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RESEARCH ARTICLE

Ecological factors shaping post-fire resilience in mature black spruce forests of eastern North America

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Abstract

1. Climate-induced fire regime shifts may reduce post-fire recovery and erode the resilience of the boreal forests. The eastern North American boreal zone is often dominated by near-monospecific stands of black spruce (BS, *Picea mariana*), a tree species with regeneration traits that are adapted to stand-replacing fire. While post-fire vulnerability of immature BS stands has been extensively studied, no study has evaluated post-fire regeneration of mature BS stands and its ecological determinants at the subcontinental scale.
2. This study assessed the fire resilience of mature BS forests and the effects of major environmental drivers on post-fire regeneration. We analysed an extensive network of 536 mature BS-dominated stands that were affected by 21 fires (1995–2016) across a 50,400 km^2 boreal landscape in eastern North America. We first quantified post-fire seedling density (seedlings/ha) of BS and co-occurring tree species to determine the proportion of plots affected by low levels of BS regeneration and potential shifts toward jack pine (JP, *Pinus banksiana*) or broadleaved species. We then analysed the effects of seed bank condition, fire characteristics (severity and seasonality) and seedbed conditions on post-fire BS regeneration.
3. One-third of the plots exhibited low-regeneration levels, particularly in stands that were dense and closed-canopy prior to the fire. A relatively minor proportion (one-fifth) also experienced compositional changes, mainly toward JP.

Generalized linear mixed-effect models indicated that higher pre-fire BS basal area and greater post-fire cover of unburned living *Sphagnum* promoted post-fire BS regeneration, whereas high-severity crown fires and spring fires had negative effects.

4. *Synthesis*. Based on a dataset of unprecedented size and spatial extent in eastern Canada, our study provides the first robust assessment of the fire resilience of mature BS forests. A third of pre-fire mature closed-canopy stands are expected to transition into open woodlands, a change that could persist for centuries. While mature BS-dominated forests are generally considered more fire-resilient than younger stands, our study raises concerns about their capacity to persist and maintain ecosystem services under the projected climate-driven increases in burned area and severity.

KEYWORDS
Composite Burn Index, ecosystem recovery, forest disturbance, forest dynamics, global change ecology, *Pinus banksiana*, post-fire regeneration, *Sphagnum*, successional trajectories

1 | INTRODUCTION

The North American boreal forest is characterized by a stand-replacing wildfire regime (Frelich et al., 2024), which influences vegetation dynamics by favouring tree species with regeneration traits that are adapted to such fires (Keeley & Pausas, 2022; Pausas et al., 2017; Ruggirello et al., 2023). Although vegetation has responded to climate change throughout the Holocene (the past ca. 11,700 years; Girardin et al., 2024; Ali et al., 2025), disturbance-induced ecosystem changes that have been observed over the last few decades are occurring at an increasing rate (Baltzer et al., 2021; Remy et al., 2017). In particular, ongoing climate change is altering fire regimes across the circumpolar boreal forest (Coogan et al., 2019; Feurdean et al., 2020; Lehtonen et al., 2016; Wang, 2024), where temperatures are rising among the fastest on Earth (IPCC, 2023). In North America's boreal forests, climate change is driving marked increase in burned areas (Jain et al., 2024) and is also increasingly favouring high-severity fires (i.e. fires that have greater impacts on vegetation and soil through combustion and heating; Keeley, 2009; Wang et al., 2025).

Most of the northeastern American boreal forest is dominated by black spruce (*Picea mariana* [Mill.] B.S.P.; hereafter BS), a conifer species that is well adapted to stand-replacing fire, and which can establish across a broad range of climatic and biophysical conditions (Johnson, 1992; Viereck & Johnston, 1990). To ensure self-replacement after fire, BS depends on a large aerial seed bank in semi-serotinous cones (Greene et al., 2013; Splawinski et al., 2022). The species reaches sexual maturity after about 50 years, but seed production peaks between 100 and 200 years, depending upon site fertility and growing degree-days (Splawinski et al., 2022; Van Bogaert et al., 2015; Viglas et al., 2013). After a fire, most seeds are released and germinate during the first 2–5 years (Greene et al., 2013; Gutsell & Johnson, 2002; St-Pierre et al., 1992), and seed availability and viability during this short time window are a sine qua non condition to ensure BS regeneration (Perrault-Hébert et al., 2017; Viglas et al., 2013). Seedling recruitment and mortality are concentrated in the first 5–10 years following fire, after which the established cohorts typically persist with little change for decades (Charron & Greene, 2002; Johnstone et al., 2004). As such, fire generates even-aged stands, which can experience modest increases in density through BS's asexual reproduction via layering during mid- to late-successional stages (>60–80 years), ensuring cohort renewal over long fire-free periods (Greene et al., 1999; Johnstone & Chapin III, 2006).

For optimal post-fire establishment and growth, BS seeds need to land on mineral soil, which can be exposed when fire burns through and consumes the organic horizons (Charron & Greene, 2002; Thomas & Wein, 1985; Wang & Kemball, 2005). Mineral soil provides a superior germination and establishment substrate for BS because it retains moisture, offers stable temperature and nutrient conditions. In contrast, thick layers of partially burned and blackened organic matter, which tend to dry out rapidly due to porous, low-density structure and lower albedo, offer a very poor substrate for BS germination and establishment. Alternatively, unburned *Sphagnum* patches can offer favourable germination conditions due to their high water-retention capacity (Boiffin & Munson, 2013; Perrault-Hébert et al., 2017), yet this substrate may hinder subsequent tree growth (Lavoie et al., 2007; Munson & Timmer, 1989; Pacé et al., 2018).

Burn severity, defined as the degree to which fire impacts the vegetation and soil through combustion and heating (Keeley, 2009), may have a dual effect on BS regeneration. On the one hand, when ground-level burn severity is too low, a thick, blackened organic layer may remain, which hinders BS regeneration (Baltzer et al., 2021; Day et al., 2023; Marty et al., 2023). On the other hand, since the species' small seeds are enclosed in thin cone scales, they are vulnerable to high temperatures (Sirois, 1993; Splawinski et al., 2022). As such, severe canopy-level burning can destroy part or all of the aerial seed bank, thereby significantly limiting post-fire regeneration (Arseneault, 2001; Reid et al., 2023; Ruggirello et al., 2023; Sirois, 1993).

When BS partially or completely fails to regenerate (i.e. BS regeneration failure), the presence of other fire-adapted species can lead to a post-fire shift in forest composition. In eastern Canada, Jack pine (*Pinus banksiana* Lamb.; hereafter JP) is the most common species that may replace BS after fire (Baltzer et al., 2021). Like BS, JP maintains an aerial seed bank in serotinous cones, but with a thicker structure that is more resistant to high-severity burning (Greene et al., 1999). Moreover, JP reaches reproductive maturity much earlier (~10 years) and produces abundant seeds by 15–30 years (Gauthier et al., 1993; Rudolph & Laidley, 1990). Consequently, stands with a low pre-fire proportion of JP frequently shift to JP dominance after fire (Baltzer et al., 2021; Boiffin & Munson, 2013; Day et al., 2023). Broadleaved (BL) boreal species (i.e. trembling aspen; *Populus tremuloides* Michx.; and white birch; *Betula papyrifera* Marsh.) may also regenerate after fire through vegetative reproduction or seed dispersion (Baltzer et al., 2021; Mack et al., 2021). When BS partially or completely fails to regenerate and no other fire-adapted species are present, fire can result in open-canopy BS woodlands or non-forest (NF) vegetation (i.e. regeneration failure; Hart et al., 2019; Baltzer et al., 2021; Burrell et al., 2021; Stevens-Rumann et al., 2022). While it is widely accepted that immature BS stands are at high risk of post-fire regeneration failure or composition shift due to underdeveloped seed banks (Girard et al., 2009; Hart et al., 2019; Perrault-Hébert et al., 2017; Viglas et al., 2013), very little information is available regarding the potential resilience and vulnerability of mature BS stands.

This study aimed to assess the fire resilience of mature BS stands and to quantify the effects of key environmental drivers on post-fire BS regeneration. We analysed an extensive network of 536 plots located within 21 fire-affected sites (burned between 1995 and 2016) distributed across a 50,400 km^2 boreal landscape in eastern North America. All sampled plots were mature (>60 years) and dominated by BS before the fires. We quantified post-fire seedling density (seedlings/ha) of BS and co-occurring tree species to determine the proportion of plots affected by low levels of BS regeneration and potential shifts toward JP or BL species, or NF vegetation (i.e. total regeneration failure). We also analysed the effects of seed bank condition, fire characteristics (severity and seasonality) and seedbed conditions on post-fire BS regeneration.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area is located in the boreal forest of eastern North America between latitudes 49°70′ N–51°90′ N and longitudes 73°58′ W–67°68′ W (Figure 1). The 21 fires under study had burned between 1995 and 2016 and are located in the BS-feather moss bioclimatic domain of Quebec, eastern Canada (Saucier et al., 2009). This bioclimatic domain is characterized by BS dominance with JP, balsam fir (*Abies balsamea* [L.] Mill.), paper birch and trembling aspen as companion species, depending upon site conditions and successional stage. The study area is mostly covered by glacial deposits, particularly undifferentiated till. Its climate is characterized by average annual temperatures varying between 0.05°C and −2.19°C, with average annual precipitation varying between 946 and 1121 mm. The growing season is short, generally extending between May and September (Environment and Climate Change Canada, 2024). The mean fire return interval varies along a longitudinal gradient, ranging from about 220 years near Lake Mistassini in the west to about 640 years near the Manicouagan Reservoir in the east (Bélisle et al., 2011; Bouchard et al., 2008; Couillard et al., 2022).

2.2 | Site selection

The studied fires were selected because: (i) they were located within the boreal closed-crown forest in the province of Quebec; (ii) they were composed of mature (>60 years) BS-dominated pre-fire stands (>50% of the basal area occupied by BS); (iii) they had burned a minimum of 3 years before field surveys to allow time for post-fire seedling establishment (St-Pierre et al., 1992); (iv) they had burned after 1984, allowing the acquisition of differenced Normalized Burn Ratio data (dNBR; see Danneyrolles et al., 2024); (v) they had not been salvage logged; and (vi) they were accessible by road. Considering the mature-old-growth age structure (mean ± SD = 158.7 ± 61.0; Supporting Information S.I.5) combined to the logging history of the area (Boucher et al., 2017), the studied stands were never clear-cut before fire. Across all selected fires, 536 circular plots of 400 m^2 (r = 11.28 m) were sampled during the summers of 2017, 2018, 2019 and 2020 following a systematic sampling design, with at least three plots distributed along the lower, middle and upper portions of each slope. Depending on the fire size and accessibility, between 4 and 152 plots were established by fire.

Finally, each plot was located at least 50 m away from any human disturbances (cutovers, roads), unburned stands, shrub-dominated vegetation or water bodies to avoid edge effects (Boucher et al., 2011; Harper et al., 2005) and were separated from one another by at least 100 m to minimize spatial autocorrelation.

2.3 | Aerial seed bank conditions

To estimate aerial seed bank conditions, we evaluated the pre-fire stand basal area and age, which are good proxies of viable seed availability (Splawinski et al., 2016; Viglas et al., 2013). In each plot, all pre-fire trees with a diameter at breast height (DBH) ≥1 cm were counted by species, and their DBH was measured to calculate stand basal area (m^2/ha). To determine the mean pre-fire stand age, transversal disks of five representative burned trees

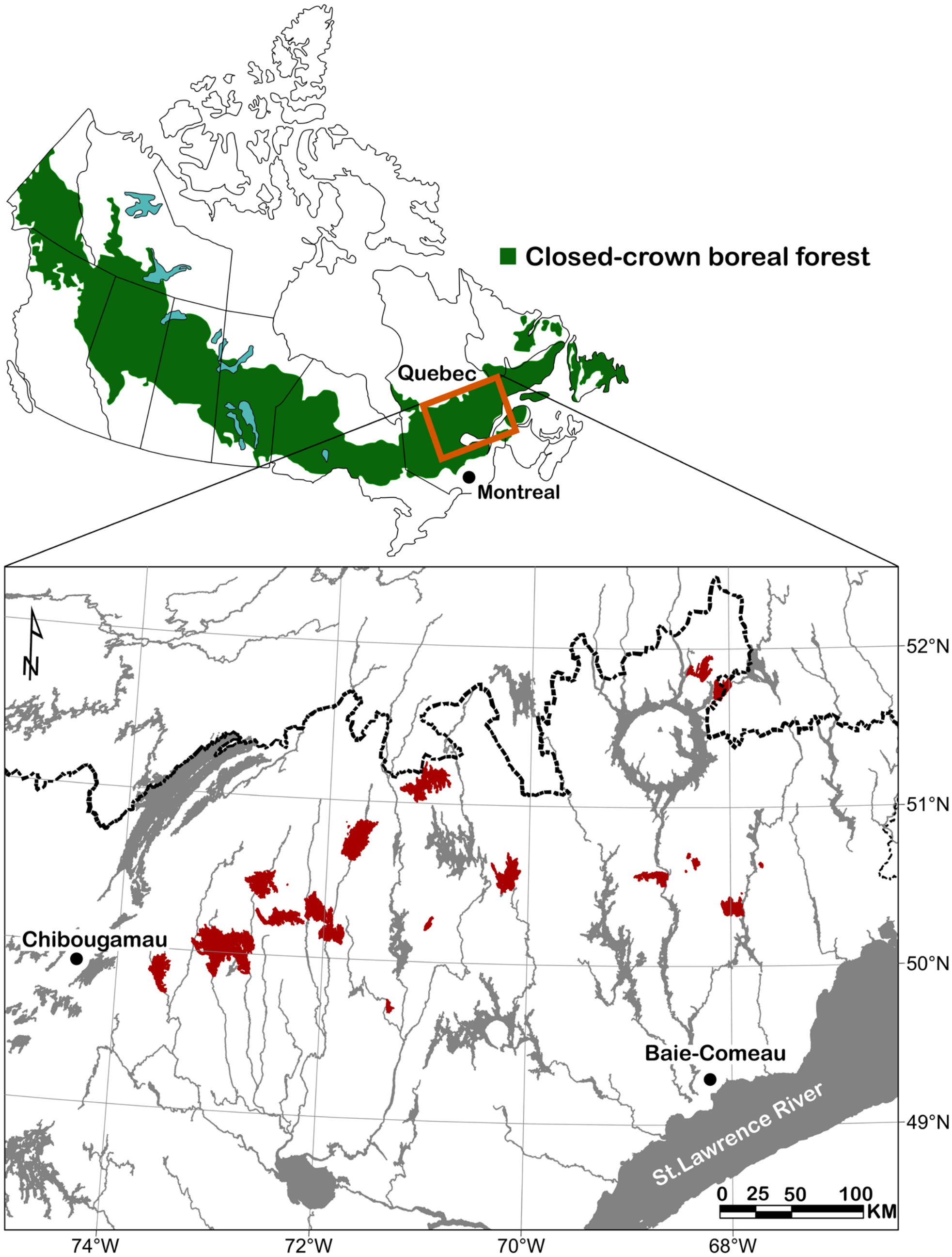

FIGURE 1 Location of the 21 studied fires (1995–2016; in red) in the closed-crown boreal forest of Quebec, eastern Canada. The hatched line corresponds to the northern boundary of the managed forest area. The closed-crown boreal forest area is drawn according to Rowe (1972).

were collected at 0.30 m from the ground surface. Samples were dried and finely sanded in the lab to count the number of annual growth rings, and tree age was adjusted to consider sampling height (Delwaide & Fillion, 2010).

2.4 | Seedbed conditions and seedling counts

The percentage cover of each understory plant species in each plot was assessed using the point-intercept method (Buckland et al., 2001). This involved two perpendicular transect lines, each measuring 22.56 m, resulting in a total length of 45.12 m across the plot. At every 0.5 m increment along these lines, 1.5-m-long metal rods were placed perpendicularly. The number of rods that were touched by each species across a plot was counted and divided by the total number of rods, yielding a percent cover value (Lutes et al., 2006). The percentage ground cover of understory plants was obtained, including living *Sphagnum* spp. moss and ericaceous shrubs. All living post-fire tree seedlings (height >0.01 m) of each of the main tree species, which included BS, JP, paper birch or trembling aspen (forming 99.9% of all tree species stems), were counted in 10 evenly distributed 4-m^2 subplots. Within-plot, stocking was also calculated as the percentage of subplots occupied by at least one seedling. The term stocking has been widely used in forestry to represent the crowdedness of stands relative to a defined norm and as a measure of the extent to which a site is occupied by trees and their potential to develop into closed-canopy forests (Yang et al., 2008). The thickness (cm) of the post-fire residual organic layer was measured at the centre of each of the 10 subplots.

2.5 | Fire characteristics

Fire seasonality was defined for each site as the date of burning using the MODIS fire-detection product (i.e. hot spots; Giglio et al., 2018). Since MODIS data has been available only since 2001, we used the Canadian National Fire Database (CNFDB; Canadian Forestry Service [CFS], 2023) to establish dates for earlier fires. With these combined data, a precise fire date could be assigned to each sample plot (Supporting Information S.I.1). To account for annual variation in the onset of the fire season, each burn date was converted into a fire season day (day 1 = start of the fire season, with subsequent days numbered sequentially). The start of the fire season was determined using BioSim 11 (Régnière et al., 2017) and was defined as either the end of snow cover at the nearest weather station for three consecutive days or a midday temperature of at least 12°C (Canadian Forestry Service [CFS], 1984).

Fire severity (sensu Keeley, 2009) in each plot was determined using the dNBR that was calculated as per Key and Benson (2006). Google Earth Engine was used to extract cloud-free pre- and post-fire images that were taken from the Landsat collection 2 imagery. The resulting dNBR values were stored in 900-m^2 pixels. A weighted average dNBR value was calculated when a 400-m^2 plot was covered by more than one pixel. The Composite Burn Index (CBI), ranging between 0 (unburned) and 3 (highest severity) (Key & Benson, 2006), was then calculated from the equations of Danneyrolles et al. (2024), which were specifically developed for the study region.

2.6 | Statistical analysis

2.6.1 | Evaluation of post-fire regeneration and changes in forest composition

Post-fire regeneration levels were assessed with two approaches. First, based on BS post-fire recovery studies (Boiffin & Munson, 2013; Perrault-Hébert et al., 2017) and forestry regeneration standards (Forestier en chef [FEC], 2023), we quantified the absolute post-fire regeneration (PFR_A) of each plot by classifying global density of BS and JP seedlings into three broad categories: low regeneration (<1750 seedlings/ha); moderate regeneration (between 1750 and 8000 seedlings/ha); or ample regeneration (>8000 seedlings/ha). These PFR_A thresholds were further validated by comparing them to stem density distribution in an independent dataset of 46,550 forest inventory plots of BS-dominated stands across Quebec's boreal forests (see Supporting Information S.I.7). This comparison indicates that even if all seedlings survive, future forests in the low-regeneration category would fall within the lowest-density quartile of BS-dominated stands in Quebec's boreal forests. In addition, within the low-regeneration category, we also determined the proportion of plots that exhibited total regeneration failure (i.e. plots with no seedlings of any species). JP was included in the analysis because it is the fire-adapted coniferous companion species to BS in the eastern Canadian boreal forest (Lavoie & Sirois, 1998; see Supporting Information S.I.2). Second, to better account for the effect of pre-fire stem density, the relative post-fire regeneration index (PFR_R) was calculated for each plot as the ratio of post-fire BS and JP seedling density to their pre-fire stem density. This index reflects the maintenance of tree species density within a plot, where a PFR_R ≥1.00 indicates post-fire regeneration density equal to or exceeding pre-fire stem density levels, independent of the post-fire regeneration classes mentioned above.

We classified changes in post-fire successional trajectories, specifically whether pre-fire mature BS stands were replaced by JP, BL species, or transitioned to NF vegetation. For each plot, we calculated the proportion occupied by seedlings of each main tree species or species group (BS, JP, or BL) after fire. A species or group was considered dominant if it comprised 50% or more of the total post-fire seedlings. Plots with no seedlings of any species were classified as NF (i.e. total regeneration failure; Stevens-Rumann et al., 2022).

2.6.2 | Environmental variables influencing post-fire BS regeneration

Based on the reproductive ecology of BS, we selected measurable and interpretable environmental variables that could influence BS post-fire regeneration (Boucher et al., 2020; Perrault-Hébert et al., 2017). These variables provide insight into (i) seed bank condition, (ii) fire characteristics and (iii) seedbed conditions (Table 1). To avoid collinearity, we used the variance inflation factor (VIF) function of the *car* package, and only the explanatory variables with a VIF <2 were retained (Dormann et al., 2013). A total of six readily measurable and interpretable variables were thus retained from which explanatory models of post-fire BS regeneration were constructed (Table 1; Supporting Information S.I.3).

Generalized linear mixed-effect models (GLMM) with a negative binomial distribution (*glmmTMB* package in R; Brooks et al., 2017) were used to model BS seedling density as a function of the different combinations of the explanatory variables. A total of 51 candidate models were constructed by combining the six explanatory variables. Normality prerequisites of residuals were met (*DHARMa* package in R; Hartig, 2022). Due to the large study area, a random effect corresponding to the identifier of each fire was included to account for unmeasured differences between fires. The Moran *I* statistic for spatial autocorrelation was used to assess whether residuals of the candidate models still exhibited spatial autocorrelation (Table 2) (*spdep* package in R; Bivand et al., 2013).

TABLE 1 Description of the six explanatory environmental variables selected to model post-fire BS seedling density.

Variable type	Variable (abbreviation)	Unit	Median [range]
Seed bank conditions	Pre-fire basal area of living BS stems (Basal area)[a]	m^2/ha	9.18 [0.5–37.34]
	Mean age of canopy trees at the time of fire (Age)[a]	Years	158.70 [63.00–358.00]
Fire characteristics	Time-of-year when fire occurs, adjusted for start of the fire season (Seasonality)[b,c]	Fire season day	68.00 [34.00–105.00]
	Composite Burn Index (CBI)[b]	Unit-less	2.16 [1.13–2.74]
Seedbed conditions	Living *Sphagnum* cover after fire (*Sphagnum*)[a]	%	0.00 [0.00–58.24]
	Ericaceous shrubs cover after fire (Ericaceous)[a]	%	39.81 [0.00–100.00]

[a]Field survey.

[b]Remote sensing.

[c]BioSIM 11.

TABLE 2 The four top-ranking models that were retained for model averaging among the 51 candidate models predicting BS seedling density, as assessed with the corrected Aikaike's information criterion (AICc).

Model rank	Variables	*K*	AICc	ΔAIC	AICwt	CUMwt	Moran's *I* (*p*-value)
1	Basal area + CBI + Seasonality + *Sphagnum*	7	4167.17	0.00	0.45	0.45	0.014 (0.16)
2	Basal area + CBI + *Sphagnum*	6	4168.13	0.96	0.28	0.73	0.014 (0.16)
3	Basal area + CBI + Seasonality + *Sphagnum* + Age	8	4168.99	1.82	0.18	0.91	0.013 (0.18)
4	Basal area + CBI + Seasonality + *Sphagnum* + Age + Ericaceous	9	4170.44	3.27	0.09	1.00	0.015 (0.15)

Note: The estimated parameters are provided, including the intercept (*K*), the AICc values, the difference in AIC (ΔAIC), the AIC weight (AICwt) and the cumulative AIC weight (CUMwt). The Moran *I* statistic for spatial autocorrelation (Moran *I*) and its associated *p*-value are also provided.

The candidate models were ranked according to their AIC values (Burnham & Anderson, 2002) using the *AICmodavg* package (Mazerolle, 2023). Since the top-ranking models had AIC weights (AICwt) <0.95, model averaging was performed. Average parameter estimates and associated unconditional standard errors and unconditional 90% confidence intervals were calculated for the top four ranking models, for which the sum of AICwt values exceeded 0.95.

Predictive models of BS seedling density were made at the population level according to the values of the explanatory variables retained during model averaging. For each explanatory variable, their values were classified according to the three PFR_A classes and the mean value of each group was compared using ANOVAs and Tukey's tests (*TukeyHSD* function of the *stats* package in R). Following the same principle, the values of each explanatory variable were separated according to post-fire species dominance. Given that the data were not normally distributed, a Kruskal–Wallis test (non-parametric one-way ANOVA) was used to determine whether the group means differed (*Kruskal.test* function of the *stats* package in R). All statistics were calculated using R software (version 4.3.2; R Development Core Team, 2023).

3 | RESULTS

3.1 | Evaluation of post-fire regeneration and changes in forest composition

Overall, 33.4% of the plots experienced low regeneration (<1750 seedling/ha), 41.0% exhibited moderate regeneration (1750 and 8000 seedlings/ha), and 25.6% had ample regeneration (>8000 seedlings/ha). Median stocking values were 20% (0%–50%, 90% CI) for the low-regeneration category, 50% (10%–100%, 90% CI) for the moderate regeneration category and 80% (20%–100%, 90% CI) for the ample regeneration category. Among all sample plots, 72.6% had a pre-fire stem density above the low-regeneration seedling density thresholds (≥1750 stems/ha) and 27.4% had a pre-fire stem density below the low-regeneration seedling density thresholds (<1750 stems/ha; Figure 2a). Notably, most cases of low post-fire regeneration occurred in plots that had pre-fire stem densities above the low-regeneration threshold (Figure 2b). Among these plots which were above the low-regeneration threshold before fire, 41.1% showed a reduction in density after fire (PFR_R <1.0); the mode of the PFR_R was 0.45, and the median

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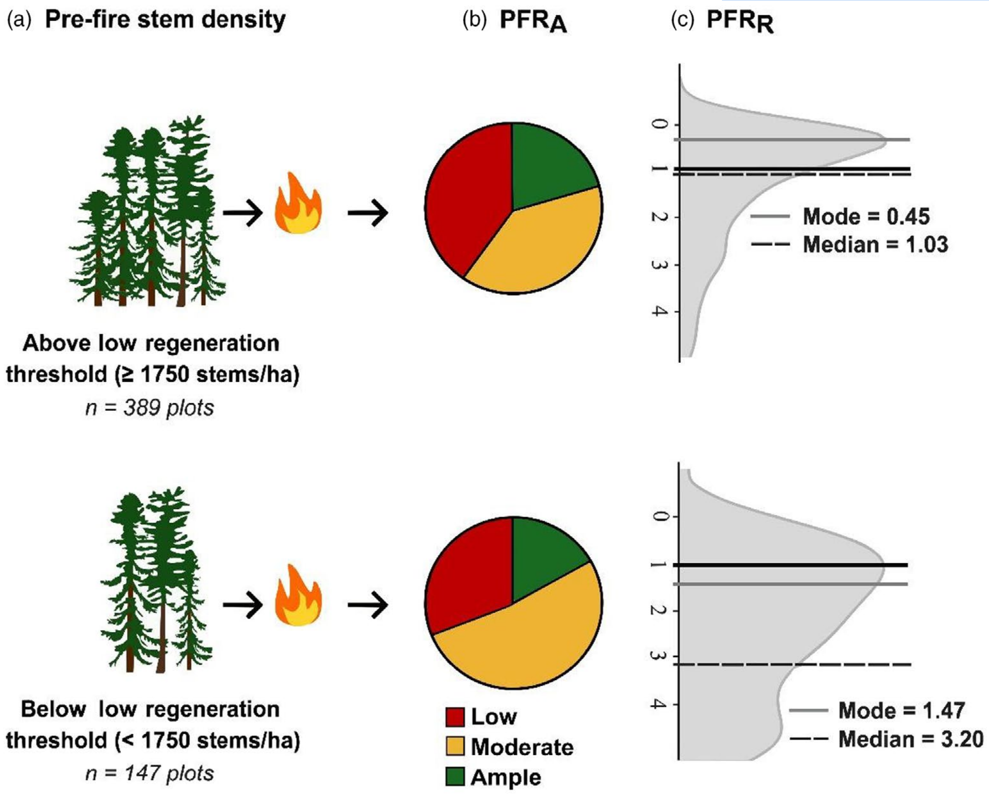

FIGURE 2 Post-fire regeneration in plots whose pre-fire stem density (a) was either above the low-regeneration threshold (≥1750 stems/ha; top row) or below the low-regeneration threshold (<1750 stems/ha; bottom row). (b) The absolute post-fire regeneration classes (PFR_A) distinguish between plots having an ample seedling density (>8000 seedlings/ha), plots with moderate seedling density (1750–8000 seedlings/ha) and plots with low-regeneration density due to an insufficient density of BS and JP seedlings (<1750 seedlings/ha). (c) Frequency distribution of the relative post-fire regeneration index (PFR_R), calculated as the ratio of each plot's post-fire seedling density (BS + JP) to its pre-fire stem density. For each distribution, the continuous black line indicates where $PFR_R = 1$, the continuous grey line indicates the mode of the PFR_R, and the hatched black line indicates the median of the PFR_R. For clarity, PFR_R values >5 are not shown.

PFR_R was 1.03 (Figure 2c). Among the plots with a pre-fire stem density below the low-regeneration threshold, 21.1% showed a reduction in density after fire (PFR_R <1.0); the mode and the median of the PFR_R were 1.47 and 3.20, respectively (Figure 2c).

Considering the entire data set ($n = 536$ plots; Figure 3a), 81.0% of the plots remained dominated by BS after fire, 12.3% became dominated by JP, 2.6% by BL and 4.1% transitioned to NF vegetation types (Figure 3b). Among the plots that remained dominated by BS, 30.9% showed low regeneration, 44.7% had moderate regeneration, and 24.4% had ample regeneration. Post-fire BS-dominated plots also experienced a reduction in density, with 41.4% showing a PFR_R <1.00 (Figure 3c,d). Among the plots in which dominance shifted to JP, more than half (54.6%) experienced low regeneration. Yet, when compared to pre-fire density, only a slight loss of density was observed (Figure 3c,d). Of the few (2.6%) plots that had recorded a change in dominance to BL species, half experienced low regeneration, while the remainder exhibited moderate regeneration. Accordingly, most plots showed a much lower density after fire (Figure 3c,d). Finally, 4.1% of all plots exhibited complete regeneration failure and had transitioned to NF types (Figure 3c,d).

3.2 | Environmental variables influencing post-fire BS regeneration

Among the four top-ranking models (CumWT of 1.00; Table 2) predicting post-fire density of BS seedlings, all of the candidates included *Sphagnum*, pre-fire BS basal area and CBI, while three also included fire seasonality. These four environmental variables were significant (within 90% CI) but the other two (Age and Ericaceous) were not (Supporting Information S.I.4). The top-ranking model (AICWT = 0.45) explained 60% of the variation in BS seedling density (conditional $R^2 = 0.60$ and marginal $R^2 = 0.43$).

BS seedling density increased with *Sphagnum* cover (average coefficient = 0.092, p-value <0.001; Supporting Information S.I.4) and, thus, plots showing ample regeneration had a higher percentage of *Sphagnum* cover than did plots that showed low regeneration, which were mostly devoid of moss (Figure 4a). A similar positive relationship was observed for pre-fire basal area (average coefficient = 0.048, p-value <0.001; Supporting Information S.I.4), with ample regeneration more frequently occurring in plots with higher pre-fire basal areas (Figure 4b). Fire seasonality was also positively correlated (average coefficient = 0.013, p-value <0.1;

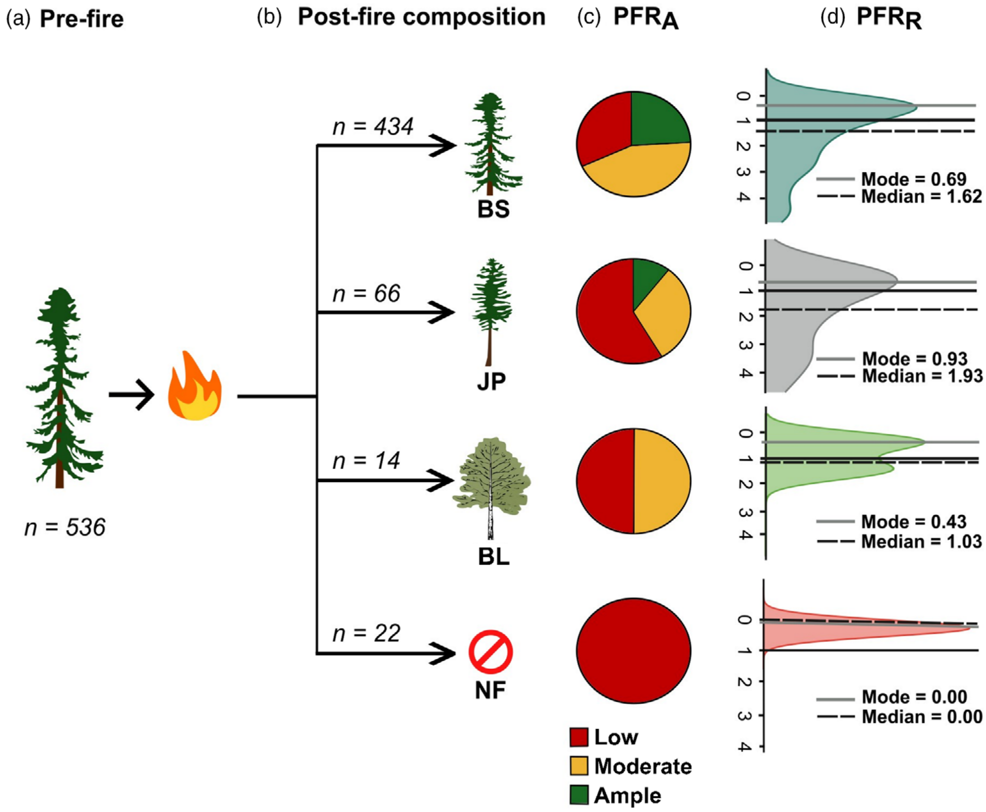

FIGURE 3 Post-fire regeneration according to post-fire stand composition. (a) Number of plots dominated by BS before fire. (b) Number of plots whose post-fire composition either stayed dominated by black spruce (BS; top row), shifted to a dominance by jack pine (JP; second row), shifted to a dominance by broadleaved species (BL; third row), or converted to non-forest (NF; bottom row) due to regeneration failure. (c) The absolute post-fire regeneration classes (PFR_A) distinguish plots having an ample BS and JP seedling density (>8000 seedlings/ha), plots with moderate seedling density (1750–8000 seedlings/ha), and plots that experienced low regeneration due to an insufficient density of seedlings (<1750 seedlings/ha). (d) Frequency distribution of the relative post-fire regeneration index (PFR_R), calculated as the ratio of each plot's post-fire seedling density to its pre-fire stem density. For each distribution, the continuous black line indicates where $PFR_R = 1$, the continuous grey line indicates the mode of the PFR_R, and the hatched black line indicates the median of the PFR_R. For clarity, PFR_R values >5 are not shown.

Supporting Information S.I.4) with BS seedling density, although the correlation was weaker than with the other variables. Low regeneration was more frequent in fires that occurred earlier in the season, whereas moderate regeneration and ample regeneration levels were more frequent later in the season (Figure 4c). The CBI was, however, negatively correlated (average coefficient = −0.61, p-value <0.001; Supporting Information S.I.4) with post-fire seedling density. Therefore, the plots that had ample regeneration had a lower CBI than those that had low regeneration. Higher CBI values tended to favour a transition to BL stands (Figure 4d).

4 | DISCUSSION

The increase in fire activity induced by climate warming is raising serious concerns regarding the resilience of boreal forests and their capacity to provide ecosystem services (Gauthier et al., 2015; Hartmann et al., 2022). The impact of climate change on wildfire activity in the eastern boreal zone of North America was highlighted during the record-breaking 2023 fire season, during which wildfires burned for months in Quebec (Boulanger et al., 2024). Based on a dataset of unprecedented size and spatial extent in eastern Canada, our study provides the first robust assessment of the fire resilience of mature BS stands. One-third of the plots exhibited low-regeneration levels, particularly in stands that were dense and closed-canopy prior to the fire, which are thus expected to transition into open woodlands in the coming decades. Our analyses also identified several key spatially explicit predictors driving the reduction in BS density, particularly the combined negative effects of high-severity and early-season fires, pre-fire BS basal area and the presence of living *Sphagnum* patches.

High-severity fires hindered BS regeneration in our study plots, a finding consistent with the literature from both eastern and western boreal forests of Canada (e.g. Baltzer et al., 2021; Day et al., 2023; Perrault-Hébert et al., 2017). However, burn severity is often discussed as having a dual effect on BS regeneration. On the one hand, insufficient ground-level burn severity leaves a thick, charred organic layer that inhibits seedling roots from accessing the mineral soil, a substrate favourable to establishment (Baltzer et al., 2021; Day et al., 2023; Marty et al., 2023). Conversely, a fire that is too

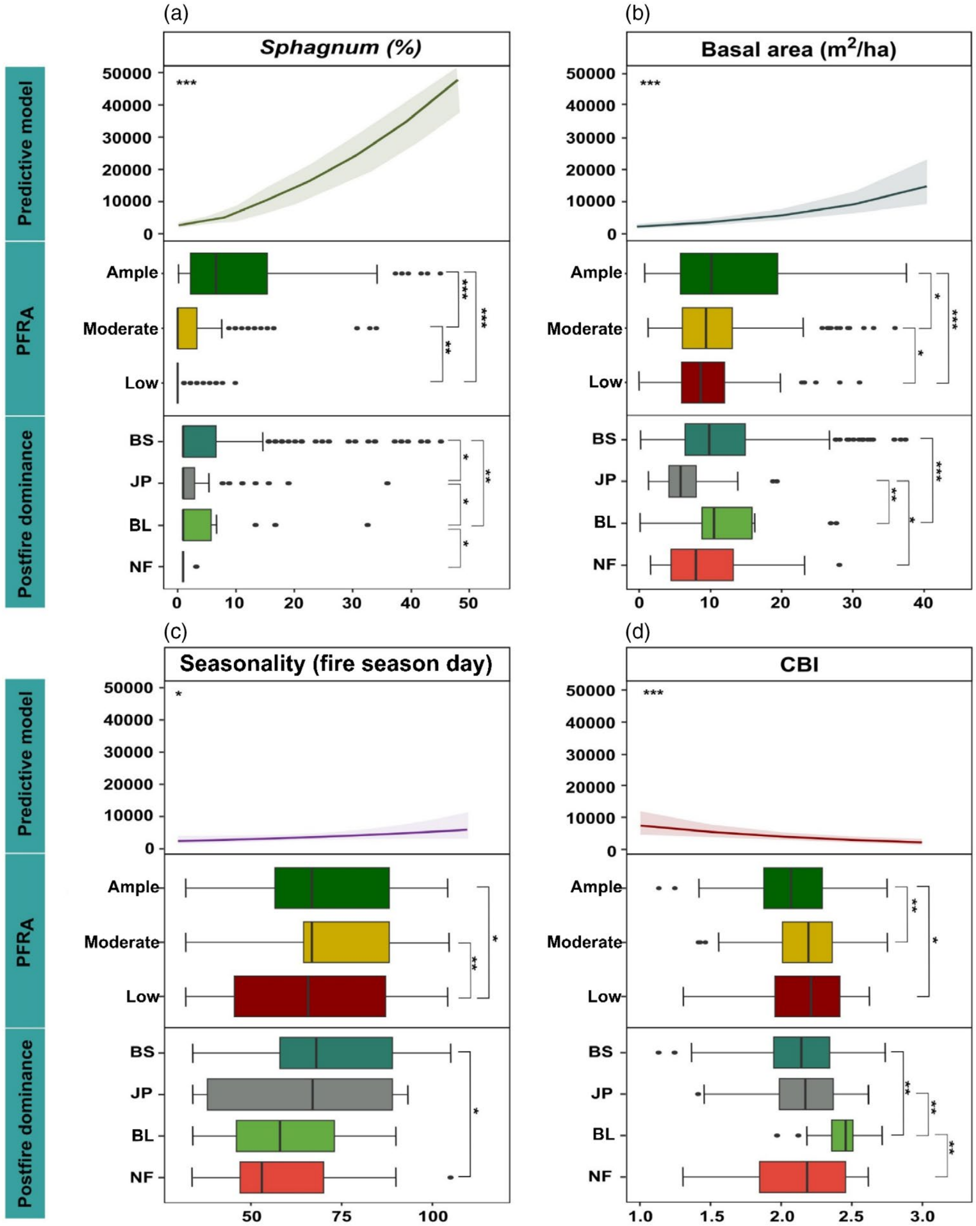

FIGURE 4 Predictive models of post-fire black spruce (BS) regeneration (seedlings/ha) and frequency distribution of predictive variable values by PFR_A classes and post-fire vegetation dominance for the following predictive variables: (a) post-fire *Sphagnum* cover, (b) pre-fire basal area, (c) fire seasonality and (d) Composite Burn Index (CBI). The 90% confidence interval is represented by the shaded area on the predictive model graphs. The asterisks represent the level of marginal significance (***=0.001, **=0.01, *=0.1). BS, black spruce; BL, broadleaved species; JP, jack pine; NF, non-forest.

severe at the canopy level can damage part or all of the aerial seed bank, thus compromising regeneration (Reid et al., 2023; Ruggirello et al., 2023; Sirois, 1993). In our study, the negative relationship between burn severity and BS regeneration, coupled with the confinement of BS seedlings to unburned *Sphagnum* patches, suggests that the combustion of the aerial seed bank is the primary mechanism limiting regeneration in plots burned at high severity.

Our results also corroborate previous studies demonstrating that BS regeneration is generally lower following spring fires than that occurring later in the fire season (Girard et al., 2009; Le Page et al., 2010; Veilleux-Nolin & Payette, 2012). A widely discussed hypothesis suggests that spring fires may lead to poor BS seedling establishment because frozen or water-saturated soils limit burn depth, reducing the exposure of mineral soil (Heinselman, 1981; Miyanishi & Johnson, 2002; Veilleux-Nolin & Payette, 2012). However, given that BS regeneration was strongly associated with unburned living *Sphagnum* patches in the stands we analysed, it seems unlikely that this phenomenon significantly affected BS regeneration. An alternative hypothesis is that early spring fires may occur when physiological processes are re-initiating, coinciding with a short period of high conifer leaf flammability due to a low water-to-carbon ratio in the needles (a phenomenon known as 'spring dip'; Jolly et al., 2014).

These particular spring conditions may increase the potential for severe canopy-level fires and damage to the BS aerial seed bank. Additional explanations may relate to as-yet-understood phenological patterns of seed production and germination. In all cases, further research is necessary to clarify the impact of fire seasonality on BS regeneration.

Stands with a higher pre-fire basal area of BS had higher seedling density after the fire. This is likely because BS basal area is positively related to the size of the aerial seed bank (Greene & Johnson, 1998; Splawinski, Greene, et al., 2019). While burned immature BS-dominated stands are at high risk of shifting to open woodlands (Girard et al., 2009; Hart et al., 2019; Perrault-Hébert et al., 2017), it is generally assumed that mature BS stands are resilient to fire (Splawinski, Cyr, et al., 2019; Viereck & Johnston, 1990). Immature trees have a small viable seed bank that limits their sexual regeneration capacity (Brown & Johnstone, 2012; Viglas et al., 2013; Whitman et al., 2019). Although most of the stands under study were dominated by trees that were older than 100 years (mean ± SD = 158.7 ± 61.0; Supporting Information S.I.5), an age at which BS seed banks usually are fully developed, one-third of the studied stands showed low to no regeneration. Outbreaks of spruce budworm (*Choristoneura fumiferana*), which primarily affect such old forests, may have occurred before fire, thereby reducing the BS seed bank by feeding on spruce flowers, cones and seeds (Schooley, 1980; Simard & Payette, 2005). However, aerial defoliation records from the decade preceding each fire revealed that spruce budworm disturbance occurred in less than 1% of the plots (Lemay et al., n.d.) and therefore is unlikely to explain the observed low levels of regeneration.

One essential result emerging from our analysis is that unburned living *Sphagnum* moss patches are high-quality substrates for post-fire BS regeneration. After fire, residual patches of living *Sphagnum* retain high moisture content and therefore provide favourable seedbeds (Lanti-Traikovski et al., 2025), in contrast to partially burned and blackened organic matter, which tends to dry out rapidly due to its porous structure and lower albedo (Boiffin & Munson, 2013; Greene et al., 2004; Perrault-Hébert et al., 2017; Veilleux-Nolin & Payette, 2012). Yet, it is generally assumed that exposed mineral soil is the most frequent and favourable seedbed for BS seedling establishment (Charron & Greene, 2002; Greene et al., 2004; Thomas & Wein, 1985; Wang & Kemball, 2005). In the 21 burns of our dataset, exposed mineral soil was quite rare, given the substantial thickness of the residual organic matter that was observed in our study sites (i.e. 17.9 ± 9.7 cm; Supporting Information S.I.6). Consequently, it is unlikely that fire could produce enough exposed mineral soil microsites to support adequate post-fire regeneration of BS (Boiffin & Munson, 2013). Indeed, eastern North American boreal forests tend to accumulate more organic matter than western North American boreal forests, due in part to the wetter climate and generally lower fire frequency observed in the east (Bergeron et al., 2004; Carcaillet et al., 2006).

Although unburned living *Sphagnum* moss provides suitable microsites for post-fire BS establishment, its continued accumulation of organic matter can raise the water table, thereby reducing nutrient availability and constraining subsequent seedling growth (Fenton & Bergeron, 2006; Lavoie et al., 2007; Munson & Timmer, 1989; Pacé et al., 2018). Moreover, in plots exhibiting low regeneration, stocking remained low largely because BS seedlings were clustered within relatively small, isolated patches of unburned *Sphagnum*. Such clustering is likely to promote self-thinning mortality over the coming decades, further exacerbating regeneration limitations. This suggests that while *Sphagnum* moss may allow some regeneration and thus contribute to BS resilience, suboptimal growth conditions and limited colonizable space may further slow stand development and strongly reduce the potential for these sites to return to closed-canopy forest over the long term.

Unlike the frequently observed decline in BS density following a fire, post-fire compositional changes were moderate. BS-dominated stands remained dominated by BS after fire, and JP was the only tree species that moderately benefited from fires to increase its dominance (~12% of plots). This expansion of JP over BS could be explained by several ecological traits favouring the species in a context of increasing fire activity. While JP reaches maximum seed production earlier than BS (10 years; Viereck et al., 1983), this trait likely did not influence its competitive ability relative to BS in our dataset, which comprises only mature stands. However, JP cones exhibit a thicker structure than those of BS, better protecting seeds and providing an advantage under severe fire conditions (Arseneault, 2001; Viereck et al., 1983). Moreover, the seeds of JP are considerably larger than those of BS (Burns & Honkala, 1990). Consequently, JP seedlings exhibit faster and longer radicle elongation, providing critical access to water resources located deeper in the underlying mineral soil (Johnstone & Chapin III, 2006; Thomas & Wein, 1985). The post-fire increase in JP dominance in our study is consistent with other studies that were conducted in the same region (see Baltzer et al., 2021; Boiffin & Munson, 2013). In contrast, transitions to BL stands were rare (<3%), probably because the fertility, drainage and climate of our study area are suboptimal for the growth of paper birch and trembling aspen (Boucher et al., 2014).

5 | CONCLUSION

Our work assesses the post-fire regeneration potential of mature BS stands in the boreal forest of eastern North America. One-third of the plots exhibited low-regeneration levels, particularly in stands that were dense and closed-canopy prior to the fire, which are expected to transition into open woodlands in the coming decades. Shifts from BS-dominated stands to JP or BL dominance did occur, but they were relatively uncommon. Our analysis also highlights the key ecological drivers of post-fire BS regeneration. Higher severity fires appear to reduce BS regeneration, likely by damaging the aerial seed bank in mature stands. Conversely, the presence of living *Sphagnum* moss after fire provides high-quality substrate for seedling establishment, thereby enhancing BS resilience.

Although our data cannot determine how long poorly regenerated forests will persist as open woodlands, several lines of evidence point to long-term, potentially quasi-permanent shifts. First, most seedling recruitment occurs within the first 5–10 years after fire, after which very few, if any, new seedlings are established from seeds (Johnstone et al., 2004; St-Pierre et al., 1992). Moreover, in poorly regenerated stands, seedling clustering on sparse living *Sphagnum* patches indicates that self-thinning will likely further reduce future mature stem density. Secondly, even-aged stands established by fire can experience modest increases in density through BS's asexual reproduction via layering during mid- to late-successional stages. However, this mechanism typically produces only a few saplings in the immediate vicinity of the living post-fire cohort (Rossi et al., 2013). Consequently, in poorly regenerated open woodlands where regenerating trees are widely scattered, canopy closure could take several centuries. As such, several previous studies have argued that fire-induced shifts from closed-canopy boreal forest to open woodland constitute a transition to an alternative stable state likely to persist for centuries to millennia (e.g. Girard et al., 2008, 2009; Jasinski & Payette, 2005; Payette & Delwaide, 2018).

Climate change is driving increases in total burned area and potential fire severity across North American boreal forests (Jain et al., 2024; Wang et al., 2025). While mature BS-dominated forests are generally considered more fire-resilient than young ones, our study raises important concerns about their ability to persist and continue providing ecosystem services (i.e. timber supply, carbon storage, wildlife and floristic habitats) under future fire regimes. Implementing robust long-term post-fire vegetation monitoring will be essential to better understand and predict these future dynamics.

AUTHOR CONTRIBUTIONS

Stelsa Fortin conceived the study, led the investigation, ensured data curation, conducted formal analysis, developed the methodology, created visualizations and wrote the original draft with revisions and editing. Yan Boucher conceptualized the study, acquired funding, supervised the project, led the investigation, ensured data curation, conducted formal analysis, developed the methodology, created visualizations and wrote the original draft with revisions and editing. Yves Bergeron supervised the project and contributed to the review and editing. Martin Simard conducted formal analysis and contributed to the review and editing. Dominique Arseneault, Hugo Asselin, Martin Barrette, Sylvie Gauthier, Francois Girard, Martin Girardin, Marc-André Parisien and Nelson Thiffault all contributed to the review and editing. Victor Danneyrolles created visualizations and wrote the original draft with revisions and editing. Osvaldo Valeria acquired funding and contributed to the review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.70260.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in the Dryad Digital Repository: https://doi.org/10.5061/dryad.ggth76j1k (Fortin & Boucher, 2026).

STATEMENT ON INCLUSION

Our study brings together authors from various universities and governmental institutions located in the country of the study area. All authors were involved early in the development of the study design, ensuring a diverse set of perspectives. Efforts were made to consider relevant work in French, the local language of the study area (Quebec, Canada).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Supporting Information S1. Date of burning of the sampling plots according to the fire identifier.

Supporting Information S2. Percentage of seedlings of each species in the 536 plots ($n = 17{,}154$ seedlings).

Supporting Information S3. Correlation matrix between the response variable (Black spruce seedling density [BS regeneration]) and the explanatory environmental variables using the corrected Pearson's correlation for spatial autocorrelation (modified *t*-test of the *SpatialPack* package in R; Vallejos et al., 2020).

Supporting Information S4. Average coefficients and 90% confidence intervals (CI) for each variable of the four top-ranking models (AICWT >0.90).

Supporting Information S5. Frequency distribution and descriptive statistics of pre-fire stand age.

Supporting Information S6. Frequency distribution and descriptive statistics of the residual organic matter (ROM) thickness.

Supporting Information S7. Comparison of the absolute post-fire regeneration threshold (PFR_A) to stem density distribution in an independent dataset of 46,550 forest inventory plots of black spruce–dominated stands across Quebec's boreal forests.

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