand). For detailed methods please consult App. 2 and Lecomte et al. (in press).

Statistical analyses

Chronosequence data set

To evaluate the factors responsible for the variation in forest understorey plant communities, the mean abundance of each taxa in the chronosequence stands were used to compute a Canonical Correspondence Analysis (CCA) using the program CANOCO Version 4 (ter Braak & Šmilauer 1999). The continuous environmental variables (mineral soil clay content, slope index and time since fire (TSF)) and categorical variables (fire severity and initial stand composition) were loaded by forward selection. Additionally, we were interested in how initial stand conditions influenced vegetation dynamics so we included the two following interactions: TSF * fire severity and TSF * initial stand composition. Significance of each variable was computed using a Monte Carlo test ($\alpha = 0.05$). Only the 17 species or groups of species occurring in over 10% of the 1-m^2 plots (App. 3) were used for the CCA. Finally, to examine the relationship between understorey species and temporally varying stand characteristics, we entered *a posteriori* (passively) in the CCA the following stand variables: forest floor thickness and total stand basal area represented by large stems (DBH > 10 cm).

The quantitative effect of fire severity and initial composition on understorey composition was assessed in the chronosequence stands using the abundance of the three dominant terricolous bryophyte and lichen taxa: *Sphagnum* spp., feathermosses and *Cladina* spp., and the two most abundant shrub taxa: *Ledum groenlandicum* and *Vaccinium* spp. (*V. angustifolium* and *V. myrtilloides*) as response variables. Since the CCA showed that slope and soil texture were not significant in explaining understorey composition, we have not included them in the analyses. As the three chronosequences, based on initial composition and fire severity, spanned different time scales: *Pinus banksiana* HS: 45-229 years, *Picea mariana* LS: 38-169 years and *Picea mariana* HS: 50-2355 years, the data were analysed at two distinct time scales: medium term (< 250 years) and long term (> 250 years). The medium term scale permitted us to assess the effects of both fire severity and initial stand composition on understorey species composition. The long-term scale allowed us to evaluate how the understorey composition of *Picea mariana* stands established after HS fires evolved in the extended absence of fire.

Medium-term effects were assessed with a Linear Model design (PROC GLM; SAS Institute 2000) with a combination of a continuous predictor variable (TSF) and categorical predictor variables (initial stand composition and fire severity). When predictor variables or interaction were not significant ($p > 0.05$) they were removed from the models. The quantitative effects of the long-term absence of fire on understorey composition were assessed with linear regression following appropriate transformation of the independent variable (TSF).

Organic matter monoliths

The vegetation changes that occurred since the last fire were assessed using Markovian transition probabilities. Using only horizons that had been accumulated since the last fire, the probabilities were computed from observed changes in abundance of plant macroremains and dead wood from one organic matter horizon (1 cm thick) to the next. Only ground species, notably *Sphagnum* spp., the feathermosses *Pleurozium schreberi*, *Ptilium crista-castrensis* and *Hylocomium splendens*, *Polytrichum* spp., *Dicranum* spp. and lichens, were considered, as they represented the majority of plant remains identified within the monoliths. Transition probabilities were separately calculated for each chronosequence, and for three different time scales: stands < 100 years old, stands > 100 years old and stands of all ages. The 100 years cut off was used because stands colonizing LS fires remain open throughout succession while comparable stands established after HS fires rapidly close and then open their canopies after 100 years (Lecomte et al. in press).

Results

Chronosequence survey – Ordination trends

In the Canonical Corrspondence Analysis of the 48 stands the canonical axes 1 and 2 explained, respectively, 14% and 10% of the variance in species composition, while the environmental variables Fire severity, TSF and the interaction Fire severity*TSF, each explained 6% of the variation (Table 1). All other environmental variables and interactions did not significantly ($p > 0.05$) explain any more of the among-stand understorey composition variability.

The ordination diagram indicates that axis 1 is mainly linked to a paludification gradient, as reflected by the positive association of the environmental variables TSF and total organic matter thickness along with the hydrophilous species, *Sphagnum* spp., *Smilacina trifolia* and *Equisetum sylvaticum* (Fig. 1A). Axis 2 is negatively associated with fire severity and total basal area represented by large stems as well as with a cluster of species associated with shaded conditions (*Pleurozium schreberi*, *Dicranum* spp., *Ptilium crista-castrensis*, *Petasites palmatus*, *Cornus canadensis* and *Maianthemum canadense*). Axis 2 is also positively associated with species typical of xeric and/or high light environments such as the ericaceous shrubs (*Vaccinium* spp., *Kalmia angustifolia* and *Ledum groenlandicum*) and *Cladina* spp. The considerable length of the vectors representing the varying stand structural attributes (canopy closure and forest floor thickness) is a testimony of the strong relationship between these variables and understorey composition.

The successional vectors, which connect the mean ordination score for each stand age-class, suggest that the understorey composition of stands evolving after HS fires gradually shifted from an assemblage of species strongly associated with shaded conditions to one that is strongly associated with wet conditions (Fig. 1B). The large overlap between identical age-class ellipses of the two composition types evolving after HS fires indicates that the initial composition (*Pinus banksiana* vs *Picea mariana*) had little effect on understorey composition (Fig. 1B). The *Pinus banksiana* vector is shorter as we did not sample any old stands (> 250 years) that were post-fire dominated by *Pinus banksiana* (Fig. 1B). The successional vector of stands evolving after low severity (LS) fires indicates that these stands underwent a change in understorey composition from species associated with high light and xeric environments to species strongly associated with wet conditions (Fig. 1B). The lack of overlap between the < 100 yr old age-class ellipses of the two severity types suggests that fire severity greatly influenced understorey composition. However, the near perfect overlap of the 100-250 yr old age-class ellipse of the LS fire chronosequence and the oldest age-class ellipse of

Table 1. Statistics of the Canonical Correspondence Analysis with a forward selection of environmental variables using the chronosequence data set. %var = % variance explained.

Variable	% var	*F*	*p*
Fire severity	6	3.15	**0.02**
Fire severity * TSF[1]	6	3.50	**0.02**
TSF	6	3.45	**0.03**
Initial composition	3	1.83	0.06
Slope index	3	1.45	0.20
Mineral soil clay content	2	1.42	0.18
Initial composition * TSF	2	1.14	0.42

[1] Time since last fire; Bold: *p*-values are significant at the 0.05 level.

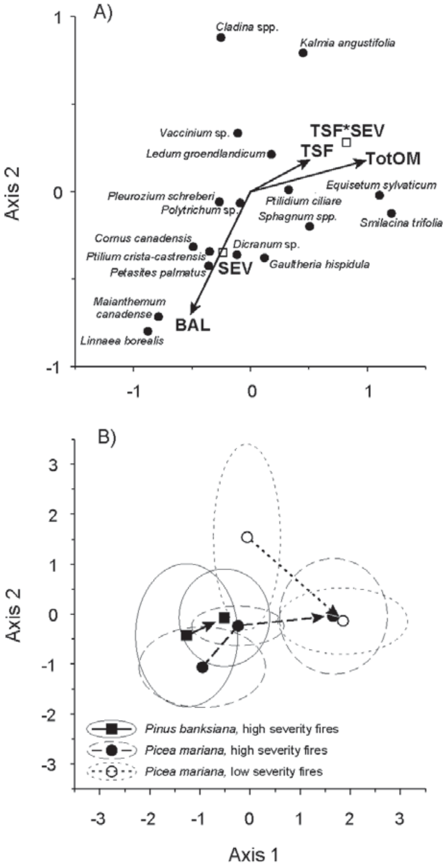

Fig. 1. Canonical Correspondence Analysis of understorey species composition using the chronosequence data set. **A.** Categorical variables indicated as points: species (●) and explanatory variables (□); continuous variables presented as vectors.. TSF = Time since last fire; SEV = Centroid of stands originating from high severity fires; BAL = Basal area of large stems (DBH > 10 cm) and TotOM = Total thickness of forest floor organic matter. The variables BAL and TotOM were loaded *a posteriori*. **B.** Successionnal vectors connecting the mean ordination score of each stand age-class (< 100, 100-200 and > 200 years), from the youngest to the oldest. SD = 1 confidence ellipses are shown.

the HS fire *Picea mariana* chronosequence suggests that (1) fire severity accelerated the rate of paludification in this landscape and that (2) the prolonged absence of fire induced a convergence in understorey composition regardless of the severity of the last fire.

Chronosequence survey – Quantitative trends in understorey composition

The initial composition did not significantly affect temporal changes in abundance of the main understorey species (Table 2). In contrast, fire severity significantly affected the evolution in the abundance of all taxa (Table 2, Fig. 2). After HS fires, while *Sphagnum* and ericaceous shrubs became more abundant, the abundance of feathermosses decreased, while few temporal changes were observed in the cover of *Cladina* spp. (Fig. 2). In contrast, LS fires appeared to accelerate the replacement of feathermosses by *Sphagnum* and initially favoured the presence of *Cladina* and *Vaccinium*, which eventually decreased in the absence of fire (Fig. 2). While fire severity did not affect the rate of change in the abundance of feathermosses and *L. groenlandicum* (no TSF * Severity interaction), the feathermosses were initially less abundant and *L. groenlandicum* more abundant after LS fires than after HS fires.

In the extended absence of fire (> 250 years), after HS fires, the trends observed during the first few centuries resumed with a continued increase in the cover of *L. groenlandicum* and a decrease in the abundance of the feathermosses (Fig. 3). Although *Sphagnum* abundance significantly increased in the absence of fire and was present in all the stands older than 250 years, there was large variability among the oldest stands. Although we observed a significant positive relationship between *Cladina* spp. cover and TSF, this was mostly due to the higher cover of this species in only the oldest stand. No significant trend in the cover of *Vaccinium* species was observed with a relatively constant low cover (< 10%).

Table 2. General linear model with initial composition, fire severity and time since fire as factors (N = 42) for the abundance of the five main understorey taxa using the medium term (< 250 years) chronosequence data set.

Variables	Source	F	p
Feathermosses	Initial composition (COMP)	-	N.S.
$R^2 = 0.23$	Fire severity (SEV)	9.03	**0.005**
	Time since fire (TSF)	4.97	**0.032**
	COMP * TSF	-	N.S.
	SEV * TSF	-	N.S.
	TSF * TSF	-	N.S.
Sphagnum spp.	Initial composition (COMP)	-	N.S.
$R^2 = 0.42$	Fire severity (SEV)	1.66	0.206
	Time since fire (TSF)	16.57	**0.0002**
	COMP * TSF	-	N.S.
	SEV * TSF	9.77	**0.003**
	TSF * TSF	-	N.S.
Cladina spp.	Initial composition (COMP)	-	N.S.
$R^2 = 0.24$	Fire severity (SEV)	9.21	**0.004**
	Time since fire (TSF)	5.90	**0.0199**
	COMP * TSF	-	N.S.
	SEV * TSF	6.36	**0.016**
	TSF * TSF	-	N.S.
L. groenlandicum	Initial composition (COMP)	-	N.S.
$R^2 = 0.34$	Fire severity (SEV)	11.84	**0.0014**
	Time since fire (TSF)	12.02	**0.0013**
	COMP * TSF	-	N.S.
	SEV * TSF	-	N.S.
	TSF * TSF	-	N.S.
Vaccinium spp.	Initial composition (COMP)	-	N.S.
$R^2 = 0.28$	Fire severity (SEV)	12.07	**0.0013**
	Time since fire (TSF)	1.24	0.2721
	COMP * TSF	-	N.S
	SEV * TSF	5.99	**0.0191**
	TSF * TSF	-	N.S.

Bold p-values are significant at the 0.05 level.

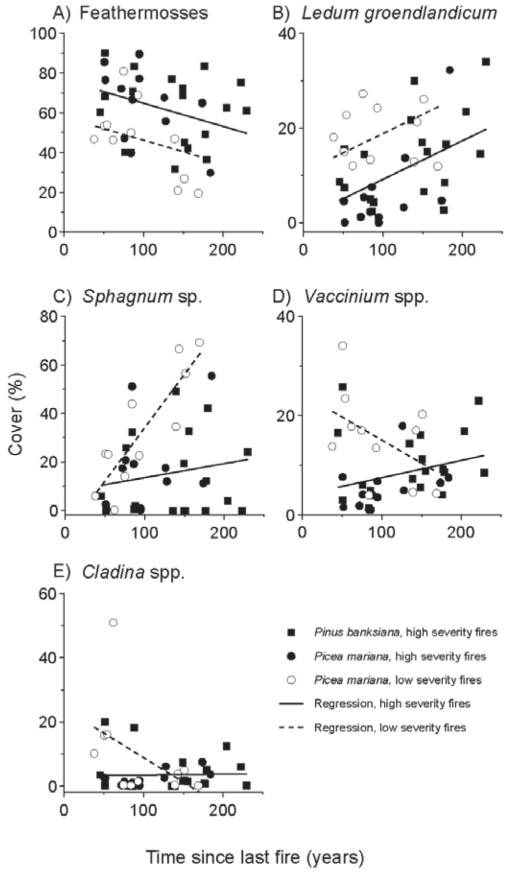

Fig. 2. Abundance of five main understorey taxa in relation to time since the last fire using the medium term (< 250 years) chronosequence data set. **A.** Feathermosses: *Pleurozium schreberi* and *Ptilium crista-castrensis*; **B.** *Sphagnum* spp.; **C.** *Cladina* spp.; **D.** *Ledum groenlandicum*; **E.** *Vaccinium* spp.: *V. angustifolium* and *V. myrtilloides*. The regression line for stands originating from high severity fires is common to both *Picea mariana* and *Pinus banksiana* because composition effect was not significant ($\alpha = 0.05$).

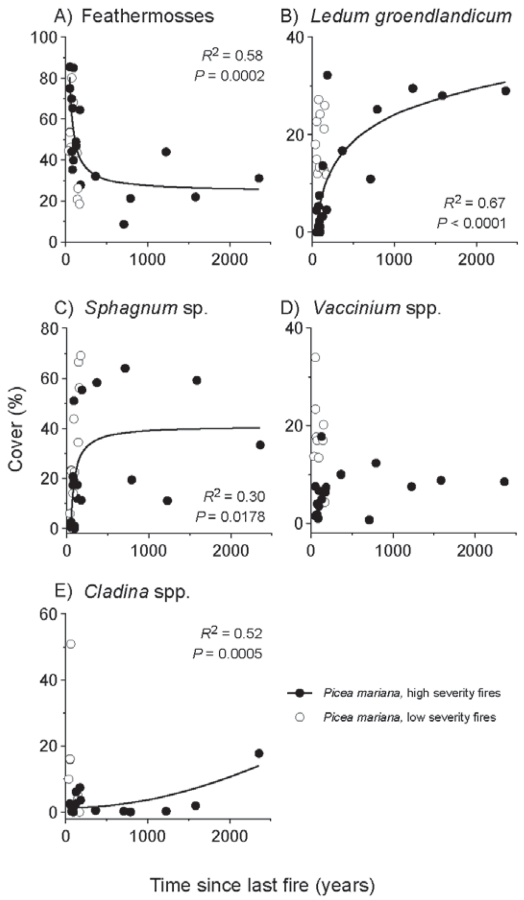

Fig. 3. Abundance of five main understorey taxa in *Picea mariana* stands evolving after high severity fires in the extended absence of fire using the long-term (> 250 years) chronosequence data set. **A.** Feathermosses – *Pleurozium schreberi* and *Ptilium crista-castrensis*; **B.** *Sphagnum* spp.; **C.** *Cladina* spp.; **D.** *Ledum groenlandicum*; **E.** *Vaccinium* spp. (*V. angustifolium* and *V. myrtilloides*). For comparison, taxa abundance is also shown for stands originating from low severity fires.

Notably, the abundance of the five main understorey taxa in stands evolving after LS fires resembled the cover values of these species in much older stands evolving after HS fires (Fig. 3).

Organic matter monoliths – In situ temporal changes in understorey composition

The soil monoliths showed organic matter accumulations since the last fire ranging from 2 cm to 56 cm (mean = 14.1 cm; SD = 9.5 cm). The transition matrices showed considerable differences between stand age classes and fire severity types (HS vs. LS in *P. mariana* stands), but few differences between overstorey tree composition (*Pinus banksiana* vs *Picea mariana* in HS fires) (App. 4, Fig. 4). In young HS stands (< 100 years), all ground species showed a high probability of being replaced by feathermosses while, in the prolonged absence of fire (stands > 100 years), species in general demonstrated a higher probability of being replaced by *Sphagnum* (Fig. 4). The transition probabilities are thus not stable in time after HS fires. In contrast, ground species in LS stands consistently showed high transition probabilities toward *Sphagnum* regardless of the age classification of stands (App. 4, Fig. 4). In all stands, *Sphagnum* always showed a strong positive feedback, i.e. a strong tendency for self-replacement. In general, *Polytrichum*, *Dicranum* and lichens showed a low probability of replacing other species and a high probability of being replaced by either *Sphagnum* spp. or feathermosses, reflecting their early successional status in this landscape.

Discussion

1. Initial tree composition

Our results contradict the hypothesis that overstorey composition (*Pinus* vs *Picea*) affects understorey composition (Légaré et al. 2001; Yu et al. 2002). In the eastern Canadian boreal forest, shortly after the first post-fire century, *Picea mariana* replaces *Pinus banksiana* (Lesieur et al. 2002; Lecomte & Bergeron 2005). Viereck (1983) demonstrated that in boreal coniferous stands, the main factors influencing the forest floor environment were changes in canopy closure and the accumulating forest floor with time. In the study area, which is prone to paludification, initial overstorey composition does not influence the evolution of stand canopy closure or thickness of the forest floor after HS fires (Lecomte et al. in press). While nitrogen concentrations in *Pinus* litter have been found to be higher than in *Picea* litter (Preston et al. 2000), no significant difference in their decay rates have been observed over a six year period (Trofymov et al. 2002). The short duration of *P. banksiana*'s domination and the minimal effect of its dominance on canopy closure, forest floor thickness or potential litter decomposition are probably the main reasons an initial *P. banksiana* dominance had no significant effect on understorey composition.

2. Temporal changes after high severity fires

After HS fires, the most important successional change in understorey composition is the shift in dominance from feathermosses in young post-fire stands to *Sphagnum* spp., concurrent with a gradual increase in organic matter thickness and opening of the canopy. After HS fires, high stem density and rapid growth leads to the rapid closure of the canopy (Taylor et al. 1987; Lecomte et al. in press).

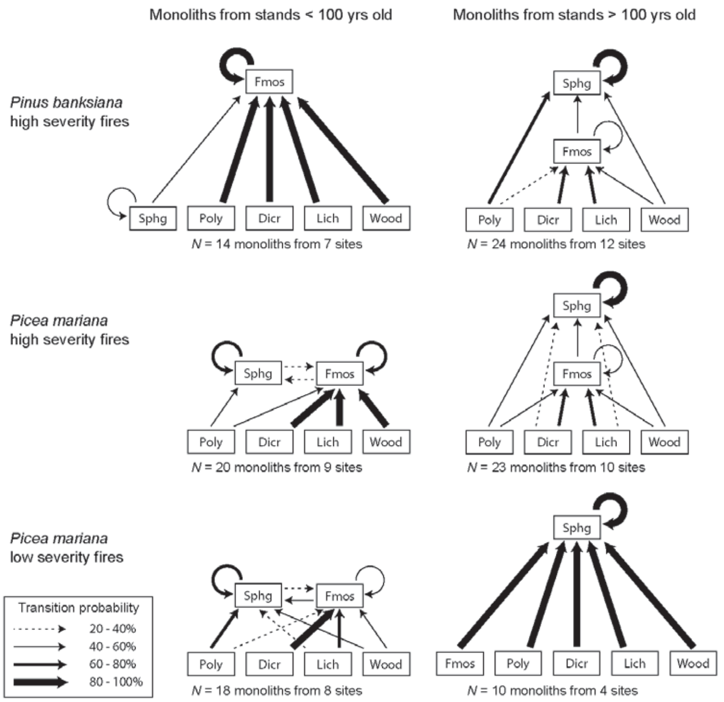

Fig. 4. Successional pathways of ground species (boxes) as deduced from transition probabilities (arrows) in plant macrofossils found in soil organic matter profiles. For each graph, bottom row shows species that never replaced another one, and top row shows species that were never replaced by another one. Middle row shows species that both replaced and were replaced. For clarity, only probabilities > 20% are shown. Sphg = *Sphagnum* spp.; Fmos = Feathermosses – *Pleurozium schreberi*, *Hylocomium splendens* and *Ptilium crista-castrensis*; Poly = *Polytrichum* spp.; Dicr = *Dicranum* spp.; Lich = Lichens; Wood = Dead wood.

However, as stands reach 100 years, the canopy gradually opens (Lecomte et al. in press) in response to secondary disturbances (insect, pathogens, windthrow) and senescence. In the extended absence of fire, the continual thickening of the forest floor lowers tree productivity (Heinselman 1963), which inhibits a ‘reclosure’ of the canopy after the post-fire tree cohort dies (Boudreault et al. 2002; Lecomte et al. In press). The opening of the canopy greatly modifies the light/moisture environment of the understorey, and consequently the abundance of bryophyte and vascular understorey species. Feathermoss ground cover competing with *Sphagnum* spp. is positively associated with overstorey canopy closure (Bisbee et al. 2001), a relationship that is probably caused by the different mechanisms by which these species can acquire moisture. While dew formation and precipitation are important sources of moisture for feathermosses, *Sphagnum* spp. can wick up water through the forest floor from the water table (Busby & Whitfield 1978). A gradual thickening of the forest floor causes the water table to rise above the forest floor-mineral soil interface, which makes water more accessible to *Sphagnum* spp. (Fenton et al. accepted manuscript). Our results suggest that the replacement of feathermosses by *Sphagnum* spp. as succession proceeds past the first century, reflects the differential response of species to the temporally varying closure of the canopy and thickness of the forest floor. These results are consistent with the ecophysiological requirements of these species and previous reports in the boreal forest (Taylor et al. 1987; Groot & Horton 1994; Boudreault et al. 2002).

The increase in understorey shrub cover probably reflects the response of these shade intolerant species to the gradual opening of the canopy. However, the greater increase in the cover of the evergreen shrub *L. groenlandicum* as opposed to the deciduous shrubs (*Vaccinium* spp.) may reflect the effects of the temporally varying availability of nutrients on these species. Deciduous shrubs frequently occur on more fertile sites than evergreen shrubs due to their greater annual nutrient demand (Chapin 1980). As stands mature and forest floors thicken, soil temperatures decrease, which slows down decomposition rates and reduces nutrient availability (Viereck 1983). We postulate that the lower availability of nutrients as stands mature gives a competitive advantage to evergreen, nutrient conserving shrub species over deciduous, nutrient demanding species (Groot & Horton 1994; Wardle et al. 1997).

Our results suggest that long fire-free intervals, by influencing ecosystem characteristics such as light transmittance and forest floor depth, greatly affect understorey composition after HS fires. In the absence of fire, the opening of the canopy and the gradual thickening of the forest floor, coupled with an increase in the cover of *Sphagnum* spp. and evergreen shrubs demonstrate the prevalence of paludification in the Clay Belt (Heinselman 1981; Taylor et al. 1987; Boudreault et al. 2002).

3. Temporal changes after low severity fires

The thick residual organic matter left after the passage of an LS (low severity) fire negatively influences post-fire tree regeneration (Greene et al. 2004), subsequent nutrient availability (Van Cleve & Dyrness 1983) and tree growth (Zasada et al. 1987). Stand development after LS fires is characterized by the maintenance of an open canopy and a consistently thicker forest floor compared to HS fires (Lecomte et al. in press). The maintenance of an open canopy during stand development after LS fires induces a rapid invasion of the site by species tolerant of high light/xeric conditions, such as the terricolous lichens *Cladina* spp. Then, as the forest floor thickens the non-vascular plant community rapidly becomes dominated by *Sphagnum* spp.

The early dominance of the understorey of stands established after LS fires by *Cladina* spp. is consistent with observations from Labrador in eastern Canada which documented the evolution of the understorey composition in *P. mariana* dominated stands after LS fires (Foster 1985; Simon & Schwab in press). However, while these authors reported a gradual replacement of the *Cladina* lichens by feathermosses, we observed a rapid invasion of the stands by *Sphagnum* spp. These differing understorey trajectories may be due to the fact that the Labrador stands were established on coarse textured morainic deposits, unlike the fine textured glaciolacustrine deposits on the Clay Belt. The lower water-holding capacity of the coarse textured deposits may have hampered the accumulation of forest floor organic matter and favoured tree growth, canopy closure and hence the feathermosses over *Sphagnum*. Furthermore, the authors of the Labrador studies reported a gradual closure of the canopy late during the first century after fire, which was to some degree accomplished by the establishment of *Abies balsamea*. However, this fire intolerant species is scarce in the Clay Belt, probably because of the fire regime that is characterized by large fires (Bergeron et al. 2004b). Large fires tend to leave a lower quantity of green trees inside the fire perimeter, which greatly reduces the post-fire establishment of *A. balsamea*.

The deeply buried reproductive organs of the ericaceous shrub species (Flinn & Wein 1977) give them an advantage after the passage of an LS fire (Nguyen-Xuan et al. 2000). Far more individuals of these species were found in LS fires, suggesting that LS fires enhanced their dominance in the immediate post-fire vegetation by not fully consuming their deeply buried reproductive organs. Our results suggest that LS fires significantly affected long-term understorey composition development, with an apparent acceleration of the paludification process. This suggests that even under similar abiotic conditions, one vegetation gradient related to time after disturbance is insufficient to account for the full complexity of long-term vegetation processes following fire in the coniferous boreal forest and that fire severity should be considered.

4. Paleovegetation and chronosequence results

The stratigraphy of plant remains within soil organic matter profiles confirmed that the mosaic of successional communities observed across this landscape provides analogues for the temporal sequence at individual stands if the severity of the last fire is accounted for. Both chronosequence and paleo-ecological data sets document the replacement of feathermosses by *Sphagnum* spp. in the absence of fire. Both indicate few differences in understorey dynamics between the *Pinus banksiana* and *Picea mariana* dominated stands and a premature replacement of feathermosses by *Sphagnum* spp. after LS fires. The stratigraphic history of fire severity and of vegetation change since the last fire at each stand strengthens the conclusions that are drawn from the detailed analysis of the chronosequence stands.

5. Landscape variability in understorey vegetation, current forestry practices and GCC

Among-stand variability in understorey composition within this boreal landscape was related to temporal changes in stand structural attributes occurring in the absence of fire and by initial stand conditions. However, differing initial coniferous tree compositions did not significantly affect understorey composition. LS fires, by favouring late successional species and hampering canopy closure, induced a premature paludification of coniferous boreal stands on fine textured deposits. Hence, by highlighting the important effects of fire interval and severity on understorey composition, we have demonstrated that changes in disturbance regime may have important effects on the distribution of understorey species within the Clay Belt of eastern Canada. Furthermore, our results indicate that the use of paleo-ecological methods along a chronosequence of stands represents a multiproxy approach which provides a novel and robust way of studying vegetation dynamics occurring over several centuries.

In most eastern Canadian boreal forest landscapes, fire frequency has been decreasing since the end of the Little Ice Age (ca. 1850) (Bergeron et al. 2004b). Moreover, simulations using the Canadian General Atmospheric Circulation Model suggest that the fire cycle may continue to increase for the decades to come (Flannigan et al. 2001; Bergeron et al. 2004a). As GCC may induce a longer fire cycle, this landscape may also be more susceptible to the passage of LS fires that only partially consume the thick forest floor that has accumulated during the long fire-free periods (Foster 1985). The combined effects of lower fire frequency and higher occurrence of LS fires may result, at the landscape scale, in fewer dense coniferous stands with an understorey dominated by feathermosses, and a concomitant increase in the frequency of open coniferous stands with an understorey dominated by *Sphagnum* species. If feathermoss dominated stands are a greater source of carbon than *Sphagnum* dominated stands (O'Connell et al. 2003), GCC may shift eastern Canadian boreal landscapes from a source to a sink of carbon in the future. This trend may be accentuated by current logging practices that protect the thick forest floor present in cutblocks, resembling the effects of LS fires. Studies should be undertaken to establish if similar stand types (based on overstorey and understorey composition) but differing with respect to fire severity and/or interval show similar or different net C-fluxes with respect to the atmosphere.

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App. 1. Characteristics of the chronosequence survey stands.

Site	Initial composition[1]	*P. banksiana* basal area[2] ($m^{-2}.ha^{-1}$)	Fire severity[3]	Residual OM[4] (cm)	Stand age (years)						
					Oldest tree[5]	Calibrated ^{14}C age (charcoal)[6]	Calibrated ^{14}C age (humus)[7]	Mineral soil			Slope Index[8]
								%sand	%silt	%clay	
30	*Pinus*	29.6	High	1.2	45	-	-	1.5	22.0	76.5	1.0
54	*Pinus*	48.2	High	1.0	51	-	-	0.0	12.7	87.3	1.9
61	*Pinus*	32.1	High	1.5	51	-	-	6.5	21.5	72.0	5.1
36	*Pinus*	39.4	High	1.6	76	-	-	1.0	23.6	75.4	0.6
38	*Pinus*	22.3	High	1.6	84	-	-	0.0	9.0	91.0	0.7
23	*Pinus*	32.0	High	1.3	86	-	-	3.5	26.9	69.7	1.4
57	*Pinus*	34.3	High	1.2	88	-	-	13.0	45.5	41.5	1.2
29	*Pinus*	40.0	High	1.2	135	-	-	19.9	30.8	49.3	1.2
69	*Pinus*	34.0	High	1.1	139	-	-	2.0	34.3	63.7	1.9
66	*Pinus*	28.5	High	1.7	149	-	-	12.5	25.0	62.5	8.7
73	*Pinus*	50.9	High	1.3	149	-	-	26.0	25.0	49.0	1.5
40	*Pinus*	35.6	High	1.1	151	-	-	25.5	27.5	47.0	2.4
49	*Pinus*	28.4	High	1.2	155	-	-	14.0	63.0	23.0	2.1
94	*Pinus*	44.7	High	1.0	176	-	-	6.0	24.5	69.5	5.1
83	*Pinus*	40.0	High	1.0	177	-	-	4.0	20.0	76.0	1.0
79	*Pinus*	20.2	High	1.1	179	-	-	2.4	29.0	68.6	0.0
65	*Pinus*	32.9	High	2.1	204	-	-	14.0	32.5	53.5	0.8
64	*Pinus*	25.8	High	1.9	222	-	-	0.0	38.4	61.6	3.9
67	*Pinus*	10.6	High	1.0	229	-	-	0.0	28.6	71.4	1.4
62	*Picea*	0.0	High	1.4	51	-	-	2.0	23.4	74.6	10.5
4	*Picea*	0.0	High	2.5	52	-	-	0.0	38.1	61.9	2.5
59	*Picea*	7.9	High	2.3	72	-	-	13.0	22.5	64.5	1.7
15	*Picea*	2.4	High	1.5	76	-	-	10.3	27.9	61.8	-4.6
2	*Picea*	0.0	High	1.9	84	-	-	0.0	21.0	79.0	0.6
56	*Picea*	0.0	High	1.3	86	-	-	13.5	28.5	58.0	0.8
12	*Picea*	0.0	High	1.1	95	-	-	0.0	20.9	79.1	2.1
55	*Picea*	0.1	High	2.5	95	-	-	14.5	30.0	55.5	0.9
18	*Picea*	0.0	High	2.0	126	-	-	15.0	18.0	67.0	1.8
75	*Picea*	0.0	High	2.0	128	-	-	3.4	24.5	72.1	-1.3
8	*Picea*	0.0	High	1.4	174	-	-	9.0	25.5	65.5	1.4
95	*Picea*	0.0	High	1.3	184	-	-	3.0	26.0	71.0	1.7
9	*Picea*	0.0	High	1.5	215	1225	-	11.5	23.5	65.0	1.6
7	*Picea*	0.0	High	1.7	217	790	-	7.5	27.0	65.5	1.1
50	*Picea*	0.0	High	2.0	222	365	-	19.0	27.0	54.0	1.3
6	*Picea*	0.0	High	3.2	280	710	555	1.0	22.7	76.4	0.4
16	*Picea*	0.0	High	2.7	286	1585	705	10.0	18.0	72.0	0.5
20	*Picea*	0.0	High	3.2	353	2355	-	5.9	22.8	71.3	1.9
11	*Picea*	0.0	Low	12.0	38	-	-	21.0	29.5	49.5	1.1
74	*Picea*	0.0	Low	13.0	51	-	-	6.0	26.5	67.5	1.3
53	*Picea*	0.0	Low	7.3	54	-	-	20.0	31.0	49.0	0.6
58	*Picea*	0.0	Low	5.8	62	-	-	23.0	30.5	46.5	2.1
78	*Picea*	0.0	Low	17.9	75	-	-	17.0	28.0	55.0	0.6
3	*Picea*	0.0	Low	16.2	93	-	-	1.9	16.0	82.0	0.0
60	*Picea*	0.0	Low	6.7	97	-	-	9.0	15.0	76.0	1.2
68	*Picea*	1.6	Low	4.6	139	-	-	1.0	22.7	76.4	0.8
63	*Picea*	0.0	Low	7.9	143	-	-	2.0	18.5	79.5	0.8
17	*Picea*	0.0	Low	17.3	151	-	-	17.5	33.0	49.5	0.8
5	*Picea*	0.0	Low	8.4	169	-	-	13.9	47.6	38.5	0.3

[1] Initial stand composition determined from the composition of dead and live trees (see App. 2) *Pinus* = *Pinus banksiana*, *Picea* = *Picea mariana*..

[2] Basal area of live and dead *P. banksiana* stems > 2 m in height.

[3] Fire severity determined from the thickness of the residual organic matter (see App. 2).

[4] Thickness of the residual organic matter, *i.e.*, the organic matter that was not burned by the last fire, located between the mineral horizon and the uppermost charcoal layer.

[5] Stand age determined from tree-ring analysis. Stands where the postfire cohort of trees was not found were given a minimum age and were radiocarbon dated.

[6] Radiocarbon dates obtained for carbonised plant remains (see App. 2).

[7] Radiocarbon dates obtained for humus accumulated just above uppermost charcoal layer (from Cyr, D., Bergeron, Y., Gauthier, S. & Larouche, A.C. 2005. Are the old-growth forests of the Clay Belt part of a fire-regulated mosaic? *Can. J. For. Res.* 35: 65-73).

[8] Slope Index integrates slope incline and landform shape, and can assume positive (mounds or regular slopes) and negative values (depressions) (see App. 2).

App. 2. Detailed methodology used in this study.

Chronosequence dataset

Stand selection and vegetation sampling

Using a stand initiation map developed for the northern part of the Clay Belt (Bergeron et al. 2004), we visited all the burned areas located < 2 km from a road during the summers of 2000-2002. We sampled 43 distinct fires. In each fire, we visually estimated the density and composition of the postfire tree composition based on living and/or deadwood trees. If within a burned area different postfire densities and tree compositions were observed, several stands were sampled. Each stand was on fine-textured mineral deposits, on a slight incline and free of any sign of anthropogenic disturbance. Within each burned area, at least one stand (10m × 10 m quadrat) was selected for detailed dendroecological analysis. In each stand, the diameter at breast height (dbh) of all live and dead stems > 2 m in height were measured. Dead trees buried under the organic matter were exhumed and measured. According to the basal area of live and dead trees, 19 of the 48 sampled stands were dominated by *Pinus banksiana* after fire (App. 1). For the remaining 29 stands, no significant traces of any other tree species apart from *Picea mariana* were apparent so these stands were all classified as being dominated by *Picea mariana* after fire.

At each stand, understory vegetation was described in ten 1-m^2 square plots located every 2 m along two randomly chosen 10-m transects. The cover of each species was estimated as a vertical projection of its above-ground live biomass on the forest floor.

Soil texture and topography

Although the mineral soil textures were hand-checked *in situ*, two mineral soil samples were taken at the centre of each stand, one at the surface and another at a depth of 1 m. Soil texture was then determined with the Bouyoucos hydrometer method (McKeague 1976). The mineral soil micro-topography, which may be masked by peat accumulation, was assessed with a theodolite in each stand along four 50-m transects each starting at the centre of the stand and passing through one of the corners. Significance of the slopes were assessed with simple linear regressions and non-significant slopes ($P > 0.05$) were given a value of zero. If the slopes of transects going in opposite directions were of opposite signs, or one or both of the slopes was null, we calculated the slope of the two transects combined (i.e., one transect of 100 m). If the slopes were of the same sign, we summed these slopes to obtain a negative slope value (depression) or positive value (mound or incline) for the 100 m transect. The Slope Index used in this study is the mean of the slopes of the two 10-m transects.

Stand age determination

Stand age (fire year) was obtained by carefully dating cross-sections taken at the base of live or dead dominant trees. Cross-sections were finely sanded and crossdated using a frost-ring chronology (M. Simard unpubl.), under a dissecting microscope at 40× magnification. Frost rings show one or several rows of distorted cells caused by growing season frosts (Bailey 1925; Glerum & Farrar 1966), and provide robust pointer years for crossdating. Crossdating was verified using the program COFECHA (Holmes 1983). In stands where the oldest tree exceeded 200 years, and no fire scars or pioneer species (*Pinus banksiana*) were present, samples of carbonised plant remains found in the uppermost charcoal layer within the humus profile were sent to IsoTrace Laboratories (Toronto) for AMS (Accelerator Mass Spectrometry) radiocarbon dating. To minimise the effect of the age of the carbonised plant remain on the determination of stand age we have exclusively dated short-lived material (needles, cone scales and twigs). The radiocarbon years were calibrated in calendar years using INTCAL98 (Stuiver et al. 1998) and are shown in App. 1, along with additional radiocarbon datings from a parallel study (Cyr et al. 2005) undertaken in two of the very old stands (> 250 years). However, Cyr et al. (2005) dated the organic matter located just above the uppermost charcoal layer in the soil, which may account for their younger dates as compared to our radiocarbon dates from carbonised material. In both cases the radiocarbon dates of humus predate the age of the oldest tree present so we have used the dates obtained from carbonised plant remains.

Organic matter monoliths

To determine if the mosaic of successional communities observed across the landscape provided analogues for the temporal sequence at individual stands, in all 48 chronosequence stands, two to four, 10 cm by 10 cm monoliths of the organic layer were cut down to the mineral soil with a Wardenaar sampler (Wardenaar 1987). The monoliths were frozen and then sliced into 1-cm sections. Subsamples of 50 cm^3 were defloculated in a 2% NaOH solution for 24 h at 60°C before a gentle manual water spray was used to sieve the samples successively through 2 mm, 1 mm and 0.25 mm mesh. Samples were then bleached in a 10-20% HCl solution and examined microscopically at 40 × magnification for identification of macroremains. The mineral soil / organic matter interface of each monolith was established where the mineral soil represented less than 25% of the sample. Individual plant remains were identified by type (cone scales, leaf fragments, seeds, etc.) and to species, genus or family depending on extent of decomposition. With respect to all macroremains present, the relative abundance of each plant remain type was then quantified (0-12.5%, 12.5-25%, 25-50%, 50-75%, 75-100%).

Fire severity

Charcoal fragments were extracted from each monolith slice, and then dried and weighed. The thickness of the postfire residual organic matter (i.e., the organic matter not consumed by the last fire) was established as the number of 1-cm layers above the mineral soil and under the last charcoal layer deposited.

In the younger black spruce stands (< 200 yrs), 2.25-m long trenches were dug about 20 cm into the mineral soil. At every 15 cm along the trench, we located the charcoal layer closest to the surface and noted its position above the mineral soil (i.e., the residual organic matter thickness). Additionally, at each *P. banksiana* stand, ten and, at each *P. mariana* stand, fifteen 25 cm × 25 cm pits were dug into the mineral soil every 2 m along two or three 10-m transects. For each pit we noted the same measurements as for the trenches.

The severity of the last fire for each stand was qualified as high (HS) or low (LS) based on the average thickness of the residual organic matter obtained from the monoliths and from the pits and trenches. Ideally, soil burn severity is quantified as the amount of organic matter consumed (*sensu* Miyanishi & Johnson 2002). Nonetheless, as it is impossible to know how much organic matter was present in the pre-fire stand, we have chosen to qualify fire severity as the amount of organic matter not consumed by the fire (*sensu* Nguyen-Xuan et al. 2000). A study of seven burns in the boreal forest has demonstrated that coniferous postfire seed germination was significantly impacted when residual organic matter approached 5 cm (Greene 2004). We used this ecologically significant threshold (5 cm) to classify soil burn severity. Among the stands sampled, 11 of the 29 *P. mariana* stands were established after the passage of a LS fire (App. 1).

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App. 3. Frequency and mean cover of the 17 taxa present in over 10% of the 1-m^2 plots for each chronosequence.

Understory species	Frequency (% of plots)				Mean cover (%)			
	Chronosequence				Chronosequence			
	Pinus banksiana HS fire	*Picea mariana* HS fire	*Picea mariana* LS fire	All stands	*Pinus banksiana* HS fire	*Picea mariana* HS fire	*Picea mariana* LS fire	All stands
Pleurozium schreberi	93.7	91.6	92.7	92.7	54.8	46.4	45.3	49.4
Sphagnum spp.	29.5	60.0	71.8	50.8	13.2	26.5	32.6	22.7
Ledum groenlandicum	71.6	66.8	87.3	73.3	14	11.4	18.6	14.0
Vaccinium spp.	88.9	64.2	90.0	79.6	10.2	5.9	15.4	9.7
Cladina spp.	41.1	35.3	60.9	43.3	4.2	2.6	9.4	4.8
Ptilium crista-castrensis	37.4	33.2	19.1	31.6	6.3	5.2	1.4	4.8
Gaultheria hispidula	46.8	70.5	55.5	58.0	3.3	6.2	1.9	4.1
Kalmia angustifolia	13.2	28.9	56.4	29.0	1.4	2.1	7.5	3.1
Cornus canadensis	63.2	30.0	24.5	41.6	3.4	1.0	0.6	1.9
Equisetum sylvaticum	12.6	27.4	33.6	23.1	0.3	1.9	3.9	1.7
Ptilidium ciliare	29.5	26.3	12.7	24.5	1.5	1.8	0.3	1.4
Dicranum spp.	47.4	49.5	30.9	44.5	1.3	1.8	0.6	1.3
Polytrichum spp.	16.3	21.6	31.8	21.8	0.8	0.6	1.0	0.8
Petasites palmatus	26.8	6.3	6.4	14.3	1.2	0.4	0.2	0.7
Linnaea borealis	23.7	6.8	0	11.8	1.3	0.3	0	0.6
Smilacina trifolia	2.6	16.8	13.6	10.6	0	0.7	0.6	0.4
Maianthemum canadense	24.2	3.2	0	10.6	0.5	0.1	0	0.3

App. 4. Transition probabilities of ground species and dead wood from one (1-cm thick) soil horizon (below in profile, or previous in time) to the next (above in profile, or following in time) using macrofossil data from soil organic matter profiles. Data is shown for the three chronosequences under study: PBA HS = *Pinus banksiana* after high severity fire, PMA HS = *Picea mariana* after high severity fires, and PMA LS = *Picea mariana* after low severity fires; and per age classification.

Species or dead wood (below in monolith)		Replacing species (above in monolith)															
		Monoliths from all stands						Monoliths from stands < 100 yrs						Monoliths from stands > 100 yrs			
PBA - HS	*N* = 38 monoliths from 19 stands						*N* = 14 monoliths from 7 stands						*N* = 24 monoliths from 12 stands				
		Sphg	Fmos	Poly	Dicr	Lich		Sphg	Fmos	Poly	Dicr	Lich		Sphg	Fmos	Poly	Dicr	Lich
	Sphg[b] (35%)[a]	0.89	0.09	0.01	0	0.01	Sphg (2%)	0.52	0.43	0	0	0.05	Sphg (43%)	0.92	0.07	0.01	0	0.01
	Fmos[c] (22%)	0.29	0.66	0	0.02	0.03	Fmos (40%)	0.01	0.93	0	0	0.06	Fmos (17%)	0.45	0.5	0.01	0.03	0.02
	Poly[d] (1%)	0.52	0.44	0.02	0	0.02	Poly (1%)	0	0.98	0.01	0	0.02	Poly (1%)	0.65	0.31	0.02	0	0.02
	Dicr[e] (< 1%)	0.06	0.86	0.01	0.07	0.01	Dicr (< 1%)	0	0.98	0	0.01	0.01	Dicr (< 1%)	0.09	0.78	0.02	0.1	0
	Lich[f] (< 1%)	0.09	0.77	0	0.04	0.1	Lich (1%)	0	0.81	0	0	0.18	Lich (< 1%)	0.16	0.73	0	0.06	0.04
	Wood[g] (3%)	0.3	0.66	0	0.01	0.03	Wood (1%)	0.08	0.91	0	0	0	Wood (3%)	0.4	0.54	0	0.02	0.04
PMA - HS	*N* = 43 monoliths from 19 stands						*N* = 20 monoliths from 9 stands						*N* = 23 monoliths from 10 stands				
		Sphg	Fmos	Poly	Dicr	Lich		Sphg	Fmos	Poly	Dicr	Lich		Sphg	Fmos	Poly	Dicr	Lich
	Sphg (38%)	0.79	0.21	0	0	0	Sphg (18%)	0.62	0.36	0.01	0	0	Sphg (47%)	0.88	0.12	0	0	0
	Fmos (11%)	0.38	0.59	0	0.02	0.01	Fmos (20%)	0.2	0.77	0	0.03	0	Fmos (7%)	0.54	0.44	0	0.01	0.01
	Poly (< 1%)	0.48	0.46	0.05	0.01	0	Poly (< 1%)	0.47	0.47	0.05	0	0	Poly (< 1%)	0.54	0.41	0.02	0.04	0
	Dicr (< 1%)	0.18	0.73	0	0.08	0	Dicr (< 1%)	0.01	0.86	0	0.13	0	Dicr (< 1%)	0.33	0.63	0.01	0.03	0
	Lich (< 1%)	0.18	0.76	0	0.01	0.05	Lich (< 1%)	0	0.98	0	0	0.02	Lich (< 1%)	0.22	0.71	0	0.01	0.06
	Wood (7%)	0.37	0.61	0	0.01	0.01	Wood (7%)	0.19	0.81	0	0	0	Wood (7%)	0.51	0.45	0	0.01	0.02
PMA -LS	*N* = 28 monoliths from 12 stands						*N* = 18 monoliths from 8 stands						*N* = 10 monoliths from 4 standss				
		Sphg	Fmos	Poly	Dicr	Lich		Sphg	Fmos	Poly	Dicr	Lich		Sphg	Fmos	Poly	Dicr	Lich
	Sphg (42%)	0.79	0.18	0.03	0	0	Sphg (37%)	0.69	0.26	0.04	0	0	Sphg (51%)	0.95	0.04	0.01	0	0
	Fmos (7%)	0.53	0.39	0.03	0	0.05	Fmos (9%)	0.4	0.5	0.03	0	0.07	Fmos (5%)	0.8	0.19	0.02	0	0
	Poly (< 1%)	0.75	0.19	0.06	0	0.01	Poly (< 1%)	0.71	0.22	0.06	0	0.01	Poly (< 1%)	0.84	0.11	0.05	0	0
	Dicr (< 1%)	0.49	0.49	0	0.01	0	Dicr (< 1%)	0.01	0.97	0	0.02	0	Dicr (< 1%)	0.98	0.02	0	0	0
	Lich (< 1%)	0.35	0.55	0	0	0.1	Lich (< 1%)	0.25	0.63	0	0	0.11	Lich (< 1%)	0.96	0.02	0	0	0.01
	Wood (5%)	0.63	0.31	0.01	0	0.06	Wood (7%)	0.5	0.4	0	0	0.09	Wood (2%)	0.85	0.14	0.01	0	0

[a] Mean abundance in macrofossil samples

[b] Sphg = *Sphagnum* spp.

[c] Fmos = Feathermosses (*Pleurozium schreberi*, *Hylocomium splendens*, and *Ptilium crista-castrensis*).

[d] Poly = *Polytrichum* spp.

[e] Dicr = *Dicranum* spp.

[f] Lich = Lichens

[g] Wood = Dead wood