



The influence of landscape-level heterogeneity in fire frequency on canopy composition in the boreal forest of eastern Canada

Dominic Cyr, Sylvie Gauthier & Yves Bergeron

Keywords

Abies balsamea; Côte-Nord; Disturbance; Landscape pattern; NMDS; *Picea mariana*

Received 6 August 2010

Accepted 24 July 2011

Co-ordinating Editor: Valerio Pillar

Cyr, D. (corresponding author, cyr.dominic@gmail.com): Centre d'études sur la forêt, Université du Québec à Montréal, C.P. 8888 Succ. Centre-Ville, Montréal, QC, H3P 3P8, Canada

Gauthier, S. (sgauthier@nrca-nrcan.gc.ca): Natural Resources Canada – Laurentian Forestry Centre, Canadian Forest Service, 1055 du P.E.P.S., P.O. Box. 10380, Stn. Sainte-Foy, QC, G1V 4C7, Canada

Bergeron, Y. (yves.bergeron@uqat.ca): NSERC-UQAT-UQAM Industrial Chair in Sustainable Forest Management, Université du Québec en Abitibi-Témiscamingue, 445 boul. de l'Université, Rouyn-Noranda, QC, J9X 5E4, Canada

Abstract

Question: Will a three-fold variation in fire frequency among large patches ($\approx 10^5$ – 10^6 ha) of boreal forest generate differences in canopy composition and, more specifically, will it influence the relative abundance of species with regard to their typical position along the succession gradient.

Location: A landscape of 1.6 Mha in the boreal forest of eastern Canada (Quebec).

Methods: We sampled 160 circular plots in closed-canopy forest in which we measured canopy vegetation composition, local fire history (time since last fire) and edaphic conditions. We conducted multivariate analyses (NMDS, multi-response permutation procedure) and pair-wise comparisons to probe differences in canopy composition between areas of contrasting fire frequency before and after controlling for the influence of local environmental factors.

Results: There are significant differences between areas of contrasting fire frequency in terms of relative species abundance, even after analytically removing the effect of important local environmental factors. In old stands, *Picea mariana* is significantly more abundant in high fire frequency areas while *Abies balsamea* is significantly more abundant in low fire frequency areas, both before and after controlling for local environmental factors, including time since last fire. Young stands do not differ in terms of individual species relative abundance but show more variability among stands in low fire frequency areas.

Main conclusion: The low fire frequency areas allow late-successional specialist *A. balsamea* to dominate over ubiquitous successional generalist *P. mariana* because of the typically longer time elapsed since the last fire. This suggests that succession from *P. mariana* to *A. balsamea* can occur long after what is typically covered by dendroecologically reconstructed fire history in this type of boreal landscape (> 200–300 yr).

Introduction

Natural disturbances are important drivers of the natural dynamics of the boreal forest (Payette 1992). At every spatial scale, natural disturbance regimes influence species composition and structure. Forest fires, which are usually considered to be the primary disturbance in coniferous boreal forest, are the foundations for a landscape mosaic within which other processes interact, hence playing a crucial role in structuring communities in space and time (Johnson 1992; Burton et al. 2008). Fire severity, type, seasonality, size distribution and frequency are all aspects

of fire regimes that influence vegetation dynamics in the boreal forest. Fire frequency, which we define as the proportion of the area burned per unit time, or the reciprocal of the mean fire return interval (Turner et al. 1994; Baker 1995; Li et al. 1999), is especially important as it determines the proportions and importance of stand age classes in the landscape and, in turn, influences the composition and structural attributes that are associated with these age classes (De Grandpré et al. 2000; Harper et al. 2005; Brassard et al. 2008). Although there is large stochasticity in all fire regimes, several determinants of fire frequency have been singled out in past studies conducted in the boreal

forest, ranging from broad-scale factors such as climate, dominant vegetation or land use (Wein & MacLean 1983; Weir et al. 2000; Bridge 2001; Lefort et al. 2003; Bergeron et al. 2004; Girardin et al. 2009) to others that are effective at finer scales, such as surficial geology (Bergeron et al. 2004; Mansuy et al. 2010), position on the slope (Cyr et al. 2007) or aspect (Gavin et al. 2003). Other physiographic determinants of fire frequency are described at intermediate scales such as distance to firebreaks (Larsen 1997; Cyr et al. 2005), proportion of wetland (Hellberg et al. 2004) or dominant aspect of the surroundings (Cyr et al. 2007). All of these factors partly explain spatio-temporal variations in frequency and/or size of fires and, considering the importance of local fire history on stand attributes and structure, they are also crucial to the understanding of where and when boreal species can be found.

Vegetation communities present prior to a fire partly determine the composition of the post-fire initial cohort, as well as the subsequent development of the stand through succession, hence generating ecological feedback from long-term, *in situ* fire history (McCune & Allen 1985; Foster et al. 1998; Motzkin et al. 1999). For instance, many species can resprout under certain conditions (Perala 1990; Safford et al. 1990) or benefit from aerial seed banks accumulated in serotinous cones that are released after the fire (Rudolph & Laidly 1990; Viereck & Johnson 1990). These strategies are often used by early-successional specialists and give them a greater chance of re-establishing when successive fires occur at short intervals. However, variable fire severity in the canopy often allows some trees to survive within recently burned areas (Eberhart & Woodard 1987; Kafka et al. 2001; Madoui et al. 2010). If the previous fire-free interval was long, the likelihood of these trees belonging to fire-sensitive, late-successional species is increased, and so is the likelihood of these species influencing early development and rate of succession after fire (Wimberly & Spies 2002; Keeton & Franklin 2005; Johnstone & Chapin 2006).

Using survival analyses, Cyr et al. (2007) showed spatial heterogeneity in fire frequency within a landscape of 15 961 km², which is comparable in magnitude to the heterogeneity that is generally observed from one such large landscape to another. A two to six-fold variation in fire frequency was indeed observed and related to topographic and geographic features. Dominant aspect within a neighbourhood of 4000–10 000 m² was found to generate a fire frequency gradient, where areas dominated by southwest-facing slopes burned up to three times more often than areas dominated by northeast-facing slopes, with intermediate values between these. Such landscape-level heterogeneity in fire frequency, which is independent of fine-scale, bottom-up types of controls, creates a landscape mosaic made up of patches of several thousand hectares in

which the fire regimes differ substantially (Fig. 1). This heterogeneity is also most likely permanent, despite changes in fire activity that might have occurred in the past since it is caused by permanent features of the physical environment.

The general objective of this study is to assess whether this landscape-level heterogeneity in fire frequency generates discernible patterns in canopy composition. Substantial differences in age structure at the landscape level are expected because it is the most direct result of any variation in fire frequency. Based on this premise and given the importance of time since fire as one determinant of canopy composition, we first assessed whether the relative abundance of the dominant tree species differs between contrasting portions of the landscape in terms of fire frequency, especially with regard to the proportions of early- and late-successional specialists. The typically longer fire-free intervals in low fire frequency areas should indeed favour late-successional specialists, and *vice versa* for the early-successional specialists in high fire frequency areas, while successional generalists should show a relatively constant abundance among high and low fire frequency areas. Second, we evaluated whether this heterogeneity in fire frequency influences the vegetation dynamics, i.e. whether differences in composition are primarily due to the fact that the last local fire-free intervals differ or if the consistently longer fire-free intervals, repeated over time, may have amplified differences between these portions of the landscape.

Methods

Study area and main tree species

The study area covers 15 961 km² of boreal forest in eastern Quebec, specifically in the North Shore region (67–69°W, 49–50.25°N (Fig. 1)). This region has a cold, maritime climate with an average annual temperature of 1.4 °C and average precipitation of 1018 mm, as measured at Baie Comeau in the southwest corner of the study area. Precipitation is evenly distributed throughout the year, and is about 70% rain (Environment Canada 1996). The topography is moderately rugged, with high hills with rounded summits and many rocky escarpments. The highest hills, located in the northeast part of the area, are just over 700-m high while other sparsely distributed hills exceed 500 m. There are rocky outcrops on slightly more than one-third of the total land area, while the rest of the land area consists mainly of shallow tills on sloping areas and deep tills at the bottom of slopes. To a lesser extent, there are sandy glaciofluvial deposits on valley floors (Robitaille & Saucier 1998).

Black spruce [*Picea mariana* (Mill.) B.S.P.] and balsam fir [*Abies balsamea* (L.) Mill.] are the dominant species, along

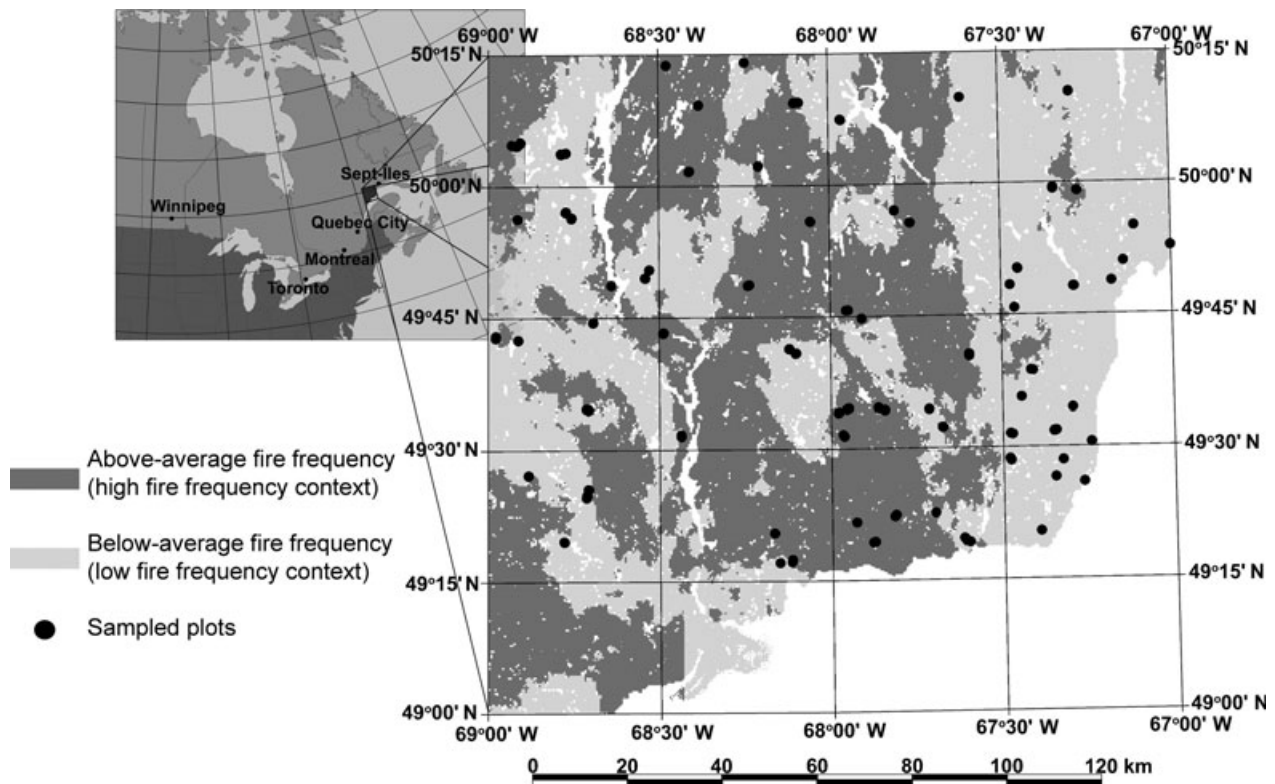


Fig. 1. Study area and spatial distribution of sampled plots. Note that some plots are clustered. These clusters are made up of two to four plots, with each pair within these clusters being separated by 100–425 m.

with white spruce [*Picea glauca* (Moench) Voss] and white birch (*Betula papyrifera* Marsh.). Trembling aspen (*Populus tremuloides* Michx.) and jack pine (*Pinus banksiana* Lamb.) can also be found, but in lower abundance. Tamarack [*Larix laricina* (Du Roi) K. Koch] can be found along with *P. mariana* in a few rare hydric stations in the region. The six most common tree species, i.e. all of the above-mentioned species except tamarack, were classified on the basis of their typical position along the successional gradient in this region. This classification is based on adaptations to fire, shade tolerance and ability to regenerate under a closed canopy. *Betula papyrifera* and *P. tremuloides* were classified as early-successional specialists (long-distance dispersal of small and abundant seeds and vegetative reproduction, shade intolerant; Perala 1990; Safford et al. 1990; Humbert et al. 2007), as was *P. banksiana* (serotinous cones that open after fire and promote early establishment, shade intolerant; Rudolph & Laidly 1990; Gauthier et al. 1993; Humbert et al. 2007). When these early-successional specialists make up the largest part of a young stand, they are typically replaced by *P. mariana*, *P. glauca* or *A. balsamea* when the initial cohort starts to break up (Bergeron 2000; De Grandpré et al. 2000). *Abies balsamea* is the main late-successional specialist in this system (no fire adaptation and shade tolerant; Bakusis &

Hansen 1965; De Grandpré et al. 2000). Consequently, it is generally abundant in stands that have not burned for a long time. *Picea mariana* is the archetypal generalist on many levels (semi-serotinous cones and seed dispersal both with and without fire, shade tolerant and vegetative reproduction; Viereck & Johnson 1990). In late-succession stages, *P. mariana* often maintains dominance or at least a strong presence alongside *A. balsamea* in this region (De Grandpré et al. 2000; Pham et al. 2004; Bouchard et al. 2008), even on mesic sites where *A. balsamea* is considered more competitive (Bakusis & Hansen 1965). Finally, we also classified *P. glauca* as a generalist (no particular fire adaptation, mast year post-fire regeneration, intermediate shade tolerance; Galipeau et al. 1997; Peters et al. 2005; Humbert et al. 2007).

Data acquisition

One hundred and sixty 400-m² circular plots showing no sign of past anthropogenic disturbance were sampled for canopy vegetation. Plots were clustered into groups of two to four plots located at distances varying between 100 to 425 m. The centre of the first plot of each cluster was systematically positioned 100 m from a randomly selected point on the road network. The other plots were

positioned 100 m from the previous one in the direction that maximized the gradient of edaphic conditions present nearby, i.e. that maximized the variety of position on the slope, surficial deposit, etc. We did not sample recently burned sites (the most recently burned site was burned 47 yr prior to fieldwork) or sites that showed signs of past harvesting. All trees with a diameter at breast height (DBH) of 1 cm or more were measured (DBH and height) and species determined. The geographic location, edaphic conditions and local fire history were noted for each station (see Table 1 for complete listing of environmental covariates) and considered as covariates, which may partly explain species composition. We make an important distinction between local fire history and fire frequency areas. Through the analysis described below, we tried to control for the influence of the number of years elapsed since the last fire, as a local determinant of canopy composition, and areas of contrasting fire frequency, as a potential broader-scale determinant of canopy composition. As our main objective is to assess whether the heterogeneity in fire frequency has a major effect on vegetation dynamics, we wanted to control for the local effect of time since fire. This factor was therefore considered within a set of local environmental covariates of which we wanted to control the influence on vegetation composition. This allowed us to evaluate whether the differences in composition were only due to the fact that the local fire-free intervals differ or because the con-

sistently longer fire-free intervals, repeated over time, may have amplified differences between these portions of the landscape.

For each plot, we attempted to date the last fire event by counting the rings of ten to 15 dominant trees that were found outside but in close proximity to the sampled plot (less than 30 m) using either cores or cross-sections. For that specific purpose, we favoured the species that were more likely to originate from a fire event. In decreasing order of preference, we selected *P. banksiana*, *P. tremuloides*, *B. papyrifera*, *P. mariana*, *P. glauca* and *A. balsamea*. The age of the oldest tree at each location was used as an indication of the time since fire because regeneration starts reestablishment almost immediately after the fire event, although the process can last for several years (St-Pierre et al. 1992; Jayen et al. 2006). This indicator was deemed sufficiently reliable and considered as a known fire-free interval if a 20-yr interval included at least 60% of the trees, especially if the growth patterns suggested open canopy conditions at establishment dates, while only a minimum time since fire was assigned when these conditions were not met. However, a visual examination of each stand's age structure suggested that a 20-yr interval was too restrictive in the case of some of the older stands that seemed in fact even-aged, probably because of increasing imprecision of dating the establishment dates as stand age increases (DesRochers & Gagnon 1997; Parent et al. 2000). We thus chose to extend this to 30 yr for stands where the older tree age was more than 200 yr. A minimum age was also assigned to stands where the only trees that could be dated were primarily of one species that usually does not establish itself directly after a fire, e.g. *A. balsamea*, independently of their age structure.

Stands were then classified as young/old based on whether they were younger or older than 150 yr, which roughly corresponds to the age at which stands break up (De Grandpré et al. 2009; Gauthier et al. 2010). The age class distribution at the landscape level was also assessed.

We partitioned the landscape into two classes based on their relative fire frequency as predicted in a previously published survival model (Cyr et al. 2007). In statistical terms, the relative fire frequency corresponds to a relative risk established with the mean fire frequency of the entire study area as a constant denominator. This survival model included longitude (as a proxy for maritime influence) and dominant aspect within a 8750-m neighbourhood radius as predictors of relative fire frequency throughout the landscape. It is noteworthy that these model predictions are independent of present vegetation and time since last fire. Using this model, we were able to create a map showing above- and below-average fire frequency areas, referred to as high and low fire frequency areas, respectively (Fig. 1). The mean fire interval (1/mean fire

Table 1. Local environmental covariates and correlations with NMDS axis (see Fig. 3). *P-values are based on 10 000 permutations. Bold characters indicate significant values under a 5% threshold.

	Spearman's Rho (Non-parametric correlation coefficient)			P-value*
	NMDS1	NMDS2	NMDS3	
Latitude (Decimal Degrees)	0.0113	0.3608	0.0509	< 0.0001
Longitude (Decimal Degrees)	-0.2367	0.0844	0.0867	0.0624
Elevation (Meters)	-0.0322	0.3229	0.0657	0.0017
Rocky outcrop (Binary)	0.0803	0.0190	-0.0046	0.6651
Shallow till (Binary)	-0.1094	0.0346	-0.1160	0.0663
Deep till (Binary)	-0.2044	0.1988	-0.0023	0.0199
Sand (Binary)	0.1572	-0.1320	0.0859	0.0023
North aspect (Binary)	0.0284	-0.0006	-0.0450	0.8073
South aspect (Binary)	0.0583	0.1473	0.0833	0.3805
Slope (Percentage)	-0.2703	0.0941	-0.1278	0.0003
Drainage (Ordinal, Seven classes)	-0.0001	0.1094	-0.0735	0.5144
Time since fire (Years)	0.0028	0.5017	-0.1014	< 0.0001
Censorship (Binary)	-0.2790	0.5319	0.12998	< 0.0001
NMDS 1st Axis	1	0.3454	-0.2373	
NMDS 2nd Axis	0.3454	1	-0.2730	
NMDS 3rd Axis	-0.2373	-0.2730	1	

frequency) in the entire study area is 226 yr (Cyr 2011), with a 95% bootstrap confidence interval ranging from 147 to 395 yr. After stratification, the high and low fire frequency areas have a mean fire interval of 164 (95% confidence interval: 126–205) and 722 yr (95% confidence interval: 353–1760), respectively.

Data analysis

As a preliminary analysis, we compared the age class distribution at the landscape level between areas of contrasting fire frequency, both visually and by means of a chi-square contingency analysis, testing for differences in the proportion of stands for which only a minimum estimate of the time elapsed since last fire is known (censored intervals).

To describe canopy composition and compare areas of contrasting fire frequency and age classes, we performed a non-metric multidimensional scaling ordination (NMDS; Kruskal 1964) based on Bray-Curtis distance matrix (Legendre & Legendre 1998) between sampled plots ($n = 161$). The distance matrix was calculated from relative basal area of stems with DBH larger than 1 cm. We used relative basal area to control for variations in absolute basal area that are related to time since last fire. NMDS was performed with R version 2.9.0 (R Development Core Team, Vienna, Austria) using the metaMDS function in the VEGAN package (Oksanen et al. 2009). It was determined that three dimensions provided the best compromise between a low stress factor (k) and the interpretability of the visual output. Aside from the number of dimensions, which was determined manually, metaMDS initiated the iterative process at random starts, and selected among similar solutions with smallest stresses after submitting the raw data and/or the dissimilarity matrix to the most appropriate transformations (e.g. scaling and rotation). We used the multi-response permutation procedure (MRPP), also in the VEGAN package, to test for differences in composition between fire frequency areas using two age strata (young: < 150 yr since last fire, old: ≥ 150 yr since last fire) as a constraint for permutations. Local environmental covariates, including time since the last fire, were fitted as vectors or centroids, depending on whether they were continuous or nominal covariates, respectively. Only significant associations under the 0.05 probability threshold are displayed on the ordination, which were also assessed based on random permutations.

Two series of ANOVA-like permutation tests were subsequently performed on each species to compare the relative abundance of individual species between fire frequency areas, again using age strata as a constraint for permutations. The first series of permutation tests was performed with no transformation of species relative abun-

dance. Then, to control for collinearity between fire frequency areas and local environmental covariates, we extracted the variance explained by a matrix of all local environmental covariates using a multiple linear regression within each age stratum, and compared the residuals values of species' relative abundance between fire frequency areas by means of a second series of ANOVA-like permutation tests. No variable selection was performed during these regressions, as the objective was to control for the most locally induced variability possible (see Appendix S1 for details).

All permutation-based tests were based on 10 000 random permutations and the significance thresholds for all series of univariate ANOVA-like permutation tests were adjusted for multiple comparisons using Holm's procedure (Holm 1979).

Results

Age class distribution at the landscape level

An approximately three-fold variation in mean fire-free intervals between areas of contrasting fire frequency produced considerable differences in age class distribution at the landscape level (Fig. 2). The relative proportion of young stands indeed seems substantially higher in high fire frequency areas when compared with low fire frequency areas, and inversely for the proportions of old stands. This general appearance of the distributions, however, must be complemented by a comparison of the proportions of stands for which only a minimum age is known. This comparison confirms a significant difference between fire frequency areas, as the proportion of stands for which only a minimum age is known is about 22% higher in low fire frequency areas ($\chi^2 = 4.585$; $P = 0.0323$; $df = 1$) than in high fire frequency areas.

Comparison of canopy composition among fire frequency areas and age strata groups

The NMDS ordination (Fig. 3) shows a relatively clear distinction between the canopy tree composition of young and old stands located in either high or low fire frequency areas. The 50% confidence interval ellipses show that the fire frequency areas can be better deciphered along the first axis of the ordination, while the age strata and most other local environmental factors are more related to the second axis. Differences between fire frequency areas are confirmed by the multi-response permutation procedure conducted using age classes as strata constraining random permutations ($P < 0.0001$). While the old stands' 50% confidence interval ellipses are distinct both on the basis of their location (composition) and spread (variability in composition) in the coordinate system, the difference

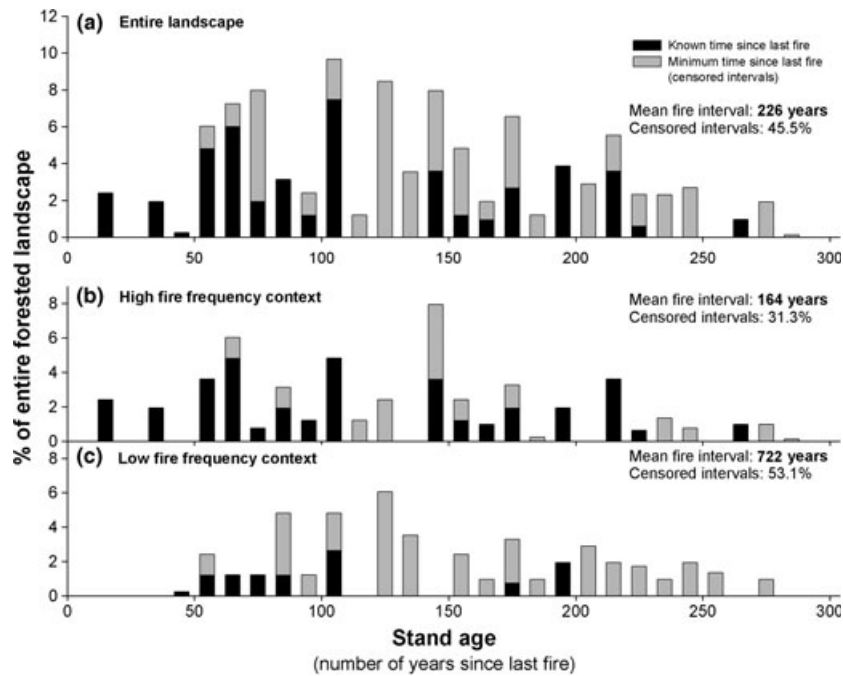


Fig. 2. Age class distribution at the landscape level for (a) the entire landscape, (b) high fire frequency areas (above average fire frequency) and (c) low fire frequency areas (below average fire frequency). The proportions shown here are representative of the forested landscape (adapted from Cyr et al. 2007) and do not exactly correspond to the number of plots sampled for the present vegetation study.

relative to fire frequency areas in young stands appears to be more related to the variability in stand composition, as the ellipses largely overlap and mostly differ in size.

Picea mariana and *A. balsamea* are the dominant species in this landscape. All species are present in young stands,

while there is an almost complete exclusion of *P. banksiana* and *P. tremuloides* in old stands (Fig. 4a). Young and old stands located in high fire frequency areas are more similar than their counterparts located in low fire frequency areas (Fig. 3a). *Picea mariana* maintains a strong

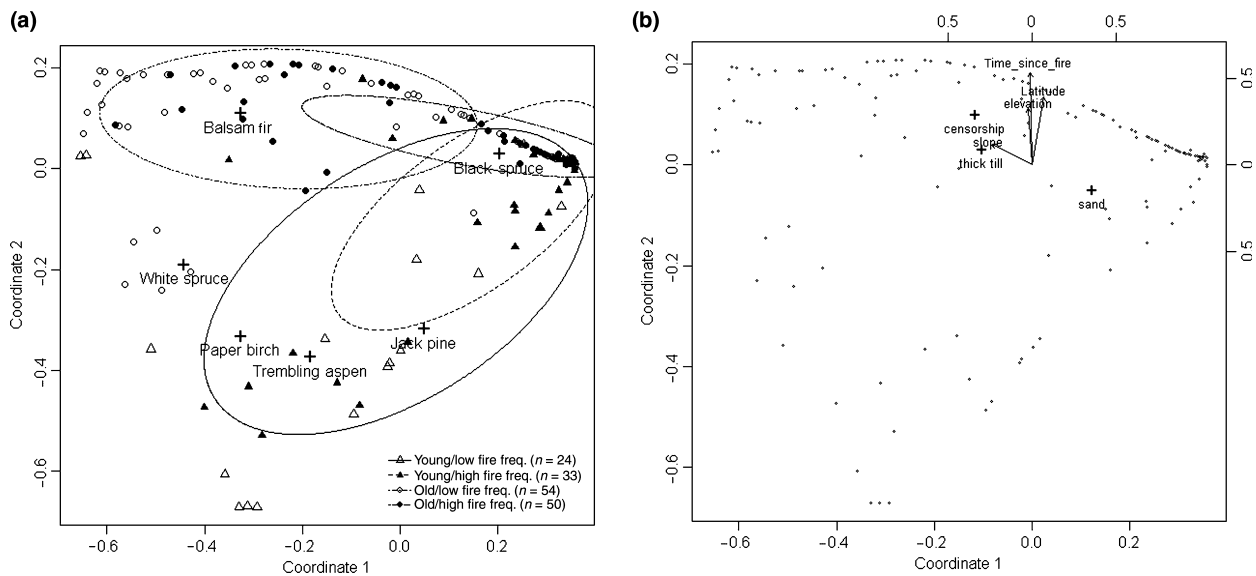


Fig. 3. NMDS ordinations showing sampled plots on the basis of the relative basal area of each species. The final stress was 5.5309 after 20 iterations. (a) 50% confidence ellipses for each group and species centroids. Groups significantly ($P < 0.0001$) differ based on 10 000 permutations within the same age class. (b) Environmental covariate fitting represented as vectors for continuous covariates and centroids for categorical covariates. Upper right axis indicates correlations between continuous covariates and ordination axis.

presence in all groups, while *A. balsamea* is mostly confined to old stands.

The first series of non-parametric ANOVA-like comparisons of the relative abundance of individual species within each age class revealed that significant differences between fire frequency areas could only be detected in old stands. *Abies balsamea* could indeed be found in greater relative abundance in low fire frequency areas, as was *P. glauca*, although it made up only a minor part of the forest landscape, while *P. mariana* had greater abundance in the high fire frequency areas (see Fig. 4 and Appendix S2 for detailed results).

The coordinate system of the NMDS, however, is significantly correlated with local environmental covariates that are known to affect species composition. The first ordination axis was negatively correlated with slope and deep tills and positively correlated with sand deposits, while the second axis was positively correlated with latitude, elevation, the age of the oldest tree and censorship. A second series of non-parametric ANOVA-like permutations on residual values of species' relative abundances was thus conducted after controlling for the influence of local environmental covariates, including time since last fire. This confirmed a significantly lower proportion of *P. mariana* in old stands located in low fire frequency areas, while *A. balsamea* is

more abundant in old forests located in low fire frequency areas (Fig. 4; Appendix S2). No significant difference in the relative abundance of *P. glauca* could be detected after controlling for the influence of local environmental covariates.

No significant differences in the relative abundances of individual species were detected in young stands, either before or after controlling for the influence of local environmental covariates (Fig. 4), despite significant differences in overall composition (Fig. 3). The most notable trend between young stands of contrasting fire frequency, however, is that *P. mariana* seems more likely to be found in high fire frequency areas, which appears to affect the variability in stand composition, as suggested by the size of the 50% confidence interval ellipses (Fig. 3).

Discussion

The first and most obvious repercussion of contrasting fire frequency at this intermediate scale is observed on the age structure at the landscape level. As the fire-free intervals are generally longer in low fire frequency areas, the proportion of old stands is much higher. Considering the number of stands for which only a minimum age is known, the actual tail of the stand age distribution is longer than it appears and thus contrasts even more with that observed in high fire frequency areas. This may explain in large part the differences between high and low fire frequency areas that were observed in old stands even after controlling for local environmental factors.

Species' relative abundance in old stands

Stands exceeding 150 yr of age make up the vast majority of this landscape. This explains why the most abundant species in the landscape are those that have the ability to thrive in late succession: *A. balsamea* and *P. mariana*. While *A. balsamea* is without doubt the main late-successional specialist in this region of the boreal forest, mainly because of the ability of its seedlings to withstand the heaviest shade conditions in order to take the opportunity to fill gaps that are eventually created in the canopy, the archetypal boreal generalist *P. mariana* is even more abundant as it can grow in a wider variety of conditions. Our results, as well as results from previous studies (De Grandpré et al. 2000; Bouchard et al. 2008), suggest that late-successional stands of this region usually converge towards either *P. mariana*- or *A. balsamea*-dominated stands or a mixture of the two (Gauthier et al. 2010). Whether an old stand will be dominated by *P. mariana* or *A. balsamea* appears to be largely determined by edaphic conditions (De Grandpré et al. 2000), which is confirmed in our study by a strong association of *A. balsamea* with deep tills. However, the generally longer fire-free intervals that characterize low fire

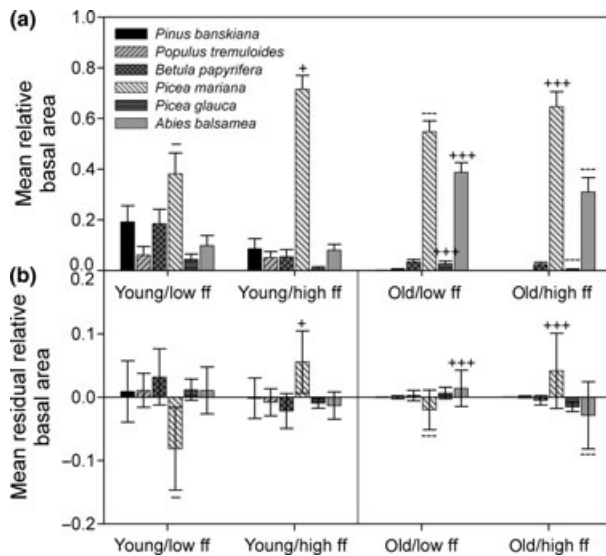


Fig. 4. (a) Mean relative abundance of the six most common tree species for each fire frequency class and age stratum (< 150 and \geq 150 yr), and (b) residual values after removing the variance explained by local environmental covariates. Error bars indicate standard error. Significant differences in mean relative basal area (and residuals) between fire frequency areas within the same age class are indicated by plus (+) and minus (-) signs. $P < 0.05$ (- or +), $P < 0.01$ (- or ++) and $P < 0.001$ (- or +++) after Holm's (1979) correction for multiple comparisons. Detailed results for all pair-wise comparisons can be found in Appendix S2.

frequency areas appear to be an additional determinant of this species' relative abundance in old forest.

We currently do not have a very clear understanding of what happens in old stands, as the time since fire exceeds what can typically be measured by dendroecological dating of fire events (200–300 yr), which of course limits our knowledge of stand dynamics in the tail of such a long chronosequence. However, we know that the influence of smaller-scale disturbances such as insects and windthrows become very important in stand dynamics and influences species' dominance (De Grandpré et al. 2000; Bouchard et al. 2008; Gauthier et al. 2010). Pham et al. (2004) showed, in a study on gap dynamics in this region, that self-replacement of these two species is most common in old stands when they dominate. Reciprocal replacement, however, is common when both species are present, with a slight advantage to *A. balsamea*. At the stand level, relatively shorter fire-free intervals in high fire frequency areas may truncate succession on some sites where *A. balsamea* would normally become dominant, allowing a higher relative abundance of *P. mariana*. This supports the idea of a generally increasing proportion of *A. balsamea* as stands become older, although this process is not irreversible and might follow a 'two steps forward, one step back' kind of dynamics. A succession from *P. mariana* towards *A. balsamea* can therefore require many successive cohorts and could occur gradually and slowly, long after what is covered by typical dendroecological analyses.

Species' relative abundance in young stands

In the case of old forest stands, the late-successional specialist *A. balsamea* showed it is favoured by a generally longer time since fire. However, the reverse hypothesis, suggesting that early-succession species, i.e. *P. tremuloides*, *B. papyrifera* and *P. banksiana*, would be favoured by higher fire frequency at this intermediate spatial scale is not supported. No clear trends in relative abundance of early-successional specialists could be detected. This result shows that the availability of propagules for the early-successional tree species is not limited by the scarcity of other young stands in low fire frequency areas, at least not more than in high fire frequency areas. Long-distance, massive seed dispersal certainly explains this in large part for intolerant hardwood species such as *P. tremuloides* and *B. papyrifera* (Perala 1990; Safford et al. 1990). The same mechanism cannot be invoked in the case of *P. banksiana* because it is known to disperse only over relatively short distances (Rudolph & Laidly 1990). Its strong association with sandy deposits possibly made it least likely to be affected by landscape-level heterogeneity in fire frequency, especially considering that anecdotal observations of multiple fire scars in such stands (pers. obs.) may indicate that a distinct, less

severe but more frequent fire regime may be at work in some exceptional stands (see also Smirnova et al. 2008).

Although we could not detect significant differences in individual species' relative abundance in young stands between areas of contrasting fire frequency, the overall species composition differs, but mainly in terms of variability. The fact that relatively shorter fire-free intervals in high fire frequency areas may favour *P. mariana* in sites where *A. balsamea* would normally become dominant by truncating succession may also increase the likelihood of *P. mariana* reestablishment after a fire event. Pre-fire composition indeed influences the outcome of early establishment in recently burned stands (McCune & Allen 1985; Motzkin et al. 1999), hence explaining the stronger similarity in stand composition between young and old stands in high fire frequency areas than in low fire frequency areas (e.g. Greene et al. 1999). *Picea mariana* indeed benefits more often from local aerial seed banks provided by its semi-serotinous cones. Comparatively, *A. balsamea* is more common in low fire frequency areas but is poorly adapted to fire and almost never successfully re-establishes itself immediately after fire, hence leaving an open site for early-successional species. Furthermore, it's been shown that stands that start succession with intolerant hardwoods seem to be more prone to faster reestablishment and future dominance of *A. balsamea* (Gauthier et al. 2010; Arbour et al. 2011). It is also possible that in the unlikely situation where successive fire events should occur in low fire frequency areas, a higher proportion of hardwoods might be favourable to the survival of some *A. balsamea* individuals through decreasing fire severity in the canopy (Kafka et al. 2001), which could also contribute to a faster reestablishment of this late-successional specialist (Bergeron et al. 2004).

Conclusions

The landscape-level heterogeneity in fire frequency influences the distribution and relative importance of the two main tree species in this boreal landscape, i.e. *P. mariana* and *A. balsamea*. We suggest that the higher relative importance of *A. balsamea* in low fire frequency areas can be in large part explained by the typically longer local fire-free intervals that cannot be accounted for in dendroecologically-based chronosequences. Stands older than 200–300 yr, for which only a minimum age can be determined, are indeed often pooled in an open age class (e.g. Christensen & Peet 1984; De Grandpré et al. 2000; Bouchard et al. 2008). Our results show that the slow replacement of *P. mariana* with *A. balsamea* on suitable sites may take much longer than that amount of time (200–300 yr) because of the combined effects of the longevity of *P. mariana* and the non-monotonous aspect of the replacement

process (Pham et al. 2004; Gauthier et al. 2010). This type of canopy succession would be truncated more often in high fire frequency areas. Therefore, this mechanism is not an effect of landscape-level heterogeneity in fire frequency *per se* as the local fire history remains the main determinant of canopy composition. However, landscape-level heterogeneity in fire frequency can be considered as an indirect determinant of stand-scale canopy composition, as it determines where in the landscape such a long successional process is more likely to be uninterrupted by a fire event.

References

- Arbour, M.-L. & Bergeron, Y. 2011. Effect of increased *Populus* cover on *Abies* regeneration in the *Picea*-feathermoss boreal forest. *Journal of Vegetation Science*. doi: 10.1111/j.1654-1103.2011.01314.x.
- Baker, W.L. 1995. Long-term response of disturbance landscapes to human intervention and global change. *Landscape Ecology* 10: 143–159.
- Bakusis, E.V. & Hansen, H.S. 1965. *Balsam fir: a monographic review*. The University of Minnesota Press, Minneapolis, MN, US.
- Bergeron, Y. 2000. Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. *Ecology* 81: 1500–1516.
- Bergeron, Y., Gauthier, S., Flannigan, M. & Kafka, V. 2004. Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec. *Ecology* 85: 1916–1932.
- Bouchard, M., Pothier, D. & Gauthier, S. 2008. Fire return intervals and tree species succession in the North Shore region of eastern Quebec. *Canadian Journal of Forest Research* 38: 1621–1633.
- Brassard, B.W., Chen, H.Y.H., Wang, J.R. & Duinker, P.N. 2008. Effects of time since stand-replacing fire and overstorey composition on live-tree structural diversity in the boreal forest of central Canada. *Canadian Journal of Forest Research* 38: 52–62.
- Bridge, S.R.J. 2001. *Spatial and temporal variations in the fire cycle across Ontario*. In: Ontario Ministry of Natural Resources – Northeast Science & Technology, ON, CA.
- Burton, P.J., Parisien, M.A., Hicke, J.A., Hall, R.J. & Freeburn, J.T. 2008. Large fires as agents of ecological diversity in the North American boreal forest. *International Journal of Wildland Fire* 17: 754–767.
- Christensen, N.L. & Peet, R.K. 1984. Convergence during secondary forest succession. *Journal of Ecology* 72: 25–36.
- Cyr, D. 2011. *Cycle des feux, vieilles forêts et aménagement en forêt boréale de l'est du Canada*. PhD Thesis, Université du Québec à Montréal, Montreal, CA.
- Cyr, D., Bergeron, Y., Gauthier, S. & Larouche, A. 2005. Are the Old-Growth Forests of the Clay Belt Part of a Fire-Regulated Mosaic? *Canadian Journal of Forest Research* 35: 65–73.
- Cyr, D., Gauthier, S. & Bergeron, Y. 2007. Scale-dependent determinants of heterogeneity in fire frequency in a coniferous boreal forest of eastern Canada. *Landscape Ecology* 22: 1325–1339.
- De Grandpré, L., Morissette, J. & Gauthier, S. 2000. Long-term post-fire changes in the northeastern boreal forest of Quebec. *Journal of Vegetation Science* 11: 791–800.
- De Grandpré, L., Gauthier, S., Allain, C., Cyr, D., Pérignon, S., Pham, A.T., Boucher, D., Morissette, J., Reyes, G., Aakala, T. & Kuuluvainen, T. 2009. Towards an ecosystem approach to managing the boreal forest in the North Shore region. In: Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpré, L., Kneeshaw, D., Morin, H., Drapeau, P. & Bergeron, Y. (eds.) *Ecosystem management in the boreal forest*, pp. 229–255. Les Presses de l'Université du Québec, QC, CA.
- DesRochers, A. & Gagnon, R. 1997. Is ring count at ground level a good estimation of black spruce age? *Canadian Journal of Forest Research* 27: 1263–1267.
- Eberhart, K.E. & Woodard, P.M. 1987. Distribution of residual vegetation associated with large fires in Alberta. *Canadian Journal of Forest Research* 17: 1207–1212.
- Environment Canada 1996. *Canadian climate normals 1947–1996*. Canadian Climate Program. Environment Canada. Atmospheric Environment Service, Downsview, Ontario, CA.
- Foster, D.R., Knight, D.H. & Franklin, J.F. 1998. Landscape Patterns and Legacies Resulting From Large, Infrequent Forest Disturbances. *Ecosystems* 1: 497–510.
- Galipeau, C., Kneeshaw, D. & Bergeron, Y. 1997. White spruce and balsam fir colonization of a site in the southeastern boreal forest as observed 68 years after fire. *Canadian Journal of Forest Research* 27: 139–147.
- Gauthier, S., Bergeron, Y. & Simon, J.P. 1993. Cone serotiny in jack pine: ontogenetic, positional, and environmental effects. *Canadian Journal of Forest Research* 23: 394–401.
- Gauthier, S., Boucher, D., Morissette, J. & De Grandpré, L. 2010. Fifty-seven years of composition change in the eastern boreal forest of Canada. *Journal of Vegetation Science* 21: 772–785.
- Gavin, D.G., Brubaker, L.B. & Lertzman, K. 2003. Holocene fire history of a coastal temperate rain forest based on soil charcoal radiocarbon dates. *Ecology* 84: 186–201.
- Girardin, M.P., Ali, A.A., Carcaillet, C., Mundelsee, M., Drobyshev, I., Hély, C. & Bergeron, Y. 2009. Heterogeneous response of circumboreal wildfire risk to climate change since the early 1900s. *Global Change Biology* 15: 2751–2769.
- Greene, D.F., Zasada, J.C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I. & Simard, M.J. 1999. A review of the regeneration dynamics of North American boreal forest tree species. *Canadian Journal of Forest Research* 29: 824–839.
- Harper, K.A., Bergeron, Y., Drapeau, P., Gauthier, S. & De Grandpré, L. 2005. Structural development following fire in black spruce boreal forest. *Forest Ecology and Management* 206: 293–306.
- Hellberg, E., Niklasson, M. & Granström, A. 2004. Influence of landscape structure on patterns of forest fires in boreal forest landscapes in Sweden. *Canadian Journal of Forest Research* 34: 332–338.

- Holm, S. 1979. A Simple Sequentially Rejective Multiple Test Procedure. *Scandinavian Journal of Statistics* 6: 65–70.
- Humbert, L., Gagnon, D., Kneeshaw, D. & Messier, C. 2007. A shade tolerance index for common understory species of northeastern North America. *Ecological Indicators* 7: 195–207.
- Jayen, K., Leduc, A. & Bergeron, Y. 2006. Effect of fire severity on regeneration success in the boreal forest of northwest Québec, Canada. *Ecoscience* 13: 143–151.
- Johnson, E.A. 1992. *Fire and vegetation dynamics: Studies from the North American boreal forest*. Cambridge University Press, New York, NY, US.
- Johnstone, J.F. & Chapin, F.S.Iii 2006. Fire interval effects on successional trajectory in boreal forests of northwest Canada. *Ecosystems* 9: 268–277.
- Kafka, V., Gauthier, S. & Bergeron, Y. 2001. Fire Impacts and Crowning in the Boreal Forest: study of a Large Wildfire in Western Quebec. *International Journal of Wildland Fire* 10: 119–127.
- Keeton, W.S. & Franklin, J.F. 2005. Do remnant old-growth trees accelerate rates of succession in mature Douglas-fir forests? *Ecological Monographs* 75: 103–118.
- Kruskal, J.B. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 29: 1–27.
- Larsen, C.P.S. 1997. Spatial and temporal variations in boreal forest fire frequency in northern Alberta. *Journal of Biogeography* 24: 663–673.
- Lefort, P., Gauthier, S. & Bergeron, Y. 2003. The influence of fire, weather and land use on the fire activity of the lake Abitibi Area, Eastern Canada. *Forest Science*. 49: 509–521.
- Legendre, P. & Legendre, L. 1998. *Numerical Ecology. 2nd English*. Elsevier, New York, NY, US.
- Li, C., Coms, I.G.W. & Yang, R.C. 1999. Fire frequency and size distribution under natural conditions: a new hypothesis. *Landscape Ecology* 14: 533–542.
- Madoui, A., Leduc, A., Gauthier, S. & Bergeron, Y. 2010. Spatial pattern analyses of post-fire residual stands in the black spruce boreal forest of western Quebec. *International Journal of Wildland Fire* 19: 1110–1126.
- Mansuy, N., Gauthier, S., Robitaille, A. & Bergeron, Y. 2010. The effects of surficial deposit-drainage combinations on spatial variations of fire cycles in the boreal forest of eastern Canada. *International Journal of Wildland Fire* 19: 1083–1098.
- McCune, B. & Allen, T.F.H. 1985. Will similar forests develop on similar sites? *Canadian Journal of Botany* 63: 367–376.
- Motzkin, G., Wilson, P., Foster, D.R. & Allen, A. 1999. Vegetation patterns in heterogeneous landscapes: the importance of history and environment. *Journal of Vegetation Science* 10: 903–920.
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G.L., Solymos, P.M., Stevens, H.H. & Wagner, H. 2009. *Vegan: Community Ecology Package*. In: R package version 1.15-2, Vienna, Austria.
- Parent, S., Morin, H. & Messier, C. 2000. Effects of adventitious roots on age determination in balsam fir (*Abies balsamea*) regeneration. *Canadian Journal of Forest Research* 30: 513–518.
- Payette, S. 1992. Fire as a controlling process in the North American boreal forest. In: Shugart, H.H., Leemans, R. & Bonan, G. B. (eds.) *A system analysis of the global boreal forest*, pp. 144–169. Cambridge University Press, New York, NY, US.
- Perala, D.A. 1990. *Populus tremuloides* Michx. Quaking aspen. In: Burns, R.H. & Honkala, B.H. (eds.) *Silvics of North America - Vol. 2 Hardwoods*, pp. 555–569. US Department of Agriculture, Washington, DC, US.
- Peters, V.S., Macdonald, S.E. & Dale, M.R.T. 2005. The interaction between masting and fire is key to white spruce regeneration. *Ecology* 86: 1744–1750.
- Pham, A.T., De Grandpré, L., Gauthier, S. & Bergeron, Y. 2004. Gap dynamics and replacement patterns in gaps of the north-eastern boreal forest of Quebec. *Canadian Journal of Forest Research* 34: 353–364.
- Robitaille, A. & Saucier, J.P. 1998. *Paysages régionaux du Québec méridional*. Les Publications du Québec, QU, CA.
- Rudolph, T.D. & Laidly, P.R. 1990. *Pinus banksiana* Lamb. Jack pine. In: Burns, R.H. & Honkala, B.H. (eds.) *Silvics of North America - Vol. 1 Conifers*, pp. 280–293. US Department of Agriculture, Washington, DC, US.
- Safford, L.O., Bjorkbom, J.C. & Zasada, J.C. 1990. *Betula papyrifera* Marsh. Paper birch. In: Burns, R.H. & Honkala, B.H. (eds.) *Silvics of North America - Vol. 2 Hardwoods*, pp. 158–171. US Department of Agriculture, Washington, DC, US.
- Smirnova, E., Bergeron, Y. & Brais, S. 2008. Influence of fire intensity on structure and composition of jack pine stands in the boreal forest of Quebec: Live trees, understory vegetation and dead wood dynamics. *Forest Ecology and Management* 255: 2916–2927.
- St-Pierre, H., Gagnon, R. & Bellefleur, P. 1992. Régénération après feu de l'épinette noire (*Picea mariana*) et du pin gris (*Pinus banksiana*) dans la forêt boréale, Québec. *Canadian Journal of Forest Research* 22: 474–478.
- Turner, M.G., Hargrove, W.W., Gardner, R.H. & Romme, W.H. 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. *Journal of Vegetation Science* 5: 731–742.
- Viereck, J.S. & Johnson, W.F. 1990. *Picea mariana* (Mill.) B.S.P. Black spruce. In: Burns, R.H. & Honkala, B.H. (eds.) *Silvics of North America - Vol. 1 Conifers*, pp. 227–237. US Department of Agriculture, Washington, DC, US.
- Wein, R.W. & MacLean, D.A. 1983. *The role of fire in northern circumpolar ecosystems*. Wiley & Sons, Toronto, CA.
- Weir, J.M.H., Johnson, E.A. & Miyanishi, K. 2000. Fire frequency and the spatial age mosaic of the mixed-wood boreal forest in western Canada. *Ecological Applications* 10: 1162–1177.
- Wimberly, M.C. & Spies, T.A. 2002. Landscape- vs gap-level controls on the abundance of a fire-sensitive, late-successional tree species. *Ecosystems* 5: 232–243.

Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Parameter estimates for multiple linear regressions conducted for removing the variance explained by local environmental covariates on each species' relative basal area. Separate regressions were conducted for (a) young ($\text{tsf} < 150 \text{ yr}$) and (b) old ($\text{tsf} \geq 150 \text{ yr}$) stands. Parameter estimates \pm standard deviations are indicated.

Appendix S2. Details of permutational comparisons of mean relative species' abundance between fire frequency

areas for each age-class. (a) Before and (b) after removal of the variance explained by local environmental covariates. **P*-value estimated based on 10 000 permutations. ***P*-values are adjusted using Holm (1979) procedure. See also Figure 4.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.