ARTICLE IN PRESS

Forest Ecology and Management xxx (xxxx) xxxx

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Forest management has reduced the structural diversity of residual boreal old-growth forest landscapes in Eastern Canada

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ARTICLE INFO

Keywords:
Forest fire
Disturbance dynamics
Forestry practices
Preindustrial landscape
Overmature forests
Ecosystem-based management

ABSTRACT

The impact of traditional even-aged forest management on landscape age structure, tree composition, and connectivity has been well documented. Very little, however, is known about the impact on stand structural diversity. This study aims to compare the structural and abiotic characteristics of forest stands disturbed by clearcut logging and by stand-replacing fire in Quebec's boreal landscapes. We hypothesized that unlike fire, logging specifically targeted stands having a higher economic value, i.e., merchantable volume, leaving altered forest characteristics on post-harvested landscapes. We compared two aerial forest surveys of a 2200 km^2 study area, one survey completed before any logging activity (preindustrial survey; 1980s), and the second survey collected > 10 years after logging activity (modern survey; 2000s). Forest stands at the time of the preindustrial survey were primary forests. We identified stands as either burned, logged, or left aside after forest management of the area (remaining stands) between the two surveys and compared their structural and abiotic characteristics using logistic regression. The structural and abiotic characteristics of burned and logged stands differed significantly. Relative to the burned stands, logged stands were older, denser, and marked by poorer drainage and a higher proportion of black spruce; therefore post-harvest and post-burn landscapes differed in terms of their structural diversities. Traditional even-aged forest management has significantly altered the boreal forest landscape by targeting specific stands having higher economic value and leaving behind stands of lower economic value. Remaining high economic stands should be protected, and a more balanced approach to harvesting must be used in the context of ecosystem-based management.

1. Introduction

The impact of anthropic activities on ecosystems has dramatically increased over the last century, resulting in major deforestation, degradation, fragmentation, and rejuvenation of the forest landscape, i.e., the replacement of a significant portion of old forest stands by regenerating and young even-aged stands (Kuuluvainen, 2002; Achard et al., 2009; Gauthier et al., 2015; Boucher et al., 2017b). In the absence of a stand-replacing disturbance over an extended period, gap dynamics—the replacement by shade-tolerant species of overstorey trees that died alone or in small groups because of secondary disturbance—develop in forest stands, initiating the old-growth succession stage (Oliver and Larson, 1996). Specific structural characteristics, such as high deadwood volume at diverse stages of degradation and ecological continuity, characterize these ecosystems and produce habitats that are often absent in younger stands (Tikkanen et al., 2006; Bergeron and Fenton, 2012; Boudreault et al., 2018). In the boreal biome, old-growth forests are a key element of the forest landscape structure (Shorohova et al., 2011; Bergeron and Fenton, 2012); however until the end of the 20th century, old-growth forests were assumed to be rare in boreal landscapes driven by recurrent stand-replacing fires (Cogbill, 1985; Johnson, 1992). A large body of studies has since demonstrated that when regional fire cycles are relatively long, they generate a forest landscape dominated by old-growth stands, particularly in Eastern Canada (Bouchard et al., 2008; Bergeron and Harper, 2009; Bergeron and Fenton, 2012).

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https://doi.org/10.1016/j.foreco.2019.117765
Received 9 July 2019; Received in revised form 4 November 2019; Accepted 10 November 2019

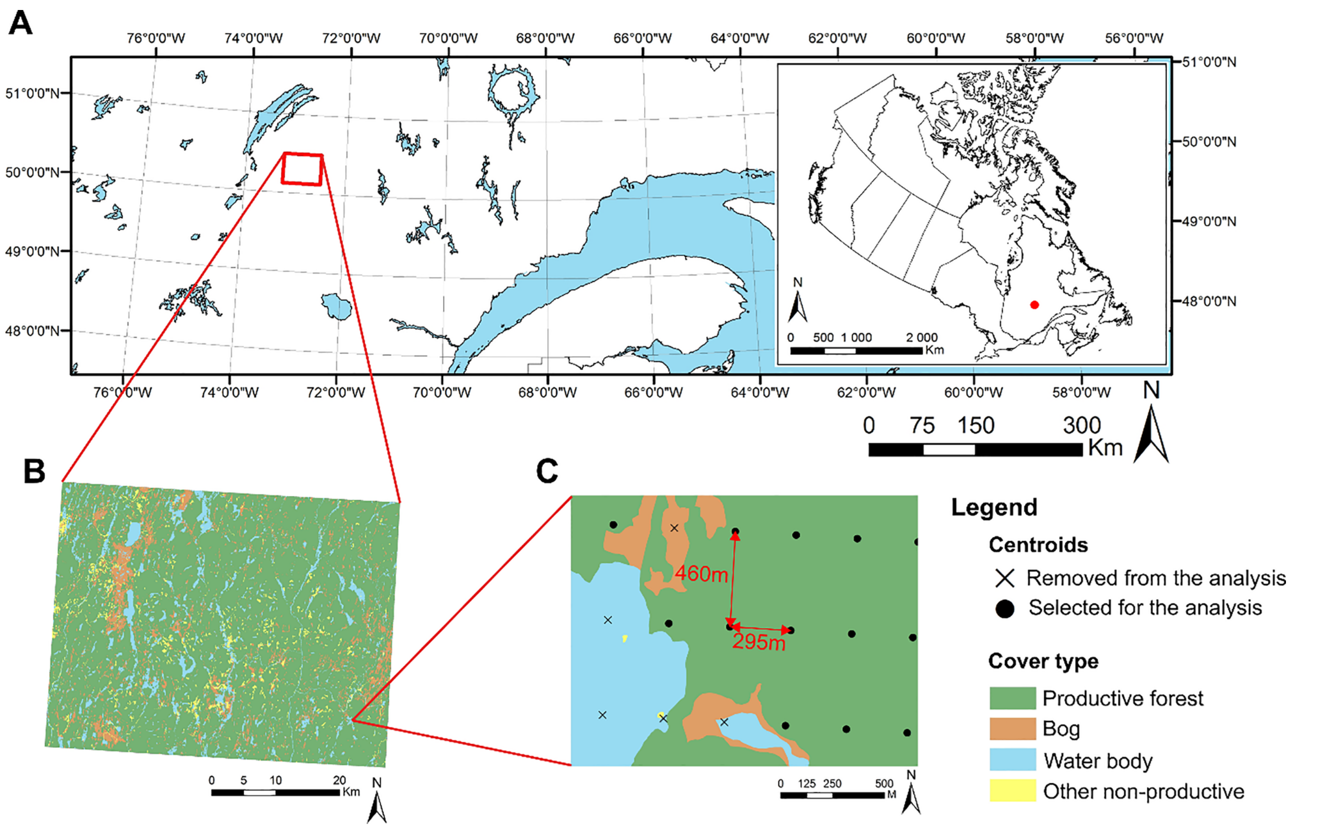

Fig. 1. A: Location of the study territory in the province of Quebec. The insert map represents its location in Canada. B: Spatial distribution of the main cover types on the study territory. C: Example of the centroid distribution on the study territory and their selection for analysis based on the cover type.

Since the early 20th century, clearcutting has been the dominant silvicultural practice in boreal landscapes (Östlund et al., 1997; Löfman and Kouki, 2003; Boucher et al., 2017b). In the past, foresters have assumed that the effects of clearcuts are analogous to those of fires, thereby justifying their extensive use (Bergeron et al., 2001; Kneeshaw et al., 2011; Halme et al., 2013). However, it has since been demonstrated that traditional even-aged forest management is not a surrogate for fire at the landscape scale, as clearcut harvesting focuses on stands that have reached economic maturity (> 70 years in eastern Canadian boreal forests). Moreover, the logging rate ($\%\cdot yr^{-1}$) in managed landscapes is often greater than the stand-replacing disturbance rate observed in natural boreal forest landscapes. Thus, in managed landscapes, fragmentation rates and the total area of early successional stands are higher than those observed in landscapes driven only by natural disturbance (Östlund et al., 1997; Fall et al., 2004; Boucher et al., 2017b). As a consequence, managed boreal landscapes currently face pressing biodiversity issues due to the loss of boreal old-growth forest area (Siitonen, 2001; Tikkanen et al., 2006; Patry et al., 2017).

To address these concerns, current ecosystem-based management strategies in boreal landscapes aim to emulate natural disturbance regimes (Kuuluvainen, 2002; Gauthier et al., 2009) or mimic stand-scale natural processes (Vanha-Majamaa et al., 2007; Kuuluvainen, 2009). In this context, logging activities aim to copy a wide range of stand structures, similar to those observed in a natural boreal landscape. Nonetheless, unlike natural disturbances, economic requirements are the main drivers of logging activities (Perry, 1998; Puettmann et al., 2009). Clearcutting-based systems—systems based almost exclusively on the use of short-rotation clearcuts—prioritize short-term benefits by maximizing the amount of wood volume logged (Halme et al., 2013; Ruel et al., 2013). There is therefore a risk that clearcut logging targets the most valuable stands, e.g., the more productive and denser stands, leaving stands having less desirable forest structural attributes in the post-harvested landscape; this practice thereby causes habitat depletion.

Assessing the structural discrepancies between logged and naturally disturbed stands requires the availability of large-scale forest surveys performed prior to large-scale forest management, i.e., surveys conducted during the preindustrial period. In Eastern Canada, the logging frontier follows a south to north spatial pattern (Boucher et al., 2017b), resulting in more recent harvests in northern areas. In Quebec, extensive and detailed forest surveys of pristine northern forests began in the 1960s. These surveys provide baseline data to allow determining how the landscape has transformed since the introduction of forest management practices. In addition, stand-replacing fires are the main natural disturbance in eastern Canadian boreal forests, and fires still occur in managed landscapes (Boucher et al., 2017a). It is therefore possible to compare the characteristics of a stands that were disturbed by logging or fire. Thus, the objective of this study is to determine whether logged stands share similar structural and abiotic characteristics as stands that were burned in eastern Canadian boreal forests. We hypothesized that compared to burn patterns, stands having a higher economic value, i.e., merchantable volume, are targeted by logging, thus leaving altered forest characteristics on the post-harvested landscapes. Here, we used the stand successional stage, density, drainage, and potential vegetation as volume proxies. Our study aimed to improve our understanding of the influence of both forestry practices and natural disturbance regimes on boreal landscapes to help develop more effective ecosystem-based forest management strategies.

2. Methods

2.1. Study territory

The study territory (50°07′23″N to 50°30′00″N and 72°15′00″W to 72°30′00″W) lies in the closed-crown boreal forest of Eastern Canada (Rowe, 1972). Based on the ecological land classification system of

Quebec, the region is in the western section of the black spruce (*Picea mariana* (Mill.))–feathermoss bioclimatic domain in the physiographic region of the Nestaocano River Hills (Fig. 1A; Blouin and Berger, 2004). It covers a 2200 km^2 area of public land covered by forest. Black spruce is the dominant tree species, often mixed with jack pine (*Pinus banksiana* (Lamb.), balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss), paper birch (*Betula papyrifera* Marsh.), and trembling aspen (*Populus tremuloides*) (Bergeron et al., 1998). The topography is dominated by rolling hills, and altitudes range between 350 and 750 m. Surficial deposits are mainly thick glacial tills, and areas located along rivers and streams are characterized by sand deposits or vast bogs (Fig. 1B). We selected this region as it encompasses the environmental diversity of the black spruce–feathermoss bioclimatic domain, ranging from poorly drained valley bottoms situated on organic deposits to well-drained till slopes. The annual regional rainfall varies between 700 and 1000 mm, mean annual temperature varies between −2.5 and 0.0 °C, and growing season length lasts 120 to 155 days. The return period of the fire cycle in this region is estimated at between 200 and 300 years (Couillard et al., 2016).

2.2. Cartographic data preparation

The first industrial logging operations started in 1991 in the study area. We used two aerial surveys completed by the Quebec government: the first survey was collected in 1983–1984 (preindustrial period), and the second survey was obtained in 2007 (modern period). The preindustrial survey divided the territory into 14-ha rectangular polygons (tessels) distributed over a 297 × 463 m grid (15″ × 15″ in geographic coordinates; Pelletier et al., 2007). The values attributed to each tessel are derived from the photointerpretation of the tessel centroid. In contrast, the modern survey defined polygons that represent the natural boundaries of forest stands, which are defined as having homogeneous abiotic and structural characteristics (Fig. 2). Nonetheless, we can compare the surveys along the preindustrial 297 × 463 m grid, taking the modern stand characteristics at the preindustrial centroid (Fig. 1C). We retained only centroids having productive forests in the preindustrial survey (13,186 centroids). We defined productive forests as forests that have the potential to reach a minimum of 30 m^3/ha of wood volume at 120 years of age (MRNF, 2008). In addition, we determined the altitude and the slope of the centroids using a topographic raster map (resolution: 20 × 20 m). From these datasets, we extracted five abiotic covariates (altitude, surficial deposit, drainage, potential vegetation, and slope) and four structural covariates (successional stage, density, dominant species, and height; Table 1). All predictors are categorical variables. Surficial deposits correspond to the organic or mineral layer lying over bedrock. Potential vegetation represents the theoretical tree species composition of the stand at a late-successional stage. For the successional stage, we defined stands older than 100 years as "old-growth." The 100-year age threshold is common and relevant for Eastern Canada as the transition toward the old-growth stage generally begins around this age in boreal stands (Bergeron and Harper, 2009; Boucher et al., 2011; Bergeron et al., 2017). We identified the centroids disturbed by stand-replacing logging or fire using archives of annual fire and logging maps provided by the Quebec government. For this analysis, we only retained fire and logging events that occurred between the preindustrial and modern periods. We then classified the centroids based on the stand-replacing disturbance they experienced between the preindustrial and modern surveys: burned, logged, or remaining (neither burned nor logged, Fig. 2).

2.3. Data preparation and statistical analysis

To test our hypothesis, we calculated the stand-replacing disturbance rate over the study territory by disturbance type (fire, logging) and successional stage (even-aged, old-growth) using the following formula:

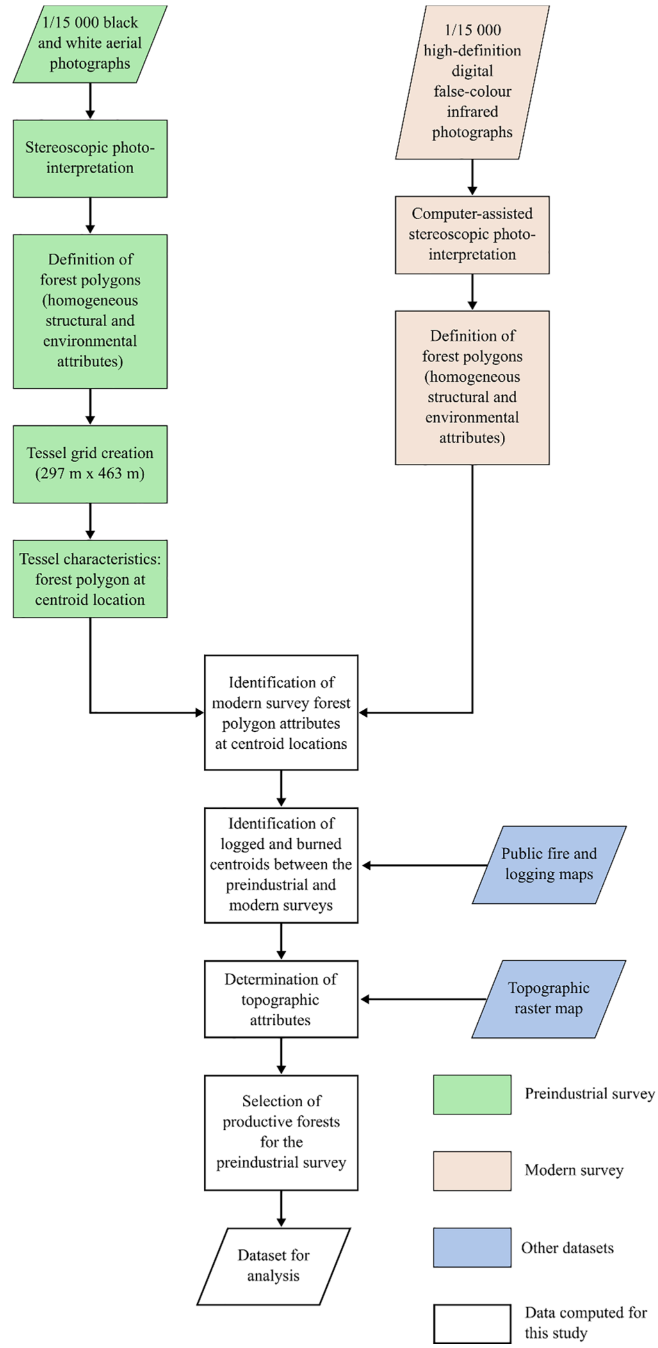

Fig. 2. Flowchart of the methodology used to obtain the datasets. Trapezoids represent inputs or outputs, rectangles represent processes.

$$standreplacingdisturbancerate = \frac{n_{disturbed\ plots}}{n_{total\ plots} \times t}$$

where $n_{disturbed\ plots}$ is the number of centroids disturbed by fire or logging over the period t, and $n_{total\ plots}$ represents the total number of plots. The stand-replacing disturbance rate is equivalent to the percent annual area burned as described by Stocks et al., (2003), except that the unit (area disturbed) is replaced by the number of centroids. For this study, t = 25, as the preindustrial survey started in 1983, and the modern survey took place in 2007 for the study territory. In addition to the stand-replacing disturbance rate, we also used a descriptive approach to illustrate the evolution of the landscape between the preindustrial and modern periods. We calculated the stand-replacing rate and undertook the descriptive approach to the landscape evolution for even-aged and

Table 1
Presentation and description of the abiotic and structural covariates and classes of the centroids.

Covariate type	Covariate name	Class	Description
Abiotic characteristics	Altitude (m)	400–449	–
		450–499	–
		500–549	–
		550–599	–
	Surficial deposit	Fluvioglacial	Fluvioglacial surficial deposit (eskers, kames…)
		Glacial	Glacial surficial deposit (tills, moraines…)
		Organic	Organic surficial deposit
		Other	Other type of surficial deposit (rocks…)
	Drainage	Subhydric	Drainage bad to complex sensu MRNF (2008)
		Mesic	Drainage moderate to imperfect sensu MRNF (2008)
		Xeric	Drainage excessive to good sensu MRNF (2008)
	Potential vegetation	Black spruce–feathermoss (BSFM)	Pure black spruce stands on mosses at the end of the succession
		Black spruce–balsam fir (BSBF)	Black spruce–balsam fir mixture at the end of the succession
		Balsam fir–white birch (BSWB)	Balsam fir–white birch mixture at the end of the succession
	Slope (%)	0–3	–
		4–8	–
		9–15	–
		16–30	–
Structural characteristics	Successional stage	Even-aged	< 100 years since the last fire
		Old-growth	≥100 years since the last fire
	Density	Regeneration	Stand at the regeneration stage (height < 7 m)
		Sparse	Percentage of canopy cover ≤ 60%
		Dense	Percentage of canopy cover > 60%
	Dominant species	Spruce sp. (SP)	Spruce sp. are the dominant species in the canopy
		Jack pine (JP)	Jack pine is the dominant species in the canopy
		Balsam fir (BF)	Balsam fir is the dominant species in the canopy
		Broadleaved (BRL)	Broadleaved species dominate the canopy
		Other	Other species dominate the canopy
	Height (m)	< 12	Height of the highest trees < 12 m
		12–17	Height of the highest trees between 12 and 17 m
		> 17	Height of the highest trees > 17 m

old-growth centroids separately. We selected this division to provide relevant complementary information regarding the problem of old-growth loss in the boreal forest of Eastern Canada.

We then identified the main structural and abiotic characteristics differentiating burned, logged, and remaining stands on the studied landscape by using the Begg and Gray (1984) approximation of multinomial logistic regression. The dependent variable was the centroid class: burned, logged, or remaining. The Begg and Gray method consists of applying simple logistic regression for each pair of dependent variable as a binary dummy variable. The logistic regression equation we used:

$$P(Y) = \frac{1}{1 + e^{-(b_0 + b_1 x_1 + \cdots + b_n x_n)}}$$

P(Y) is the probability that Y happens, e is the base of the natural logarithm, b_0 is the y-intercept, b_1 is the parameter of the first independent variable x_1, and b_n is the parameter of the n^{th} independent variable x_n. We chose this approximation instead of a multiple logistic regression because it is more conservative and thus reduces the risk of type I errors (Begg and Gray, 1984). We performed three simple logistic regressions comparing the probability of being one of a pair of centroid classes: burned/logged, burned/remaining, or logged/remaining.

The independent variables were the abiotic and structural covariates extracted from the preindustrial survey. To reduce collinearity, we selected variables having little association with each other as measured with φ or Cramer's V values (Sheskin, 2002). When two variables showed a strong association because of an infrequent class, we removed the sites belonging to this class from the dataset. As all the centroids defined by the "regeneration" density class belong to the "even-aged" successional stage class, we removed them from the analysis. The centroids retained for this analysis were therefore only merchantable stands (height > 7 m). Selected independent variables were successional stage, density, drainage, and potential vegetation.

For each of the three regressions, we first ran a model containing all the selected independent variables. We then performed a stepwise Akaike information criterion (AIC; Akaike, 1974) selection on the full model to remove independent variables that did not improve model fit, as AIC allows the ranking of candidate models (Venable and Ripley, 2002). Therefore, the final model was the one having the lowest AIC value. We assessed the goodness-of-fit of the final model using a log-likelihood test. In addition, we estimated the model's predictive ability using the area under the receiver operating characteristic curve (AUC, Zweig and Campbell, 1993) and the Tjur's coefficient of determination (COD, Tjur, 2009). An AUC > 0.7 and a COD > 0.1 indicate a significant predictive ability. To facilitate the interpretation of our results, the models' coefficient estimates were then transformed so that the sum of the estimates for all the values of one categorical predictor were equal to 0 (effect coding). The results of the logistic regressions were then summarized by defining a stand type before disturbance (hereafter "stand type") for each of the analysed centroids. The purpose of the stand type was to illustrate our results at the scale of the forest stand by regrouping for each centroid its structural and environmental characteristics. Stands types were defined by merging the classes of the structural and abiotic covariates that showed significant differences based on the centroid class in the logistic regressions. We then compared the percentage of the burned, logged, and remaining centroids in each stand type. To simplify our analysis, we only studied the ten most abundant stand types in the study area.

The analyses were run using the R-software, version 3.3.1 (R Core and Team, 2016) with the *ROCR* (Sing et al., 2005), *MASS* (Venable and Ripley, 2002), and *DescTools* (Signorell, 2017) packages. We applied a significance threshold of 0.05.

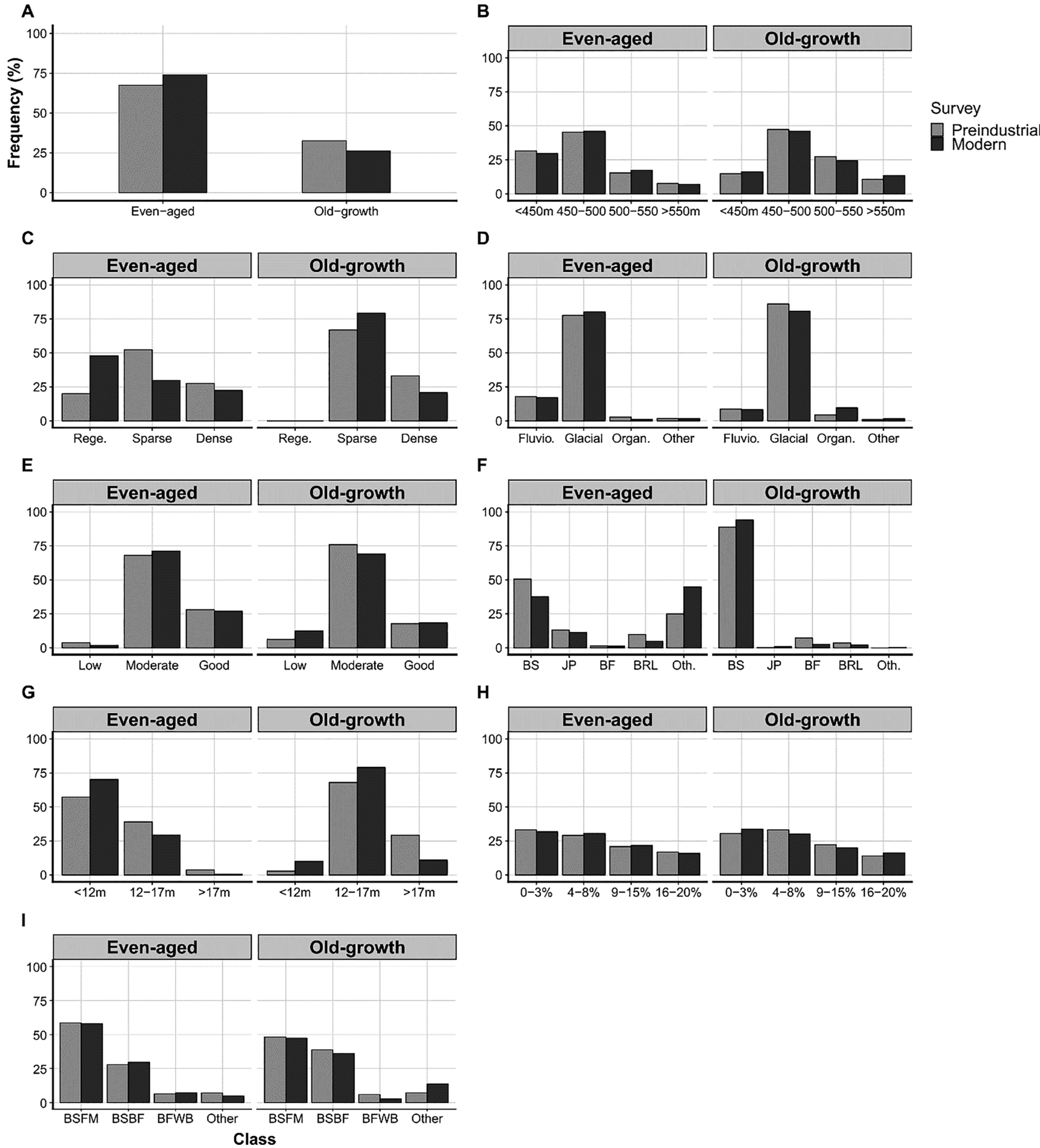

Fig. 3. Distribution of the even-aged and old-growth centroids in the preindustrial and the modern surveys based on their (A) successional stage, (B) altitude, (C) density, (D) surficial deposit, (E) drainage, (F) dominant species, (G) height, (H) slope and (I) potential vegetation. Rege.: Regeneration, Fluvio.: Fluvioglacial, Organ.: Organic, SP: Spruce sp., JP: Jack pine, BF: Balsam fir, BRL: Broadleaved, Oth.: Other. BSFM: Black spruce–feathermoss. BSBF: Black spruce–balsam fir. BFWB: Balsam fir–white birch.

3. Results

3.1. Evolution of the landscape between the preindustrial and modern surveys

Overall, between the preindustrial and the modern surveys, the old-growth forest abundance decreased by 20% (Fig. 3). When even-aged and old-growth forests were examined individually, stand characteristics differed between the two successional stages. Even-aged centroids belonging to the “regeneration” density class increased by 240% in the modern survey compared to the preindustrial survey, while those belonging to the “sparse” density class decreased by 43%. For the old-growth stage, centroids belonging to the “dense” density class or the “ > 17 m” height class, decreased by 37.4% and 62.4%, respectively. There were few changes in the dominant species between the surveys, as black spruce dominated most of the studied centroids regardless of the period. Overall, we observed few differences in the relative frequency of the classes for the abiotic covariates, i.e., altitude, surficial

Table 2
Annual stand-replacing disturbance rate on the study territory between the preindustrial and the modern surveys, based on the centroid class and the successional stage.

Centroid class	Annual stand-replacing disturbance rate (%·yr^{-1})	
	Even-aged	Old-growth
Burned	1.7	1.4
Logged	0.2	1.1

deposit, drainage, slope, and potential vegetation, between the two surveys for both successional stages. Therefore, between the two surveys, even-aged and old-growth stands showed important changes in their structural characteristics but few changes in their abiotic characteristics.

The annual stand-replacing disturbance rate due to fire was equivalent in even-aged and old-growth stands at 1.7%·yr^{-1} and 1.4%·yr^{-1}, respectively (Table 2). In contrast, the stand-replacing disturbance rates due to logging differed more than fivefold between the even-aged (0.2%·yr^{-1}) and old-growth stands (1.1%·yr^{-1}). Moreover, the fire and logging annual stand-replacing disturbance rates observed for the old-growth stands were relatively close (1.4 and 1.1%·yr^{-1}, respectively). Therefore, logging activities generally increased the annual stand-replacing rate of old-growth stands yet had little influence on even-aged stands.

3.2. Differences in the characteristics of centroids by stand-replacing disturbance type

According to the Begg and Gray (1984) approximation of multiple logistic regression, the model comparing the characteristics of the burned and logged centroids (Model 1) was the only model that identified significant effects for the abiotic and structural covariates (AUC = 0.71, COD = 0.1; Table 3). In Model 1, all retained covariates had a significant effect. The successional stage was the covariate having the highest influence on the model (Fig. 4), and old-growth stands were more logged than even-aged stands in comparison to the amounts affected by fire. Density was the second most influential covariate, followed by potential vegetation and drainage. Relative to fire, logging disturbed the older and denser stands, mainly belonging to the black spruce–feathermoss potential vegetation type with subhydric drainage. In the model that compared the remaining and logged centroids (Model 3), we observed a trend toward abiotic and structural differences between disturbance types; however, we recorded no significant differences (AUC = 0.66, COD = 0.05). The model comparing the remaining and burned centroids (Model 2) showed neither significant differences nor any trends (AUC = 0.59, COD = 0.02).

We defined the stand types for each centroid by merging their successional stage, density, potential vegetation, and drainage classes. The ten most abundant stand types represented 82.8% of all centroids. Among these ten stand types, a single one—Even-aged/Sparse/Mesic/BSFM stand type—represented 21% of all centroids (Fig. 5A), almost twice as many as the second most abundant stand type—Old-growth/Sparse/Mesic/BSFM, 11.2% of the centroids. The Even-aged/Dense/Xeric/BSBF stand type was the least abundant, representing 2.7% of the centroids. Stand types were unequally burned or logged (Fig. 5B). The percentage of burned centroids per stand type between the preindustrial and the modern surveys ranged from 13.9% to 38.6%. Similarly, the percentage of logged centroids per stand type between the two surveys ranged from 3.4% to 19.5%. Moreover, for a given stand type, the proportion of logged centroids was not equal to that of the burned stands. Most of them were more burned than logged, and this difference was often large (ratio burned/logged > 3); for example, centroids from the Even-aged/Sparse/Xeric/BSFM stand type were 7.6 times more likely to be burned than logged. In contrast, the proportion of logged centroids was greater than the proportion of burned centroids for two stand types. The Old-growth/Dense/Mesic/BSFM stand type was twice as likely to be logged than burned, while this ratio was only slightly superior to 1 (ratio centroids logged vs. burned = 1.1) for the Even-aged/Dense/Mesic/BSFM stand type. Therefore, specific stand types are targeted or avoided by logging.

4. Discussion

The impact of forest management has significantly altered structural diversity within the boreal forest landscape, as fire and logging do not affect the same types of old-growth stands. At the time of the modern survey in 2007, logged areas only covered a small fraction of the landscape. However, with ongoing harvesting, there is a risk that logging activities will modify the structural diversity of the landscape and, as a consequence, alter regional biodiversity.

4.1. Logging activities modify the structural diversity of remaining old-growth stands

Stand age class was the main characteristic discriminating between burned and logged stands. Timber harvesting aims to maximize wood volume logged per unit area (Perry, 1998; Halme et al., 2013). In eastern Canadian boreal forests, stand volume increases continuously during the 125–150 years following the last stand-replacing disturbance (Harper et al., 2005; Garet et al., 2009; Portier et al., 2018). Consequently, stands older than 100 years, i.e., old-growth forests, are more profitable than younger stands, i.e. even-aged forests. Logged stands were also denser; a higher stand density implies a greater wood volume. Moreover, logged areas contained a higher proportion of black spruce, a

Table 3
Results of the logistic regression models. AIC: Akaike information criterion, AUC: Area under the ROC curve, COD: Tjur's coefficient of discrimination, Succ. stage: Successional stage, Pot.Veg.: Potential vegetation.

Model	Dependent variable	Resid.Df	Resid.Dev	Df	Deviance	*Pr*(> Chi)	AIC	AUC	COD	Parameter	Df	Deviance	Resid.Df	Resid.Dev	*Pr*(> Chi)
Model 1	Fire/logging	4019	5004.1	−6	−476.68	< 0.001	4541.4	0.71	0.12	Succ. stage	1	317.09	4017	4607.6	< 0.001
										Density	1	79.39	4018	4924.7	< 0.001
										Pot.Veg.	2	56.03	4013	4527.4	< 0.001
										Drainage	2	24.16	4015	4583.5	< 0.001
Model 2	Remaining/fire	9449	11,410	−6	−212.79	< 0.001	11,211	0.59	0.02	Succ. stage	1	10.92	9447	11,259	< 0.001
										Density	1	139.91	9448	11,270	< 0.001
										Pot.Veg.	2	39.34	9443	11,197	< 0.001
										Drainage	2	22.61	9445	11,237	< 0.001
Model 3	Remaining/logging	7955	6962.9	−6	−354.2	< 0.001	6622.7	0.66	0.05	Succ. stage	1	316.12	7953	6645.7	< 0.001
										Density	1	1.04	7954	6961.9	n.s.
										Pot.Veg.	2	25.04	7949	6608.7	< 0.001
										Drainage	2	12	7951	6633.7	< 0.01

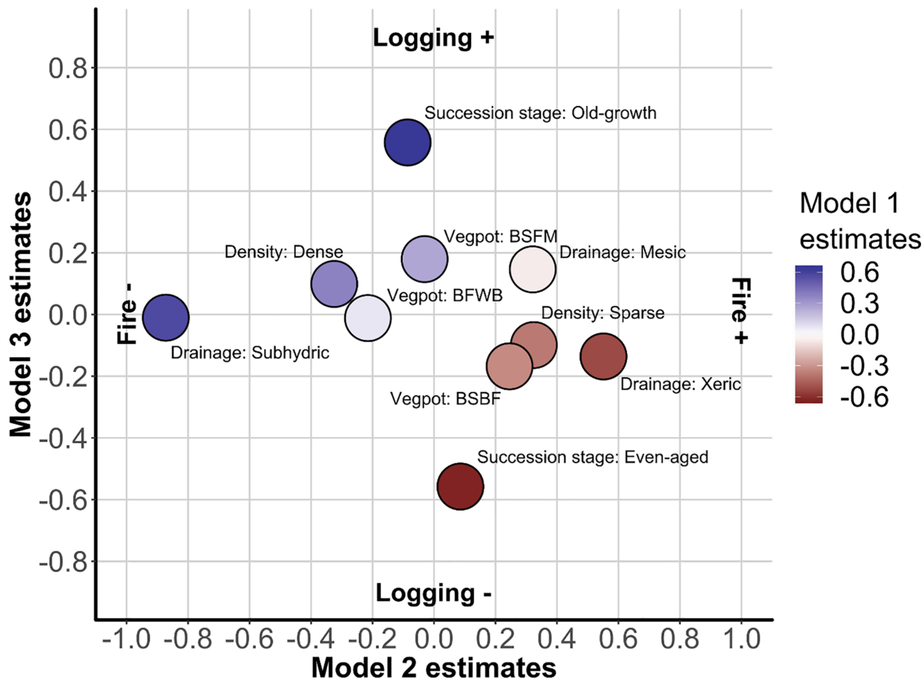

Fig. 4. Distribution of the estimates of the studied classes according to the logistic regression models that compare the characteristics of burned, logged, and remaining centroids. Positive estimate values for Model 1 indicate those characteristics that are more abundant in logged stands than in burned stands. In contrast, negative estimate characteristics indicate those characteristics that are more abundant in burned stands than in the logged stands. Similarly, Model 2 estimates represent the comparison of the characteristics of burned centroids relative to remaining centroids, while Model 3 estimates represent the comparison of the characteristics of logged centroids relative to remaining centroids. "Fire +" then indicates characteristics more abundant in burned centroids, while "Fire −" indicates those characteristics more abundant in remaining centroids. "Logging +" indicates characteristics more abundant in logged centroids, while "Logging −" indicates characteristics that are more abundant in remaining centroids. BSFM: Black spruce–feathermoss; BSBF: Black spruce–balsam fir; BFWB: Balsam fir–white birch.

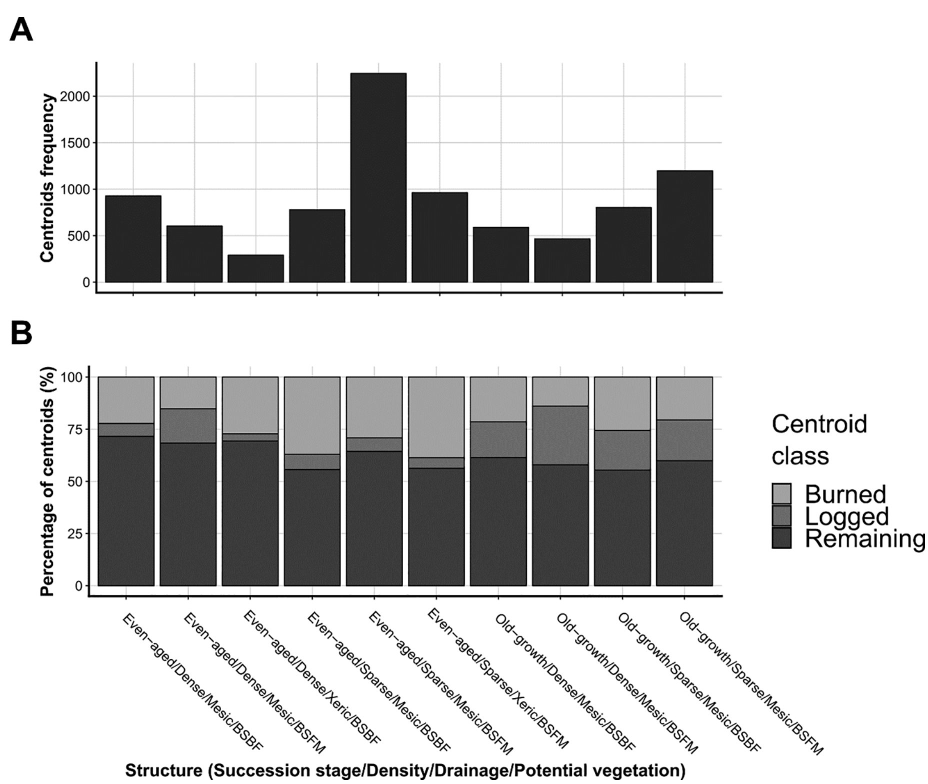

Fig. 5. (A) Centroid absolute frequency and (B) proportion of the centroids based on the nature of disturbance of the ten most abundant stand types across the study territory. BSFM: Black spruce–feathermoss; BSBF: Black spruce–balsam fir; BFWB: Balsam fir–white birch.

tree having a wood quality and value superior to most of the other boreal tree species (MFFP, 2018). These results, therefore, support our hypothesis, as logged stands were those presenting the highest merchantable wood volume.

In contrast to logging, fire is a stochastic disturbance driven by a combination of climatic factors as well as the biotic and abiotic characteristics of the landscape (Bergeron et al., 2004; Stevens-Rumann et al., 2016). The high frequency of fires over the studied time span, when compared with the estimated fire rate for the study territory over the last 150 years (Couillard et al., 2016), suggests that modern fire influence on the study territory was representative of the long-term natural disturbance regime for the region despite the short period considered by our study. This fire occurrence rate was almost equal between even-aged and old-growth stands. Stand age is often assumed to have no influence on the risk of fire occurrence (Van Wagner, 1978; Bergeron et al., 2006). This assumption, however, has been debated recently for the youngest boreal stands (time since the last fire < 50 years; Héon et al., 2014). In this study, we only analysed merchantable stands (height > 7 m), stands that are generally > 50 years old. Our results therefore underscore that fires burn stands independent of their age, at least for mature stands.

Stand types targeted by logging differed from the burned stand types. Specifically, two stand types were primarily logged, and both were defined by a dense canopy and abiotic characteristics that favour pure black spruce stands. The two stands differed only in their successional stage, one being even-aged and the second being old-growth. The old-growth structure was more logged than the even-aged structure stands. In contrast, the stand types that were primarily burned were generally younger and less dense. These results highlight that the differences between the characteristics of logged and burned stands involve specific stand types, defined by a particular combination of structural and abiotic characteristics. The influence of logging on previously unmanaged boreal landscapes is thus not only a concern for rejuvenation and fragmentation, but these practices also result in a loss of stand diversity. The diversity of stand types observed across managed landscapes will differ from that observed in unmanaged landscapes. In particular, stands having the highest economic value, i.e., old and dense pure black spruce stands, will be significantly less abundant in managed landscapes.

Fire and clearcuts are both 'contagious' disturbances (Peterson, 2002; Boucher et al., 2017b) that can affect the accuracy of our models (Valcu and Kempenaers, 2010). However, our dataset consists of a complete survey of the study territory based on a 297 × 463 m grid. Thus, our methodology limits the influence of spatial autocorrelation in our models, as we are not attempting to generalize from a subsample of points to a larger territory. Our results can therefore be considered as an accurate description of the evolution of the forested landscape based on the nature of the disturbances over the study period. Nevertheless, further research should determine to what extent structural and abiotic attributes influence the 'contagion' patterns of fires and clearcuts.

4.2. Influence on landscape dynamics and the diversity of boreal old-growth forests

The importance of boreal old-growth forests for forest biodiversity has largely been acknowledged. First, it is pointed out that these stands often contain habitats that are absent or less abundant in younger stands (Lõhmus et al., 2005; Schmiegelow and Monkkonen, 2009; Schowalter, 2017). Second, the temporal continuity of these stands is very important for species having a limited dispersal capacity (Desponts et al., 2004; Fenton and Bergeron, 2008; Boudreault et al., 2018). Recent studies have emphasized boreal old-growth forest structural and dynamics diversity (Martin et al., 2018; Portier et al., 2018; Moussaoui et al., 2019). By targeting the dense old-growth stands, logging activities may thus threaten species associated with these particular old-growth structures. From one old-growth stand to another, species composition may change due to differences in the structurally induced microclimates, differences in the abundance and the characteristics of the available deadwood, or differences in the stand disturbance history (Baker et al., 2013; Schowalter, 2017; Boudreault et al., 2018). The results of our study therefore highlight the importance of accounting for the structural diversity of boreal old-growth forests, as specific old-growth types, and hence specific habitats, may be disappearing in logged areas.

Furthermore, remaining old-growth boreal stands were often either recently disturbed (Smirnova et al., 2008; Martin et al., 2018; Portier et al., 2018) or low-productive stands (Fenton et al., 2005). In stands marked by low productivity or in stands burned by moderately severe fires, regeneration is often not sufficiently vigorous (e.g., St-Denis et al., 2010) or too scarce (e.g., Smirnova et al., 2008) to efficiently close the canopy. Moreover, a high frequency of compound secondary disturbances may also reinitiate forest succession by gradually killing the majority of the overstorey, even in stands having a dense and productive regeneration (Buma and Wessman, 2012; Donato et al., 2012; Sánchez-Pinillos et al., 2019). Recently disturbed stands are thus more vulnerable to new disturbances than those that have not been disturbed in a relatively long time. This vulnerability may also be reinforced by the characteristics of the main secondary disturbance agents in eastern Canadian boreal forests, i.e., spruce budworm (*Choristoneura fumiferana* (Clem.)) or windthrow, that can kill a significant fraction of the overstorey (De Grandpré et al., 2018; Martin et al., 2019). This supposes that the remaining stands in logged landscapes tend to have lower resilience—the ability of a stand to recover from a disturbance, sensu Perry and Amaranthus (1997)—in comparison to burned landscapes, as they are potentially more vulnerable to subsequent secondary disturbances. Therefore, logging activities in boreal landscapes may decrease the abundance, diversity, and functionality of boreal old-growth forests.

Forest management may also increase the probability of compound stand-replacing fires and may reduce the overall resilience and productivity of the landscape. By increasing the area covered by stands at the first stages of forest succession (i.e., stand initiation and stem exclusion, sensu Oliver and Larson, 1996) in the studied landscape, logging increases the risk of regeneration failure. Indeed, even fire-adapted species, such as black spruce and jack pine, cannot produce enough seeds to permit natural stand regeneration if the interval between two stand-replacing disturbances is too short (< 50 years) (Smirnova et al., 2008; Côté et al., 2013; Boucher et al., 2017b).

5. Conclusion and implications for management

The results of our study highlight the differences in the structural and abiotic characteristics of logged and burned stands. As logging activities are driven primarily by economic requirements, the most productive old-growth stands are logged first. In contrast, burns occur more often in younger and sparser stands. The effects of these disturbances thus decrease the structural diversity of the landscape. In addition, the removal of the most productive stands and the logging-induced rejuvenation process may have increased the sensitivity of the landscape to future fires or secondary disturbances.

The extensive use of clearcuts coupled with high logging rates are the main factors explaining boreal landscape simplification under traditional even-aged forest management (Östlund et al., 1997; Boucher et al., 2015; Boucher et al., 2017b). Moreover, even if there is a significant increase in the burn rate because of climate change, the overuse of short-rotation clearcuts would remain the main factor leading to boreal old-growth forest loss in the next century (Bergeron et al., 2017). Recent studies have emphasized management strategies having a greater focus on short-rotation plantations to reach the objectives of wood production (Côté et al., 2010; Tittler et al., 2015). In this context, the logging rate would increase for even-aged stands, i.e., stands < 100 years, thereby reducing the elevated logging pressure observed for old-growth stands in this study. Meanwhile, alternative forest treatments, such as partial cuts or stem-selection harvests, would be favoured in old-growth stands. Hence, enhancing alternative forest management strategies should help maintain sufficient areas of old-growth forest in managed landscapes and mitigate the incoming effects of climate change.

The province of Quebec adopted ecosystem-based forest management principles (Gouvernement du Québec, 2010) three years after the end of our study period. Therefore, the results of our study depicted the effects of past logging practices in Quebec's boreal landscapes, before this major shift in forest management policy. Indeed, and as defined by ecosystem-management principles, the current and future effects of forest practices on boreal landscapes should be closer to natural disturbance dynamics (Gauthier et al., 2009). In the next decades, further studies are required to assess how the application of ecosystem-based management is affecting the structural and abiotic characteristics of the managed forest landscape.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank the Ministère des Forêts de la Faune et des Parcs du Québec for sharing their data for the study territory. We also thank the two anonymous reviewers for their helpful comments on an earlier version of this manuscript and Murray Hay for the language revision of the manuscript. Funding for this project was provided by the Fonds Québécois de la Recherche sur la Nature et les Technologies (FQRNT), Ministère des Forêts de la Faune et des Parcs du Québec, and the Natural Sciences and Engineering Research Council of Canada (NSERC) – Université du Québec à Chicoutimi (UQAC) NSERC Industrial research chair "Industrial Research Chair on Black Spruce Growth and the Influence of Spruce Budworm on Landscape Variability in Boreal Forests."

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.117765.

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