



# Salvage logging affects early post-fire tree composition in Canadian boreal forest



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## ABSTRACT

Salvage logging following fire has become increasingly used during the last few decades as a way to mitigate economic losses caused by fire. The removal of burned mature trees including their aerial seedbanks immediately after fire could have impacts on post-fire tree recruitment but specific effects are still unknown. We conducted a study of a fire in the boreal forest of Québec, Canada, to answer the following questions: Does fire severity influence tree compositional changes after fire? Does salvage logging affect these changes by favouring species that can reproduce vegetatively? Does salvage logging reduce among-site heterogeneity relative to natural post-fire forests? To address these questions, we measured pre- and post-fire tree stocking (2 years after fire) of burned forest of different pre-fire stand composition types both in salvaged and non-salvaged sites, whereas fire severity was measured in the latter only. Species composition was evaluated using a Principal Component Analysis, and mixed models were used to test the effects of canopy fire severity, residual organic layer thickness, stand type and salvage logging on pre- to post-fire composition changes. In non-salvaged sites, fire severity had a significant effect on composition changes, and the effect depended on stand type. Low fire severity favoured species that can reproduce vegetatively such as *Populus tremuloides*, whereas moderate and high fire severity favoured the aerial seedbank species such as *Pinus banksiana* and *Picea mariana*. We found no effect of residual organic layer thickness on post-fire composition changes. Salvage treatment had a significant effect on post-fire composition changes and the effect depended on stand type. Overall, salvage logging tended to favour species relying upon vegetative reproduction more than fire alone, which favoured *P. banksiana*. Although among-site heterogeneity after salvage logging was not smaller than after fire only, salvage alters species composition more than does natural fire alone. Since salvage logging and low severity portions of the burn, which are generally not salvaged, both favour tree species with vegetative reproduction, our results suggest that these species will increase their dominance throughout the landscape if burned forests are systematically salvaged. We suggest strategies that can help to attenuate this divergence from natural post-fire conditions.

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## 1. Introduction

Fire is a major disturbance driving species compositional change in many forest biomes (Heinselman, 1981; Johnson, 1992). For instance, between 1990 and 2008, on average *circa* 5800 km<sup>2</sup> (0.42%) of the Canadian commercial boreal forest was disturbed annually by fire (Gauthier et al., 2014). Salvage logging,

introduced as a way to decrease the negative economic impacts of forest fire by recovering timber volume, has become increasingly common during the last 15 years in North America, Europe, and Australia (Greene et al., 2006; Lindenmayer and Ough, 2006; Lindenmayer et al., 2008; Nappi et al., 2011).

In the fire-prone ecosystems of the boreal forest, many tree species are well-adapted to regenerate after burning (Noble and Gitay, 1996; Greene et al., 1999). Some species, such as *Pinus banksiana* Lamb. and *Picea mariana* (Mill.) B.S.P., have multi-year aerial seedbanks that are mostly dispersed after fire (Lamont et al., 1991; St-Pierre et al., 1992; Lavoie and Sirois, 1998), whereas others such as *Populus tremuloides* Michx. have the ability to spread asexually

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after fire via new stems arising from the cork cambium of the roots (Barnes, 1966; Schier et al., 1985). While post-fire tree composition is often similar to that existing before fire (Greene et al., 2006; Jayen et al., 2006; Johnstone and Chapin, 2006; Ilisson and Chen 2009a,b), many studies report a shift toward species, such as *P. tremuloides*, with a high capacity for asexual reproduction, at the expense of species relying upon aerial seedbanks (Anderson and Romme, 1991; Greene and Johnson, 1999; Ilisson and Chen, 2009a,b; Gärtner et al., 2014).

Fire severity is one of the factors that are known to affect post-fire forest composition (Schimmel and Granström, 1996; Turner et al., 1999; Johnstone and Kasischke, 2005; Johnstone et al., 2010; Hollingsworth et al., 2013). The effect occurs on two levels: (i) on the forest floor, fire severity affects suitable seedbed availability by reducing soil organic layer depth (Johnstone and Chapin, 2006; Greene et al., 2007), and (ii) at the canopy level, it affects both seed availability and sucker production. At one extreme, a very severe fire may kill a significant part of the aerial seedbank via flaming combustion as well as the sucker-producing roots via smoldering combustion (Wang, 2003; Johnstone and Chapin, 2006). At the other extreme, in a very low-severity fire, the temperature may be insufficient to open the serotinous cones protecting the aerial seedbank (Jayen et al., 2006) and the organic layer reduction by smoldering may be insufficient to enhance the germination success of small-seeded plant species (Greene et al., 2007). Wildfires usually create a mosaic of patches with variable fire severity, and the differential responses of tree species to fire severity may therefore result in a markedly heterogeneous post-fire composition (Turner et al., 1994; Chappell and Agee, 1996; Turner et al., 1999; Haire and McGarigal, 2010).

A second severe disturbance event immediately following fire, such as salvage logging, will interact with the regeneration processes and alter post-fire tree recruitment (Greene et al., 2006). However, the impact of salvage logging on ecosystems is still poorly known (Lindenmayer et al., 2008) and few studies have been conducted on its effect on tree regeneration after fire in the boreal forest (but see Fraser et al., 2004; Greene et al., 2006; Donato et al., 2006; D'Amato et al., 2011). Salvage logging affects post-fire forest composition in three ways. First, the removal of burned mature trees including their aerial seedbanks immediately after fire, before the release of most of the seeds, decrease the quantity of available seeds in the field, as suggested by Donato et al. (2006) and Greene et al. (2006, 2013). Secondly, salvage logging is likely to have a direct impact on the site, especially by reducing the thickness of the charred organic material and decreasing shade (as burnt boles are removed). It has been suggested that salvage logging accelerates soil drying due to snag removal (Purdon et al., 2004; Kurulok and Macdonald, 2007), disadvantaging the seedlings of species that are less tolerant to drought. Finally, many studies noted mechanical negative impacts of salvage logging, i.e. saplings or suckers were killed or strongly injured by the machinery (Fraser et al., 2004; Donato et al., 2006; Greene et al., 2006; Fernandez et al., 2008). Salvage logging is mainly applied in moderately to severely burned forests and its application systematically throughout these burned areas could therefore reduce the heterogeneity naturally induced by fire. For example, Purdon et al. (2004) found that understory plant composition after salvage logging was within the range of variability but did not cover all the variability observed in composition after fire alone.

The present study assessed the combined effect of fire and salvage logging on early post-fire composition in a fire that occurred in the boreal mixedwood forest of Quebec. We first assessed the effect of fire severity on post-fire composition. Since salvage logging is only practiced in moderately to severely burned forests, this allowed us to determine variation in post-fire composition in all severities and to take these effects into account in further analysis.

We hypothesized that severe fire will favour the recruitment of seedbank conifer species, whereas low severity fire will favour species that can reproduce vegetatively. We also hypothesized that the removal of seeds in burned trees of aerial seedbank species in salvaged sites will drastically change the post-fire composition by favouring species that can reproduce vegetatively. Further, we hypothesized that the compositional change caused by salvage logging, by favouring systematically the same species, will decrease the among-sites heterogeneity relative to the natural post-fire forest created by contrasting fire severities.

## 2. Methods

### 2.1. Study area

The study area is located in the boreal zone, in northwestern Quebec, Canada, near the town of Val-Paradis (49°09'N–79°17'W; Fig. 1). Thin soils characterize the area as there are mainly lacustrine soils in the lower areas and tills and sandy fluvio-glacial soils in the higher areas (Tremblay, 1974). The nearest weather station is located 50 km to the south, in La Sarre (48°47'N–79°13'W), 244 m above sea level. Mean January and July temperatures for the normal period 1971–2000 are –18.2 °C and +16.9 °C respectively, with 148 days without frost (Environment Canada, 2013). Annual precipitation amounts to 890 mm, including 246 mm as snowfall (Environment Canada, 2013).

*P. mariana* and *P. banksiana* are the dominant tree species in the study region. Some mixed stands of *P. tremuloides*, *Populus balsamifera* L., *Betula papyrifera* Marsh., *Picea glauca* (Moench) Voss, with occasional *Abies balsamea* (L.) Mill., can also be found. Both *P. banksiana* and *P. mariana* have aerial seedbanks and thus can disperse *in situ* from burnt trees. The former abscises the majority of its seeds within a few months whereas the latter releases seeds far more slowly (Splawinski et al., 2014). Thus, *P. mariana* is more negatively affected by early post-fire salvage than is *P. banksiana* because far more its seeds remain in cone-bearing branches in slash piles or at the landing (Saint-Germain and Greene, 2009). While *P. mariana* is also able to reproduce vegetatively by layering, this reproductive mechanism is not useful for immediate post-fire recruitment (Greene et al., 1999). *P. tremuloides* has abundant, reliable sprouting following fire (Schier et al., 1985; St-Pierre et al., 1992; Greene and Johnson, 1999; Ilisson and Chen, 2009a,b), the ability to sprout has been observed in even very young *P. tremuloides* (Burns and Honkala, 1990). It is a masting species that very occasionally produces extremely large crops of very small wind-dispersed seeds in the late spring; as there is no aerial seedbank, the seeds must come from living trees at the fire edge or the within-burn residual stands. The seeds (and thus, the germinants) are so small that they have the most exacting seedbed requirements of any boreal tree species (Greene et al., 2007).

The studied fire burned 12,540 ha on June 9–11, 1997 (Bordeleau, 1998). The fire was characterized as an intermittent crown fire (Hély et al., 2003). The forest soil was still partially frozen at that time. The preceding fires occurred between 1910 and 1930 (Bergeron et al., 2004) implying that the trees at the time of the 1997 fire were 65–85 years old and thus sexually mature and that aspen was able to produce asexual regeneration (Burns and Honkala, 1990).

In the late summer and autumn of 1997, salvage logging was conducted on most of the burned area, only bogs and steep hills were left out.

### 2.2. Site selection

During the summer of 1997, we selected 36 blocks of approximately 1 ha each in different forest stands where salvage logging

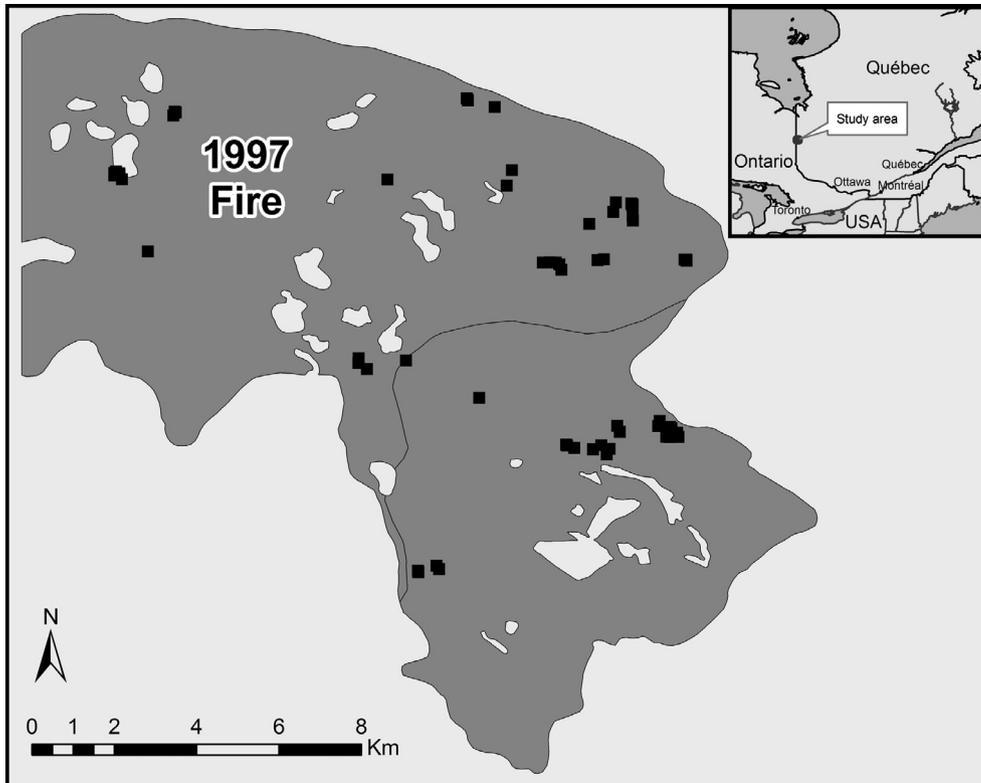


Fig. 1. Map of study area showing the fire of 1997 (grey polygon), with preserved islands, and study sites (black squares).

was excluded. Blocks were selected to control for stand age, soil moisture regime, slope and soil thickness. The 36 blocks were initially selected amongst three overstorey compositions: deciduous (>75% cover of deciduous species), mixed (25–75% deciduous) and coniferous (<25% deciduous) based on forest inventory map data. For each composition type, blocks were equally distributed into three fire severity classes at the crown level as defined by tree mortality rates: light (<25%), moderate (25–75%) and high (>75%).

Twenty-four other blocks of the same dimensions were established in 1998 in salvaged areas in the same fire, and distributed equally amongst the three overstorey compositions. Fire severity at the crown level could not be assessed in salvaged plots since we selected them only after logging. It should be noted however that salvage logging occurred only in stands where mortality level was >25% (moderate and high severity levels).

### 2.3. Field sampling

In the middle of each block, a plot of  $20 \times 20$  m ( $400 \text{ m}^2$ ) was established. For each mature tree in the  $400\text{-m}^2$  plots, the following measures were recorded: species, diameter at breast height (DBH) and whether the tree was dead or alive. In case of salvaged plots, species and basal diameter were recorded from the remaining stumps.

We measured the residual organic layer thickness at each meter along a 30-m transect established in the middle of each plot. This variable could be used as an indicator of fire severity at the soil level (more specifically, the intensity of smoldering combustion), but since the pre-fire organic layer thickness was unknown, it was used to infer the post-fire seedbed quality.

### 2.4. Estimation of stocking

As seedling density is generally much higher than the density of mature trees, the use of stocking rather than the absolute number

of individuals allowed us to compare pre- and post-fire composition on the same basis. Based on the Quebec Department of Natural Resources standards, we assumed that at least one seedling per sampling unit of  $4 \text{ m}^2$  would reach maturity (MRNQ, 2002). To evaluate the pre- and post-fire stocking, each  $400 \text{ m}^2$  plot was divided into a grid of  $4 \text{ m}^2$  sampling units and among them 25 were randomly selected for sampling. To estimate pre-fire stocking, the presence-absence of each tree species (DBH > 9 cm) was recorded in each of these units. For salvaged plots, pre-fire stocking was estimated from the presence-absence of stumps (diameter > 9 cm) of each species (it was still possible to identify the species of burned trees and stumps). For each plot, stocking values of each species were then expressed as the proportion of the 25 units where the given species was present. To estimate post-fire stocking (i.e. regeneration), presence-absence of seedlings and root suckers (1–3 years old) of each species was recorded in each of the 25 sampling units in July and August of 1999. At that time, most of the regeneration establishment is likely to be completed (Greene et al., 2004). Similarly, post-fire stocking values were reported as the proportion of the 25 units where the species was present.

Although all blocks were initially classified into three pre-fire composition types based on cartographic forest inventory data, this classification did not always reflect the observed pre-fire composition in the plot. The plots were thus newly classified into four stand composition types, based on the stocking of the three main species, *P. mariana* (*Pma*), *P. banksiana* (*Pba*) and *P. tremuloides* (*Ptr*). The new stand composition types, named *PmaPtr*, *PtrPba*, *PbaPma* and *Mixed* (all three species) according to their dominant species, are described in Table 1.

### 2.5. Data analysis

Data analysis involved several steps, which are schematized in Fig. 2 and described below.

**Table 1**

Classification of the four stand pre-fire composition types based on the plot relative stocking (%) of the three main species. X = presence, 0 = absence.

Stand type	N	<i>P. banksiana</i> (Pba)	<i>P. mariana</i> (Pma)	<i>P. tremuloides</i> (Ptr)
<i>PmaPtr</i>	18	0	X	X
<i>PtrPba</i>	10	X or 0 <sup>a</sup>	0	X
<i>PbaPma</i>	22	X	X	0
<i>Mixed</i>	10	X	X	X

<sup>a</sup> 3 of the 10 plots in the *PtrPba* type were composed only of *P. tremuloides*.

### 2.5.1. Ordinations

In order to evaluate the effect of fire severity on plot composition (rather than on the change of individual species), we used an ordination technique. As the pre-fire stocking established the composition baseline for further comparison, the ordination was performed first on the pre-fire stocking of the three main tree species, *P. mariana*, *P. banksiana* and *P. tremuloides*, in each plot using Canoco 4.5 (ter Braak and Smilauer, 2002). The Principal Component Analysis (PCA) was selected based on the short gradient length, suggesting linear data (ter Braak and Smilauer, 2002). PCA has the advantage of preserving the exact distance between objects in the reduced space and axis coordinate values can therefore be used in linear models. PCA is recognized to be sensitive to double zeros, i.e. the absence of a species in two plots will bring them closer in the ordination space. This could be a problem for communities with numerous species but in our case, with only three species, double zeros are meaningful (i.e. two plots with the absence of one of the three species are actually compositionally closed).

Once the PCA was produced using the pre-fire stocking, the same plots were passively positioned in the ordination space using their post-fire stocking data. In all analyses, species data were centered by species and log-transformed to attenuate their skewed distributions, though multinormality is not an assumption of the PCA (Legendre and Legendre, 1998).

### 2.5.2. Effect of fire severity on pre- to post-fire compositional changes

As we could not include the canopy fire severity and organic layer thickness factors in the same analysis given the small number of plots, two separate analyses were conducted. The effect of fire severity on post-fire composition was tested using a mixed model for repeated measurements (MIXED procedure; SAS Institute Inc., 2002) with the 36 non-salvaged plots. The model response variable was the composition as expressed by the coordinates of the plots on the first two PCA axes. Repeated measurements were the composition before and after the fire in each plot. Stand type was included in the model since compositional changes are likely influenced by pre-fire composition. The explanatory variables included fixed effects for stand type (four types), fire severity (high, moderate and low), time (before/after fire) and all interactions. Note that as we are interested to the composition changes through time (before/after), only the interactions implying time will be interpreted. The random effect for plot constituted the residual error. After testing different matrix structures, the variance-covariance matrix of the residual errors was assumed to be block-diagonal following a compound symmetry. To evaluate specifically if the pre- to post-fire compositional change in low severity fire is different from the change in high severity fire, we computed a contrast for each stand type on the two PCA axes coordinates.

The effects of residual organic layer thickness on pre- to post-fire compositional changes were tested in a distinct analysis using the same structure as for fire severity in the canopy. In this case, the explanatory variables included fixed effects for organic layer thickness (continuous variable), stand type (four types), time (before/after fire) and interactions involving time.

### 2.5.3. Effect of salvage logging on pre- to post-fire compositional change

Effect of salvage logging on post-fire composition was also tested using a mixed model for repeated measurements (MIXED procedure; SAS Institute Inc., 2002). To compare salvaged with non-salvaged plots, we had to exclude non-salvaged plots with low fire severity

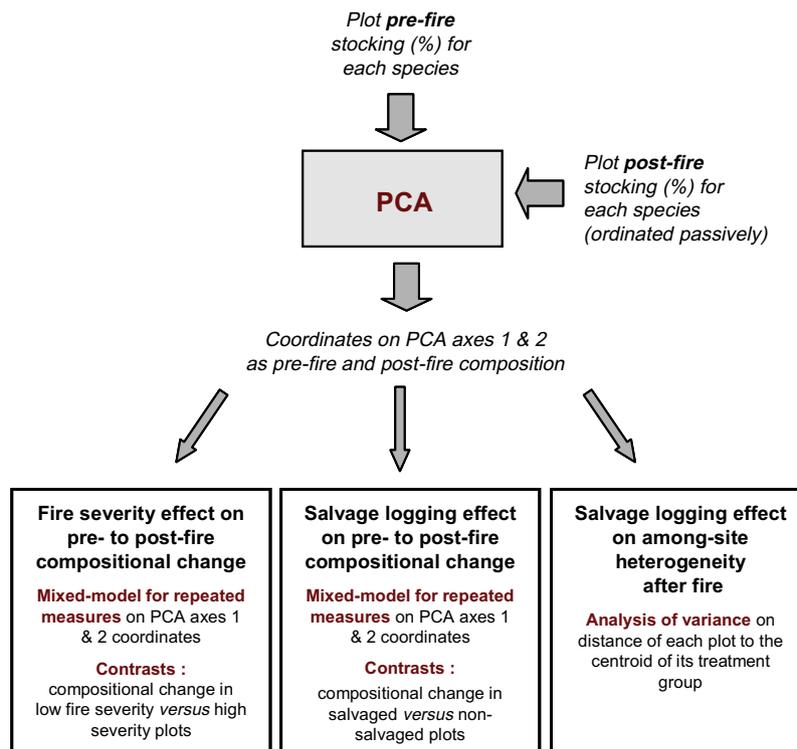


Fig. 2. Diagram of the main data analysis steps.

as these sites are usually not salvaged. Fire severity could not be included in this model since it was not measured in salvaged plots. The model response variable was the composition as expressed by the coordinates of the plot on the first two PCA axes. The explanatory variables included fixed effects for treatment (salvaged or non-salvaged), residual organic layer thickness, stand type (four types), time (before/after) and interactions implying time. The random effect for plot was also included. After testing different matrix structures, the variance–covariance matrix of the residual errors was assumed to be block-diagonal following a compound symmetry. To evaluate specifically if salvage logging affected the change in composition, we computed a contrast comparing the pre- to post-fire compositional change in salvaged plots versus the change in non-salvaged plots for each stand type on the two PCA axes coordinates.

#### 2.5.4. Effect of salvage logging on among-site heterogeneity

To test if the salvage logging reduced the among-site compositional heterogeneity relative to the natural post-fire forests, we computed the Euclidean distance of each plot to the centroid (i.e. mean of coordinates) of its treatment type (salvaged/non-salvaged) in the ordination space (Anderson, 2006). We performed an analysis of variance with the distance to the centroid as the response variable and the treatment (salvaged/non-salvaged) as the explanatory variable. All stand types were included in this analysis as we wanted to assess the global among-site heterogeneity. A treatment type with a higher mean of distances with its centroid would be more heterogeneous than one with a lower mean.

### 3. Results

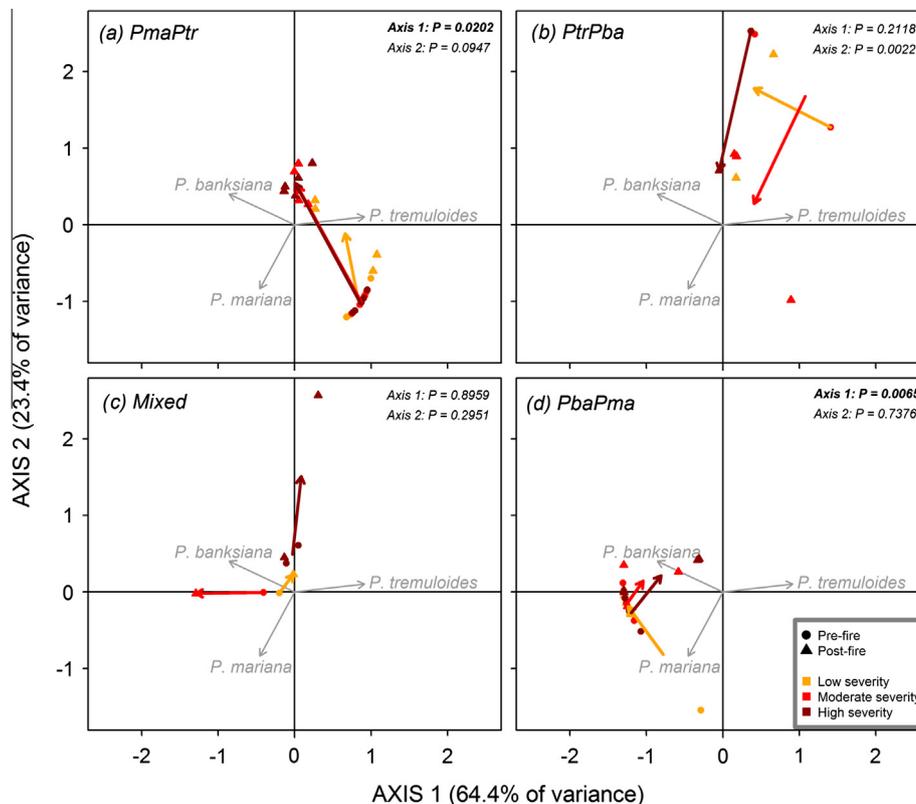
The three axes obtained by PCA performed on the three main tree species' pre-fire relative stocking explained respectively

64.4%, 23.4% and 12.2% of the variance. Axis 1 discriminated the deciduous plots from the coniferous ones whereas axis 2 discriminated *P. mariana* plots from the *P. banksiana* dominated ones (Figs. 3 and 4). Since the first two axes explained 87.8% of composition variation, only the coordinates of these two axes were included in further analyses.

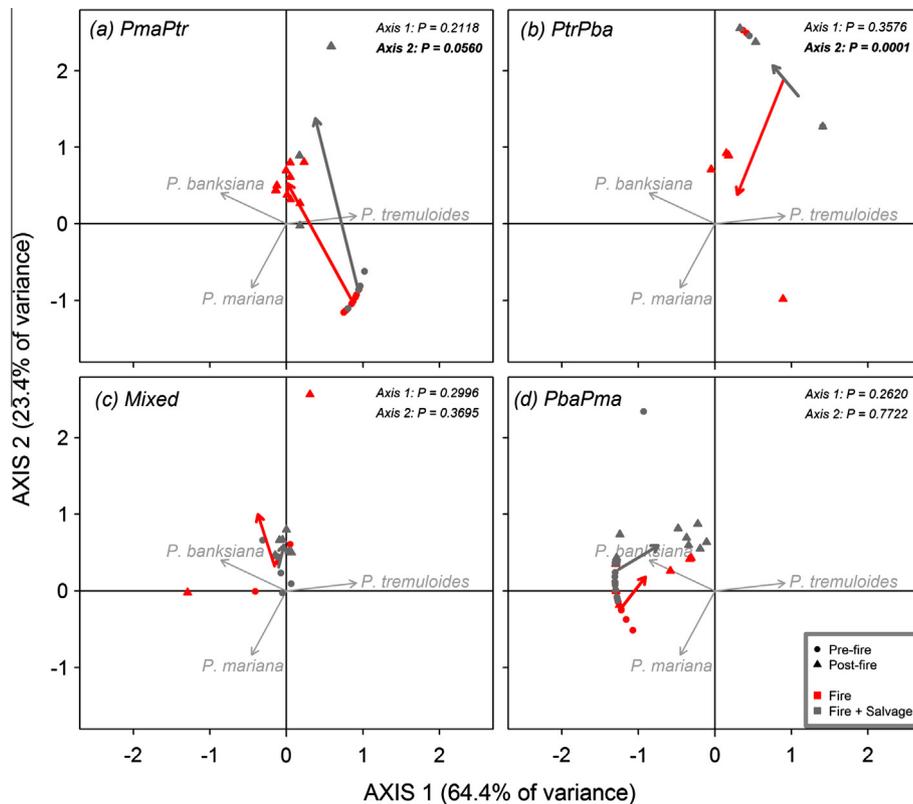
#### 3.1. Effect of fire severity on pre- to post-fire compositional change

Results from the mixed model on PCA axes 1 and 2 coordinates are shown in Table 2. Since the model is structured on a repeated design, our interpretation of the results will be limited to the interactions involving the Time factor. For the model including canopy severity, the significant Severity  $\times$  Stand type  $\times$  Time interaction indicates that the pre- to post-fire compositional change depends both on fire severity and stand type (Table 2).

In plots dominated by *P. mariana* and *P. tremuloides* (*PmaPtr* type), the pre- to post-fire change in composition in high fire severity areas was significantly different. In plots dominated by *P. mariana* and *P. tremuloides* (*PmaPtr* type), the pre- to post-fire change in composition in high fire severity areas was significantly different from that of low severity fire (contrast on axis 1:  $F = 6.19$ ,  $p = 0.0202$ ; Fig. 3a). Within low fire severity plots, the pre- to post-fire compositional change was low, marked by an increase in *P. tremuloides* and a decrease in *P. mariana* (Figs. 3a and A1). In high and moderate fire severity, compositional change was characterized by an appearance of *P. banksiana* and a decrease in *P. mariana* (Figs. 3a and A1). In the *PtrPba* type, compositional change was also different between low and high fire severities (contrast on axis 2:  $F = 11.79$ ,  $p = 0.0022$ ; Fig. 3b). *P. tremuloides* slightly decreased in the three fire severities, but in low fire severity, *P. banksiana* appeared after fire (Fig. 3b), whereas in high and moderate fire



**Fig. 3.** Composition change after different fire severities in the Principal Component Analysis space among the four stand types: (a) *PmaPtr*, (b) *PtrPba*, (c) *Mixed*, and (d) *PbaPma* types (see Table 1 for the type descriptions). Note that these results are from a single PCA but stand type data are shown separately. The length of the arrows is proportional to the extent of the composition change. Probabilities associated with contrasts testing the difference in composition changes between low and high fire severities are shown for each stand type.



**Fig. 4.** Composition change after fire only and after fire and salvage logging in the Principal Component Analysis space among the four stand compositional types: (a) *PmaPtr*, (b) *PtrPba*, (c) *Mixed*, and (d) *PbaPma* groups (see Table 1 for the type descriptions). Note that these results are from a single PCA but stand type data are shown separately. The length of the arrows is proportional to the extent of the composition change. Probabilities associated with contrasts testing the difference in composition changes between treatments are shown for each stand type.

**Table 2**

Analysis testing the difference in pre- to post-fire compositional change among fire severities and stand types. Mixed model for repeated measurements was performed on composition as expressed by the two PCA axes coordinates of non-salvaged plots and included the effects of time, fire severity and stand type. Although all interactions were included in the model, only those involving Time are shown. Axes 1 and 2 explained respectively 64.4% and 23.4% of the variance in plot composition (see Fig. 3).

Effect	PCA axis	Num. Df	Den. Df	F
Fire severity	1	2	24	5.05*
(High, moderate, low)	2	2	24	3.25
Stand type	1	3	24	119.87***
( <i>PmaPtr</i> , <i>PtrPba</i> , <i>PbaPma</i> , <i>Mixed</i> )	2	3	24	26.65***
Time	1	1	24	21.05***
(Before/after fire)	2	1	24	7.70*
Severity X Time	1	2	24	1.65
(Testing pre- to post-fire compositional change among fire severities)	2	2	24	1.40
Stand type × time	1	3	24	6.93**
(Testing pre- to post-fire compositional change among stand types)	2	3	24	18.89***
Severity × stand type × time	1	6	24	3.80**
(Testing pre- to post-fire compositional change among fires severities and stand types)	2	6	24	4.08**

\*  $p < 0.05$ .

\*\*  $p < 0.01$ .

\*\*\*  $p < 0.001$ .

severity, it was instead the relative stocking of *P. mariana* that slightly increased (Figs. 3b and A1).

In plots dominated by *P. banksiana* and *P. mariana* (*PbaPma* type), the pre- to post-fire change in composition was significantly different between high and low fire severities (contrast on axis 1:  $F = 8.90$ ,  $p = 0.0065$ ; Fig. 3d). In both high and moderate fire severity, we observed an increase in *P. banksiana* and a decrease in *P. mariana*. In low fire severity, the increase in *P. banksiana* was less

pronounced while *P. mariana* stocking remained the same (Figs. 3d and A1). In *Mixed* stands, no difference was observed between low and high fire severities (Fig. 3c), compositional changes were not important in any fire severity.

In non-salvaged sites, the four stand types had on average a different thickness of post-fire residual organic layer (Table 3a). The *PbaPma* type had a higher mean, and *PtrPba* had the lowest value. Despite these differences, when the residual organic layer

**Table 3**

Mean  $\pm$  standard deviation of residual organic layer thickness within the four stand pre-fire composition types (a) in non-salvaged plots and (b) in salvaged and non-salvaged plots where fires were of moderate or high canopy severity. See Table 1 for the description of stand types.

(a) Non-salvaged only (low to high fire severities)				
	N		Mean $\pm$ SD (cm)	
<i>PmaPtr</i>	14		9.04 $\pm$ 2.66	
<i>PtrPba</i>	7		7.89 $\pm$ 2.59	
<i>PbaPma</i>	11		13.17 $\pm$ 6.09	
<i>Mixed</i>	4		11.30 $\pm$ 3.01	

(b) Salvaged and non-salvaged (moderate and high fire severities)				
	Non-salvaged		Salvaged	
	N	Mean $\pm$ SD (cm)	N	Mean $\pm$ SD (cm)
<i>PmaPtr</i>	10	8.78 $\pm$ 2.35	4	6.59 $\pm$ 1.13
<i>PtrPba</i>	4	9.19 $\pm$ 2.02	3	5.25 $\pm$ 3.02
<i>PbaPma</i>	7	10.92 $\pm$ 3.82	11	7.39 $\pm$ 2.81
<i>Mixed</i>	3	11.68 $\pm$ 3.46	6	10.68 $\pm$ 2.07

thickness was included in the mixed model (instead of canopy severity), results revealed only a significant effect in *Mixed* stand type on axis 1 ( $F = 4.61$   $p = 0.0097$ ; results not shown).

### 3.2. Effect of salvage logging on pre- to post-fire compositional change

On axis 1, the interaction Treatment X Stand type X Time was not significant, but both Treatment X Time and Stand type X Time interactions were significant (Table 4). The significant interaction Stand type X Time on axis 1 indicated that the trends of compositional changes among stand types were similar irrespective of the treatment: in both treatments, *P. tremuloides* stocking increased in the *PbaPma* type, *P. banksiana* increased in the *PmaPtr* type, whereas *P. tremuloides* decreased in *PtrPba* type. Compositional changes were less important in *Mixed* stands (Table 4 and Figs. 4 and A2).

The significant interaction Treatment X Time indicates that salvage logging had a significant effect on the pre- to post-fire compositional change in axis 1, irrespective of the stand type, which manifested in three ways: (1) whereas fire induced an increase in *P. banksiana*, this increase was less pronounced in the salvaged plots; (2) salvage logging negatively affected *P. mariana* compared with fire alone; and (3) *P. tremuloides* was favoured by salvage logging compared with fire alone (Figs. 4 and A2).

On axis 2, salvage logging had a significant effect on post-fire compositional changes compared with non-salvaged sites, with a significant interaction with stand types (Table 3). This means that

changes on axis 2 differed according to the stand types. In the *PmaPtr* type, the difference in compositional change between salvaged and non-salvaged plots was nearly significant (contrast on axis 2:  $F = 3.87$ ,  $p = 0.0560$ ; Fig. 4a): the increase in *P. tremuloides* was higher after salvage logging to the detriment of *P. banksiana* (Figs. 4a and A2) compared with the exclusive effect of fire. In the *PtrPba* type, compositional changes after fire only and after fire and salvage logging were significantly different (contrast on axis 2:  $F = 17.83$ ,  $p = 0.0001$ ; Fig. 4b). No *P. mariana* was observed after salvage logging, while this species increased after fire only and the decrease in *P. tremuloides* was a little less pronounced after salvage logging (from 93.3% to 82.6%) than after fire (from 85.4% to 65.9%) (Figs. 4b and A2). In *PbaPma* and *Mixed* types, compositional changes were less pronounced but a noticeable trend that salvage logging favours *P. tremuloides* to the disadvantage of *P. mariana* and *P. banksiana* was still observed (Figs. 4c and d and A2).

Salvage sites tended to have a thinner residual organic layer than non-salvaged sites (restricted to only moderate to high fire severities; Table 4b). Nevertheless organic layer thickness had no significant effect on either of the two axes (the effect was removed from the model).

### 3.3. Effect of salvage logging on among-site heterogeneity

Difference of distances with the group centroid between post-fire plots (moderate to high severity) and post-salvaged plots was not significant ( $F = 1.128$ ,  $df = 1$ ,  $p = 0.294$ ), suggesting that the extent of the among-site heterogeneity after fire and after fire in conjunction with salvage logging was of similar size. The ellipses of the two treatments partially overlapped while the salvaged plots ellipse extended more at the upper right part of the ordination space and less at the lower right part (e.g. a higher *P. tremuloides* component) compared with non-salvaged plots (of all fire severities or only sites of moderate to high severity; Fig. 5). Thus, salvage logging does not lessen among-site heterogeneity, but alters species composition beyond what fire alone might do.

## 4. Discussion

### 4.1. Effect of fire severity

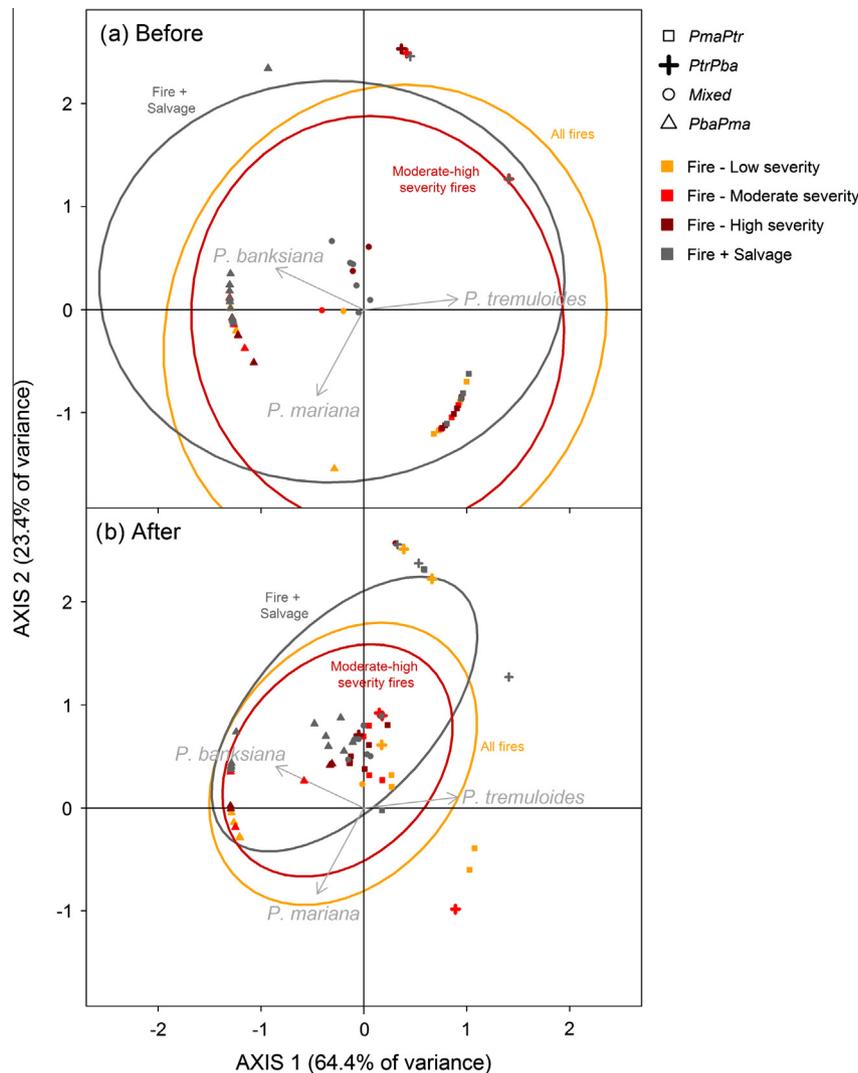
The fire near Val-Paradis showed a high variability in canopy severities, allowing us to study the early post-fire compositional changes after fire at low, moderate and high severity. Although

**Table 4**

Analysis testing the difference in pre- to post-fire compositional change between salvaged and non-salvaged plots and among stand types. Mixed model for repeated measurements was performed on composition as expressed by the two PCA axes coordinates of all plots and included the effects of time, salvage/non-salvaged and stand type. Although all interactions were included in the model, only those involving Time are shown. Axes 1 and 2 explained respectively 64.4% and 23.4% of the variance in plot composition (see Fig. 4).

Effect	PCA axis	Num. Df	Den. Df	F
Salvaged vs non-salvaged	1	1	40	5.09*
	2	1	40	7.67**
Stand type ( <i>PmaPtr</i> , <i>PtrPba</i> , <i>PbaPma</i> , <i>Mixed</i> )	1	3	40	106.67***
	2	3	40	21.11***
Time (Before/after fire)	1	1	40	11.09**
	2	1	40	32.26***
Salvage $\times$ time (Testing pre- to post-fire compositional change between salvaged and non-salvaged plots)	1	1	40	4.55*
	2	1	40	7.80**
Stand type $\times$ time (Testing pre- to post-fire compositional change among stand types)	1	3	40	21.49***
	2	3	40	27.61***
Salvage $\times$ stand type $\times$ time (Testing pre- to post-fire compositional change among salvaged/non-salvaged and stand types)	1	3	40	0.03
	2	3	40	6.04**

\*  $p < 0.05$ .\*\*  $p < 0.01$ .\*\*\*  $p < 0.001$ .



**Fig. 5.** Principal Component Analysis of species composition before (a) and after (b) fire only and fire and salvage logging. Ellipses correspond to 80% of the plots of each group: fire of all severities (yellow), fire of high and moderate severities (red), fire of high and moderate severities followed by salvage logging. Note that the post-fire composition location on the ordination space has been computed passively.

the effect of fire severity differed between stand types, a general trend was observed: high-severity fire at the crown level favoured *P. banksiana* to the detriment of *P. mariana* and *P. tremuloides* whereas low severity fire favoured *P. tremuloides*.

When mixed with *P. mariana*, *P. banksiana* increased its relative stocking when fire was severe, despite the fact that both species are well adapted to fire (Noble and Gitay, 1996; Greene et al., 1999). Similarly, Lavoie and Sirois (1998) found that when both *P. mariana* and *P. banksiana* were present in a stand before fire and the interval between the last two fires was relatively short (e.g. 100 years), there was a shift from spruce to pine dominance since *P. banksiana* produces large numbers of seeds earlier than *P. mariana* (Rowe and Scotter, 1973). Considering that our stands were mainly aged between 65 and 85 years at the time of fire, we propose that the shift from spruce to pine dominance observed in our data, particularly when the fire severity was high, can be explained by a greater number of seeds carried by *P. banksiana* compared with *P. mariana* at the time of fire. Furthermore, seedling establishment and growth of *P. mariana* is known to be very poor on organic soils (Lavoie and Sirois, 1998; Johnstone and Kasischke, 2005; Ilisson and Chen, 2009a,b), worse than *P. banksiana*, probably due to the small size of *P. mariana* germinants (Greene et al., 1999; Johnstone and Chapin, 2006).

In most of our non-salvaged stands, low fire severity highly increased the proportion of *P. tremuloides* in contrast to high fire severity. Conditions after a low severity fire were favourable for *P. tremuloides*, as this species can readily recolonize the site by suckers, but they were less suitable for the germination of *P. mariana* and *P. banksiana* as organic layers remain quite thick. In contrast, severe fire could kill the near-surface roots that sponsor *P. tremuloides* suckers (Wang, 2003; Greene et al., 2004) and favour the germination of conifer seeds by reducing the organic layer (Thomas and Wein, 1985; Johnstone and Chapin, 2006).

*P. tremuloides* seeds are very small compared with conifer ones and have few reserves to support initial root growth and have access to a stable moisture supply (Schier, 1981; Johnstone and Chapin, 2006). Although there are occasional reports of massive sexual regeneration (e.g. Romme et al., 1997), particularly after very severe fire (Johnstone et al., 2010), *P. tremuloides* recruitment is more often asexual (e.g. Greene and Johnson, 1999). In our study, the low density of *P. tremuloides* seedlings after severe canopy fire where it was previously absent can be explained by the thick residual organic layer.

Even though a third of the non-salvaged sites showed canopy mortality >75%, severity at the soil level within the Val-Paradis fire was not very high. Greene et al. (2004) observed that only 5% of the

area they studied at this same fire had a residual organic layer <2 cm and we found an average thickness of 9.5 cm. Presence of interstitial ice in the organic layer at the time of the fire likely limited the duration of the smoldering combustion (Greene et al., 2004). Typically, with a residual organic layer less than about 5 cm, small seeded species' establishment is greatly reduced (Greene et al., 2007; Johnstone and Chapin, 2006; Hesketh et al., 2009).

#### 4.2. Effect of salvage logging

Our results confirm that salvage logging clearly affected the post-fire composition of the stands compared with the changes induced by fire only. Salvage logging favoured regeneration of *P. tremuloides* at the expense of *P. mariana* and *P. banksiana* (i.e. *P. tremuloides* increased more or decreased less than after fire only, depending on stand type). At the time of logging, soon after the fire, most of the *P. mariana* and *P. banksiana* viable seeds were probably still on the burned trees (Greene et al., 2013). The removal of a great part of the conifer aerial seedbank likely reduced seedling establishment, as was suggested by Greene et al. (2006), while the strong capacity of *P. tremuloides* to re-colonize burned sites by suckers increased its proportion in salvaged stands. Meanwhile, as argued by Greene et al. (2006), the trampling of post-fire *P. tremuloides* suckers on skidpaths is partially recouped by a second cohort of asexual stems.

Generally, fires are heterogeneous in severity and thus, even in severely burned parts, patches that are less severely burned are seldom so far from other areas that they could not serve as seed sources for the more severely burned sites (Turner et al., 1994; Kafka et al., 2001; Lindenmayer and McCarthy, 2002; Donato et al., 2009; Johnstone et al., 2009; Madoui et al., 2010). The occurrence of a second disturbance may alter this natural heterogeneity, as suggested by Purdon et al. (2004) who found a decreased heterogeneity in understory plants after salvage logging compared to non-salvaged sites in the fire of Val-Paradis. For tree composition, we found that the heterogeneity induced by salvage logging was not smaller than that produced by fire, although the compositional range extended partly outside of the variability typical of fire, thus increasing the importance of *P. tremuloides* stems while decreasing that of *P. mariana*. The difference between our results and those of Purdon et al. (2004) may be explained by the fact that we only had three tree species which are all present in all conditions.

*P. tremuloides* regeneration is favoured by salvage logging and this has a significant impact on post-fire composition at the landscape level. Salvage logging was only conducted in the portions of fire that had moderate to high severities, precisely the areas where *P. tremuloides* was not favoured by fire alone. Consequently, both the low severity (non-salvaged) portions of fires and the salvaged areas will tend towards an increase in *P. tremuloides*, and therefore *P. tremuloides* would be favoured everywhere in the landscape. The presence of *P. banksiana* in the landscape, which usually benefits from fire, could be reduced compared with the natural post-fire conditions, while the abundance of *P. mariana* would be more sharply curtailed. Preserving some intact burned areas could attenuate this divergence from natural conditions, but few management policies at present require retention patches during salvage logging (Lindenmayer and Ough, 2006; Schmiegelow et al., 2006; Lindenmayer et al., 2008).

## 5. Conclusion

Our results suggest that salvage logging induces compositional changes, different from those induced by fire only, by favouring vegetatively-reproducing species, but does not significantly alter

the among-sites compositional heterogeneity. Since salvage logging and low severity portions of the burn, which are generally not salvaged, both favour trees species with vegetative reproduction, our results suggest that these species would increase their dominance throughout the landscape. Since the main problem related to salvage logging comes from the removal of aerial seedbanks, the time after fire at which the logging occurs is crucial. Delaying logging operations would certainly help promote black spruce and jack pine regeneration (Greene et al., 2013; Splawinski et al., 2014), although salvage has to occur early to minimize xylophagous beetle damage as well as drying of standing burned trees (Saint-Germain and Greene, 2009). Alternatively, retention of burned patches throughout the salvaged area as well as of burned forest stands of all severities and all composition has been proposed as an ecosystem-based management solution not only to favour natural conifer regeneration after salvaged logging but also to maintain the ecological integrity of burned forest (Nappi et al., 2011). At the stand level, the maintenance of snags of different sizes and different species has also been proposed (Nappi et al., 2004). The optimal strategies to adopt should aim at preserving the heterogeneity in the landscape, both by retention at different scales and by conducting salvage logging a different times. The development of such strategies would likely attenuate the divergence of salvaged forest composition from the post-fire natural composition.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2014.04.002>.

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