# Boreal old-growth forest structural diversity challenges aerial photographic survey accuracy

**Maxence Martin**[*1], **Hubert Morin**[1], **Nicole J. Fenton**[2]

[1] Département des Sciences fondamentales, Université du Québec à Chicoutimi, 555 boul. de l'Université, Chicoutimi, Québec G7H2B1, Canada

[2] Institut de Recherche sur les Forêts, Université du Québec en Abitibi-Témiscamingue, 445 boul. de l'Université, Rouyn-Noranda, Québec J9X 5E4, Canada

* Corresponding author: Tel.: +1 581 882 8651; maxence.martin1@uqac.ca

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## Abstract

The erosion of old-growth forests in boreal managed landscapes is a major issue currently faced by forest managers. However, quantifying this phenomenon requires accurate surveys. The intention of our study was to determine if aerial forest surveys accurately identify boreal old-growth forests in Québec, Canada. We first compared stand successional stages (even-aged vs. old-growth) in two aerial surveys performed in 1968 (preindustrial aerial survey) and 2007 (modern aerial survey) on the same 2200 km$^2$ territory. Second, we evaluated the accuracy of the modern aerial survey by comparing its results with those of 74 field plots sampled in the study territory between 2014 and 2016. The two aerial surveys differed significantly; 80.8% of the undisturbed stands that were identified as "old-growth" in the preindustrial survey were classified as "even-aged" in the modern survey. 60% of the stands identified as old-growth by field sampling were also erroneously identified as even-aged by the modern aerial survey. The scarcity of obvious old-growth attributes in boreal old-growth forests, as well as poorly adapted modern aerial survey criteria (i.e. criteria requiring high vertical stratification and significant changes in tree species composition along forest succession), were the main factors explaining these errors. It is therefore likely that most of Québec's boreal old-growth forests are currently not recognized as such in forest inventories, which could challenge the effectiveness of sustainable forest management policies.

## Résumé

L'érosion des superficies des vieilles forêts boréales est actuellement un enjeux majeurs pour les gestionnaires forestier. Répondre efficacemment à cette problématique demande néanmoins l'accès à des données d'inventaires fiables. Ainsi, l'objectif de cette étude était de déterminer si les inventaires forestiers aériens identifient correctement les vieilles forêts dans les paysages boréaux du Québec, Canada. Nous avons comparé les stades de succession (forêt équienne ou vieille forêt) de deux inventaires aériens réalisés en 1968 (inventaire aérien préindustriel) et en 2007 (inventaire aérien moderne) sur un territoire de 2200 km$^2$. Nous avons aussi comparé les résultats de l'inventaire aérien moderne avec ceux obtenus à partir de 74 placettes de terrain échantillonnés entre 2014 et 2016. Les deux inventaires aériens étaient très incohérents : 80.8% des peuplements non-perturbés identifiés comme « vieilles forêts » par l'inventaire préindustriel étaient classés comme « équiens » par l'inventaire moderne. 60% des placettes de terrain identifiées comme vieilles forêts étaient aussi classées « équiens » par l'inventaire aérien moderne. Le manque d'attributs de vieilles forêts évidents ainsi que l'utilisation de critères inadaptés (c'est-à-dire nécessitant une forte complexité verticale et d'importants changements de composition en espèces arborescentes durant la succession forestière) étaient les principaux éléments expliquant ces erreurs. Il est ainsi possible que la majorité des vieilles forêts boréales du Québec ne soient pas identifiés comme telles, limitant l'efficacité des stratégies de gestion durable.

## Introduction

Boreal old-growth forests, i.e. stands driven by gap-dynamics, are defined by specific structural attributes as well as strong temporal continuity due to the absence of stand-replacing disturbances over a significant period (Kneeshaw and Gauthier 2003; Bergeron and Harper 2009; Drapeau et al. 2009a). They contain many habitats features that are absent in younger stands, making them key elements for biodiversity (Tikkanen et al. 2006; Bergeron and Fenton 2012; Boudreault et al. 2018). However, since the middle of the 20th century, industrial-scale clear cut harvesting has primarily focussed on the oldest forest stands, leading to a decrease of boreal old-growth forest area all around the circumboreal zone (Östlund et al. 1997; Shorohova et al. 2011; Boucher et al. 2015). Moreover, the short rotation of clearcutting systems, which have been the dominant harvesting approach in boreal forests, inhibits the recruitment of new old-growth stands (Kuuluvainen 2009). Consequently, managed boreal landscapes currently face significant biodiversity issues because of the erosion of the abundance of boreal old-growth forest habitats (Drapeau et al. 2009b; Tikkanen et al. 2006; Patry et al. 2017).

To mitigate the impact of logging on boreal old-growth forests, forest management practices now often aim to maintain remaining boreal old-growth forests in managed landscapes or to employ silvicultural treatments that preserve old-growth structural attributes (Bergeron et al. 1999; Bergeron et al. 2002; Bergeron et al. 2007; Bauhus et al. 2009; Gauthier et al. 2009; Drapeau et al. 2009b, Drapeau et al. 2016). To ensure that old-growth habitats in managed landscapes were representative of that present in natural landscapes, an emphasis has been placed on management strategies that are based on natural disturbance regimes or stand scale processes (Gauthier et al. 2009; Kuuluvainen 2009). Yet, boreal old-growth forests are complex and diversified ecosystems. The shift from even-age to old-growth stage does not occur in the same way from one stand to another, varying with tree species, abiotic conditions and secondary disturbance characteristics (Bergeron and Harper 2009; Martin et al. 2018; Martin et al. Accepted). In addition, this shift is not discrete but continuous, making the distinction between the two stages hard to define (Pesklevits et al. 2011). Finally, once the old-growth stage has been reached, boreal old-growth forests continue to exist as structurally diverse and changing ecosystems (Martin et al. 2018; Portier et al. 2018; Moussaoui et al. 2019).

To ensure that remnant boreal old-growth forests are retained during forest harvesting, we have to be able to identify them in forest inventory surveys. These surveys must also be consistent over time in order to evaluate the impacts of forest management. Exhaustive field surveys are not practical in boreal forests because of their vast area. For this reason, aerial photographic surveys are commonly used as a proxy for field surveys. Yet, the efficacy of aerial photographic surveys in identifying structurally complex stands (i.e. old-growth forests) has been challenged based on evidence that such stands can be erroneously classifed as structurally simple (i.e. even-aged) (Boucher et al. 2003; Côté et al. 2010). This implies a potential underestimation of boreal old-growth forest abundance by aerial surveys, which may then limit the efficacy of subsequent management strategies in protecting boreal old-growth stands. Moreover, it is important to assess if this underestimation applies equally to all boreal old-growth forest structures. If not, specific boreal old-growth forest structures may be particularly threatened because they are not well recognized by aerial surveys.

Boreal old-growth forests are abundant in Québec's unmanaged landscapes because of relatively long (>200 years) fire cycles (Cyr et al. 2005; Grandpré et al. 2009; Bélisle et al. 2011), making Québec an appropriate region to study aerial photographic survey accuracy. In addition, complete aerial photographic surveys of boreal forests have been completed in the province since the end of the 1960s. Industrial scale logging started in the southern edge of the boreal forests in the 1940s and has progressed northward since (Boucher et al. 2017). Thus, the first surveys often inventoried landscapes where anthropogenic influences were almost inexistent, i.e. preindustrial landscapes. Our study therefore aimed to determine if aerial forest surveys accurately identify boreal old-growth forest in Québec's landscapes dominated by black spruce - feather moss forests, the main closed-forest type in Québec's boreal territories (Rowe 1972). Specifically, our objectives were: (1) to determine if old-growth stands are consistently identified by aerial surveys over time, (2) to evaluate the accuracy of the most recent aerial survey in identifying different boreal old-growth forest types, and (3) to identify old-growth types that are the most likely to be confused with even-aged stands. We expected that the accuracy of the aerial photographic surveys increased over time and thus most of the old-growth forests would be accurately identified by the most recent survey. However, we also predict that stands at the beginning of the old-growth stage will be those most commonly mistaken for even-aged stands because of the absence of any clear transition between the two stages. This study evaluates the accuracy of aerial photographic surveys, first by discriminating even-aged and old-growth stands and second by identifying how well the entire structural diversity of boreal old-growth forest developemental stages is determined. We discuss how efficient is the photographic survey approach to integrate boreal old-growth forests in managed landscapes and what are the potential biases and errors.

## Methods

### *Study area and field sampling*

In this study we used the same 2200 km$^2$ area described by Martin et al. (2018) and Martin et al. (Accepted), situated to the south east of Lake Mistassini (72°15'00" W to 72°30'00" W, 50°07'23" N to 50°30'00") (**Figure 1**). This territory is public land and part of the black spruce (*Picea mariana* (Mill.)) – feather moss bioclimatic domain. Black spruce and balsam fir (*Abies balsamea* (L.) Mill.) are the dominant tree species. They are sometimes found with jack pine, (*Pinus banksiana* (Lamb.), white spruce (*Picea glauca* (Moench) Voss), paper birch (*Betula papyrifera* Marsh.) and trembling aspen (*Populus tremuloides*). The dominant surface deposits are thick glacial tills but watercourses are often surrounded by sand deposits or vast bogs. The topography of

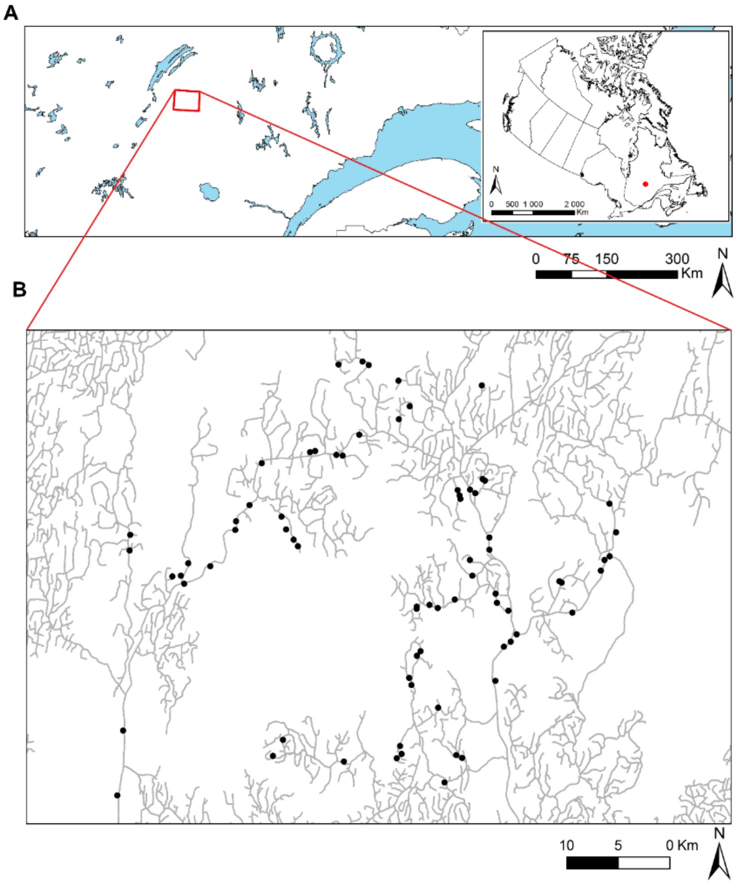

**Figure 1** (A) Location of the study territory (red rectangle) in the province of Québec. The red dot in the insert map indicates its location in Canada. (B) Field plots (black dots) sampled in the study territory. Grey lines represent the forest road network.

the study territory is dominated by gentle hills with altitudes ranging from 350 to 750 m. Mean annual temperature ranges from -2.5 to 0.0°C, annual rainfall (rain and snow) from 900 to 1100 mm and growing season length is from 140 to 150 days (Robitaille and Saucier 1998). Timber exploitation started in 1991 at a low level until the year 2000, when harvest levels increased. Consequently, all surveys performed on this territory before 1991 represent forests free from any industrial logging activity

Martin et al. (2018) and Martin et al. (Accepted) surveyed 74 stands between 2014 and 2016 on this territory (**Figure 1**). Stand selection was based on stratified random sampling of the six dominant environmental types on the study territory, as defined by Québec's Ministry of Forests, Wildlife and Parks (MFWP) ecological classification (Blouin and Berger 2004), and two stand minimal age classes. The dominant environmental types can be defined by the following Potential vegetation/Slope/ Superficial deposit/Drainage associations: Balsam fir – white birch/Medium/Till/ Mesic; Black spruce  balsam fir/Medium/Till/Mesic; Black spruce – feather moss (BSFM)/Low/Sand/Mesic; BSFM/Low/Till/Mesic; BSFM/ Low/Till/Subhydric; BSFM/Low/Organic/Hydric. These represent over 72% of productive forest area on the study territory. The age classes corresponded to the theoretical stages of the transition process toward the old-growth stage in Québec boreal forests: 80-200 years (beginning of the transition) and greater than 200 years (end of the transition). Site age was assessed by a preliminary survey through tree core sampling of five dominant and codominant trees per site. Only sites accessible by road were selected and plots were systematically placed 125m away from the stand edge to limit edge effects.

In each stand we collected data on: merchantable trees (diameter at breast height [dbh] ≥9 cm), saplings (trees with a dbh < 9 cm and a height > 1.30m), gap fraction and coarse woody debris volume using one 400m$^2$ plot with nested subplots and transects (see **Table 1** for details). To determine the minimum stand age, we performed a destructive sampling of basal discs on ten trees. Sampled trees were randomly selected according to their crown class (dominant, codominant, intermediary and suppressed). At least three of these trees were dominant trees and their height was measured once the tree was felled to estimate the maximum stand height. Two or three trees were then sampled for each of the remaining crown classes, depending on their availability within the plot. The sampled basal discs were then sanded and the tree rings measured along two radii to determinate tree age.

**Table 1** Description of the sampling design and the attributes sampled for each type of data studied in field plots.

| **Data** | **Sampling design** | **Attributes sampled** |
|---|---|---|
| Merchantable trees | All individuals in one 20 × 20m (400m$^2$) square plot | Diameter at breast height, species, vitality (alive, senescent, dead) and position in the canopy as de by the Québec’s Ministry of Wildlife, Fauna and Parks typology (MRNF 2008):<br>- Dominant: highest trees in the stand<br>- Codominant: height ≥ 2/3 of dominant tree heig<br>- Intermediary: height < 2/3 and ≥1/2 of dominan height<br>- Suppressed: height < 1/2 of dominant tree heigh |
| Saplings | All individuals in two 10 × 10m (100m$^2$) square plots within the 400m$^2$ plot | Diameter at breast height, species |
| Gap fraction | All gaps along five 25m long transects starting from the centre of the 400 m$^2$ plot. “Gaps” were all sections of the transects where the canopy height was less than the 2/3rds of the height of the dominant trees for a distance of > 2m along the transect | Gap length |
| Coarse woody debris (CWD) | All coarse woody debris that intersected four 20m long transects that followed the edge of the 400m$^2$ plot. When a piece of CWD crossed two transects, any second encounter was skipped to avoid double-counting. | Diameter at the intersection |

### *Cartographic data*

The government of Quebec has conducted five decadal forest surveys; the fifth survey is still in progress. All these inventories use aerial photographs to describe forest stands. We chose to focus on the results of the first (preindustrial aerial survey) and the fourth (modern aerial survey) decadal forest inventories, because they represent the two extremes in terms of technological evolution over the time period. On our study area, 1/15 000 aerial photographs were taken at an average altitude of 2 295m in 1968 for the preindustrial aerial survey (black and white photographs) and in 2007 for the modern aerial survey (high definition numeric false-colour infrared photographs). For both surveys, the boundaries of forest stands were defined according to their cartographic structural characteristics (tree species composition, age, structural complexity, height and density classes) and abiotic characteristics (slope, drainage, superficial deposit and potential vegetation classes). These characteristics were interpreted by stereoscopic photo-interpretation with the help of topographic maps for the preindustrial aerial survey or a stereoscopic analysis software for the modern. The MFWP then simplified stand boundaries for the preindustrial survey only: the territory was divided in 297 m x 463 m large rectangles (15 seconds x 15 seconds in geographic coordinates, 14ha) named "tessels" (**Appendix A**). The cartographic structural and abiotic values attributed to each tessel were the characteristics of the preindustrial forest stand polygon situated at the tessel centroid location. Preindustrial and modern aerial surveys can therefore be compared along the tessel grid, where each centroid represents the results of both forest surveys at the centroid location.

### *Identification of the old-growth stages*

Based on Martin et al. (2018), the old-growth stage starts when new cohorts begin to replace the first cohort or when the tree diameter distribution shifts from a Gaussian to an irregular diameter distribution. However, field and cartographic data, as well as preindustrial and modern aerial surveys, use different parameters to describe stand structural complexity. Therefore, a preliminary analysis was necessary to homogenise the descriptors of stand structural complexity in order to identify old-growth stands for both field and cartographic data.

For field data, we identified the old-growth stages using the methodology of Martin et al. (2018). First, we fitted the diameter distribution of all merchantable stems and saplings in each plot with the Weibull distribution (Bailey and Dell 1973). A Weibull's shape parameter (WSP) $\geq 1.5$ indicates a normal diameter distribution and a WSP $< 1.5$ indicates an irregular diameter distribution. Second, we counted tree rings along two radii for each of the ten basal discs sampled and the maximum value was considered as the minimum age of the tree. We identified the cohort of the trees for each stand. If the age difference between the youngest and the oldest tree did not exceed 30 years, we considered that they were all first cohort trees. If some trees exceeded the 30-year threshold, we considered these trees as belonging to old-growth cohorts replacing the first cohort. In this case, we looked for evidence of suppression on juvenile trees in the trees under the 30-year threshold (i.e. sustained low radial increment starting from the pith). Trees that presented no evidence of juvenile suppression were categorized as first cohort trees while the others were categorized as old-growth cohort trees. Finally, when the majority of the trees belonged to a single 30-year age class but were mixed with individuals more than 30 years older, the older individuals were considered as survivors of the previous stand-initiating disturbance and removed from the analysis. The remaining trees were classified as first cohort trees. Then, we calculated the Cohort Basal Area Ratio (CBAP) according to the Kneeshaw and Gauthier (2003) formula:

$$CBAP = \frac{(BA_{Old-growth\ cohort\ trees} + 0.1)}{(BA_{Old-growth\ cohort\ trees} + BA_{First\ cohort\ trees} + 0.1)}$$

where *BA* is the basal area. Stands were defined as even-aged if WSP$\geq 1.5$ and CBAP$< 0.3$ and old-growth in all other cases (Martin et al. 2018). For each field plot, we also computed the eight following field structural attributes: tree density, basal area, sapling density, balsam fir proportion, coarse woody debris volume, gap fraction, maximum height, merchantable trees' Shannon Index and minimum time since the last fire (i.e. age of the oldest tree sampled) (**Appendix B**).

For cartographic data from the modern aerial survey, stand structure was classified in one class among four (even-aged, uneven-aged, irregular and layered classes, MRNF 2008), based on cohort composition and stand vertical structure, estimated during photo-interpretation. We considered that the uneven-aged, irregular and layered classes indicated old-growth forests because their complex vertical structure and/or the presence of different cohorts implied gap-dynamics (**Table 2**). In contrast, in the preindustrial aerial survey data, there were only two stand structure classes for the mature plots: "Regular" and "Irregular" (Pelletier et al. 2007), also estimated by photo-interpretation. Therefore, we assumed the "Regular" class to be "Even-aged" while the "Irregular" class was assumed to be "Old-growth". The cartographic structural attributes computed for the analyses were: preindustrial dominant species, preindustrial and modern canopy densities, modern and preindustrial tree height, modern black spruce abundance (i.e. black spruce proportion in stand canopy), modern balsam fir abundance, modern jack pine abundance, modern broadleaved species abundance (**Appendix C**), using the classes defined by the MFWP.

**Table 2** Characteristics of the different age structures classes used by the preindustrial and modern surveys and of the developmental stage extrapolated (even-aged or old-growth) for this study

| Survey | Structure class | Age structure | Structural complexity | Old-growth stage extrapolated | Frequency (%) |
|---|---|---|---|---|---|
| Preindustrial | Regular | - | One canopy layer *(regular)* | Even-aged | 49.1 |
| | Irregular | - | High variation in the canopy height, multiple canopy layers *(irregular)* | Old-growth | 50.9 |
| Modern | Even-aged | One single cohort represent more than 75% of the canopy *(monocohort)* | One canopy layer *(regular)* | Even-aged | 80.6 |
| | Layered | Two cohorts represent each more than 25% of the canopy *(multicohort)* | Two canopy layers, with a tree height amplitude superior to 5m *(irregular)* | Old-growth | 0.5 |
| | Uneven-aged | Three cohorts represent each more than 25% of the canopy *(multicohort)* | One canopy layer *(regular)* | Old-growth | 15.3 |
| | Irregular | Three cohorts represent each more than 25% of the canopy *(multicohort)* | Multiple canopy layers, with a tree height amplitude superior to 8m *(irregular)* | Old-growth | 3.6 |

### *Statistical analysis*

For our first objective, to determine if old-growth stands are consistently identified by aerial surveys over time, we compared the classification of stands in the two time periods (preindustrial and modern) using the 3417 undisturbed, mature centroids. We computed the error-matrix and the overall accuracy (proportion of the centroids or field plots mapped correctly) of the even-aged and old-growth stands in the preindustrial and modern aerial surveys using the Olofsson et al. (2013) methodology. Yet, forests are dynamic ecosystems and their structure may change over time, however as we selected only undisturbed sites, the main consistent structural change should be a shift from the even-aged to the old-growth stage. In contrast, any shift from the old-growth stage to the even-aged in the absence of any natural stand-replacing disturbance or logging activities is unlikely and would be the result of errors in old-growth identification in at least one of the aerial surveys. Then, we used logistic regressions to determine if centroids presenting these erroneous dynamics were the result of a specific bias. The classes of the dependent dummy variables were "Consistent dynamics" (same stage between the two surveys or shift from the even-aged stage to the old-growth) and "Inconsistent dynamics" (shift from old-growth to even-aged). We selected as independent variables only the cartographic structural attributes that were not associated with each other based on the $\varphi$ or Cramer's V values (Sheskin 2002). If a strong association between two attributes was caused by low-abundant classes, we removed the sites defined by these classes from the dataset. Thus, centroids belonging to the ">80%" preindustrial or modern canopy density classes were strongly associated with each other but they only represented 255 centroids. We therefore removed these sites from the final dataset (255 centroids removed from the analysis, total remaining = 3162). The independent variables retained for the logistic regression were preindustrial canopy density, modern balsam fir abundance and modern canopy tree density. The model was run a first time with all the variables and a second time with only the significant variables, in order to obtain the most parsimonious model. Then, we used log-likelihood test, Receiver Operating Characteristic (ROC) (Zweig and Campbell 1993) and Tjur's coefficient of discrimination (COD, Tjur 2009) to assess the model predictive ability.

For our second objective, evaluating the accuracy of the most recent aerial survey in identifying different boreal old-growth forest cover types, we compared the age structure (monocohort or multicohort), the diameter distribution (regular or irregular) and the old-growth stage (even-aged or old-growth) of the 74 field plots based on our field inventories with the results of the typology of the recent survey.. Error-matrixes were computed and the overall accuracies (proportion of the area mapped correctly) were calculated for each matrix. In addition, we compared the differences in field-sampled structural attributes according to the accuracy of the modern aerial survey in identifying their age structure, structural complexity or old-growth stage (Identical: same result between field and aerial surveys; Different: different result between field and aerial surveys). Student tests were used to assess the statistical significance of these differences between surveys if requirements (homoscedasticity and normality of the independent variable for each group) were fulfilled, otherwise we used the Wilcoxon test. Four field plots belonged to the "unproductive" class in the modern aerial survey were not assigned to structural complexity or age structure classes. These sites were removed for this analysis, leaving 70 fields plots.

Finally, for our third objective, to identify old-growth types that are more likely to be confused with even-aged stands, we aimed to discriminate the vertical structure of the sampled stands based on the structural parameters that challenged aerial survey accuracy. First, we determined the proportion of trees from each crown class (dominant, codominant, intermediate and suppressed) in each plot. Then, we performed a multivariate regression tree analysis (De'ath 2002) with 100 repetitions using the structural parameters having a significant impact on survey accuracy in the previous analyses (logistic regression, Student or Wilcoxon tests). We considered that balsam fir proportion in basal area, gap fraction and maximum height computed for the field plots corresponded to the respective attributes computed for aerial surveys: modern balsam fir abundance, modern canopy density (inverse of the gap fraction) and modern stand height. We selected the optimal regression tree based on the best balance between a low relative error and a limited number of groups. This analysis was performed using only the field plots sampled in 2015 and 2016 identified as productive by the modern aerial survey (67 plots), as some field structural attributes were missing for the field plots sampled in 2014. We then computed old-growth stage error-matrixes and overall accuracies between modern aerial and field surveys for each cluster.

All the statistical analyses were performed using R-software, version 3.3.1 (R Development Core Team 2016), using the *fmsb* (Nakazawa 2017), *ROCR* (Sing et al. 2005), *sjstats* (Lüdecke 2018), *vegan* (Oksanen et al. 2018) and *mvpart* (Therneau and Atkinson 2014) packages. A *p*-threshold of 0.05 assess the tests significance.

## Results

### *Comparison of the aerial surveys*

Nearly fourty percents of the centroids (40.9%) presented an even-aged structure in both aerial surveys (**Table 3**). Yet, 39.7% of the plots showed an inconsistent structural evolution, i.e., an old-growth structure in the preindustrial aerial survey and an even-aged structure in the modern aerial survey. Hence, 80.1% of the undisturbed centroids identified as old-growth in the preindustrial survey were identified as even-aged in the modern. The remaining old-growth stage combinations were less abundant (10% shifted from even-aged to old-growth and 9.4% of centroids were stable old-growth centroids). The strong changes between the two surveys (49.7% of the plots presenting a different structure) resulted in a low overall accuracy (50.3%) and most of these changes were inconsistent with natural forest dynamics in the absence of any stand-replacing disturbance. This implied a significant bias in at least one of the aerial surveys.

**Table 3** Error-matrix between the preindustrial and modern aerial surveys. Bold results refer to inconsistent structural evolution, i.e. the shift from old-growth to even-aged between the preindustrial and modern aerial surveys in the absence of any stand-replacing disturbance.

| | **Preindustrial survey** | | | **Error matrix** | | | **Overall accuracy** |
|---|---|---|---|---|---|---|---|
| **Modern survey** | **Even-aged** | **Old-growth** | ***Total*** | **Even-aged** | **Old-growth** | ***Total*** | |
| Even-aged | 1398 | **1356** | *2754* | 40.9 | 39.7 | *80.6* | 50.3 |
| Old-growth | 342 | 321 | *663* | 10.0 | 9.4 | *19.4* | |
| *Total* | *1740* | *1677* | *3417* | 50.9 | 49.1 | *100.0* | |

All the explanatory variables of the logistic regression model comparing centroid structural evolution between the surveys (i.e. consistent or inconsistent) were significant (**Appendix D**). In addition, the model presented a good predictive ability, with a ROC = 0.71 and a COD = 0.14. The parameters associated with inconsistent structural evolution were: lower modern abundance of balsam fir, generally lower pre-industrial canopy density and higher modern canopy density. Although balsam fir was present in more than 25% of the centroids showing a consistent structural evolution, this species was almost absent in the plots with an inconsistent structural evolution (**Figure 2**). Furthermore, centroids presenting a consistent structural evolution mainly belonged to the preindustrial canopy density class [60%-79.9%]. In contrast, centroids defined by an inconsistent structural evolution mainly belonged to the preindustrial canopy density classes [25%-39.9%] and [40%-59.9%]. Centroids belonging to the modern canopy density classes [60-79.9%] were more abundant in the inconsistent structural evolution group in comparison to consistent structural evolution group. Yet, differences in modern canopy density according to the structural evolution were less striking than those observed for the preindustrial canopy density. Therefore, stands that shifted from the old-growth to the even-aged stage between the two surveys are mostly pure black spruce stands with a sparse canopy.

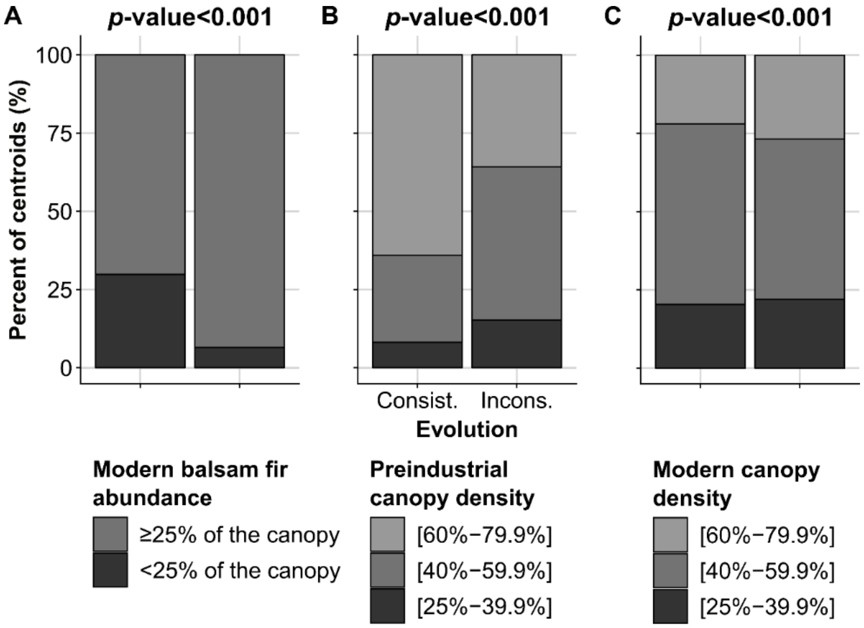

**Figure 2** Histogram of the class distribution and *p*-value of the significant parameters according to the logistic regression model comparing centroids defined by a consistent or an inconsistent structural evolution, separated depending on the binary dependant variable: (A) Modern balsam fir abundance, (B) Preindustrial tree density, (C) Modern tree density. Consist.: consistent structural evolution; Incons.: Inconsistent structural evolution. Consistent structural evolution refers to the same stage between the two surveys or shift from the even-aged stage to the old-growth between the preindustrial and modern aerial surveys. Inconsistent refers to shift from old-growth to even-aged between the preindustrial and modern surveys. The characteristics of the independent variables' classes are presented in **Appendix B**.

### Comparison of cartographic survey with field survey

The modern aerial survey was more accurate in discriminating monocohort and multicohort stands (Overall accuracy = 56%, **Table 4A**) than regular and irregular stands (Overall accuracy = 21.4%, **Table 4B**), even if all these results were low. As a consequence, the modern aerial survey failed to correctly identify the successional stage for half of the field plots (Overall accuracy = 44%, **Table 4C**). This error was specifically related to old-growth stands, as 40% of the old-growth field plots were

**Table 4** Error-matrixes between the field and modern aerial surveys for stand (A) structural complexity, (B) age structure and (C) old-growth stage.

**A**

| | **Field plots** | | | **Error Matrix** | | | **Overall** |
|---|---|---|---|---|---|---|---|
| **Modern survey** | **Regular** | **Irregular** | ***Total*** | **Regular** | **Irregular** | ***Total*** | **accuracy** |
| Regular | 7 | 55 | *62* | 10.0 | 78.6 | *88.6* | 21.4 |
| Irregular | 0 | 8 | *8* | 0.0 | 11.4 | *11.4* | |
| *Total* | *7* | *63* | *70* | 10.0 | 90.0 | *100.0* | |

**B**

| | **Field plots** | | | **Error Matrix** | | | **Overall** |
|---|---|---|---|---|---|---|---|
| **Modern survey** | **Monocohort** | **Multicohort** | ***Total*** | **Monocohort** | **Multicohort** | ***Total*** | **accuracy** |
| Monocohort | 17 | 27 | *44* | 24.3 | 38.6 | *62.9* | 55.7 |
| Multicohort | 4 | 22 | *26* | 5.7 | 31.4 | *37.1* | |
| *Total* | *21* | *49* | *70* | 30.0 | 70.0 | *100.0* | |

**C**

| | **Field plots** | | | **Error Matrix** | | | **Overall** |
|---|---|---|---|---|---|---|---|
| **Modern survey** | **Even-aged** | **Old-growth** | ***Total*** | **Even-aged** | **Old-growth** | ***Total*** | **accuracy** |
| Even-aged | 5 | 39 | *44* | 7.1 | 55.7 | *62.9* | 44.2 |
| Old-growth | 0 | 26 | *26* | 0.0 | 37.1 | *37.1* | |
| *Total* | *5* | *65* | *70* | 7.1 | 92.9 | *100.0* | |

**Table 5** Mean values, standard deviation (in italics) and *p*-values, based on the Student or Wilcoxon test of the structural parameters of the field plots between those for which the diameter structure or the age structure have been correctly identified (identical) by the modern aerial survey and those incorrectly identified (different). The absence of values in the *p*-value column indicates a non-significant result. TD: Tree density (n/ha), BA: basal area ($m^2$/ha), BFP: balsam fir proportion (%), WSP: Weibull's shape parameter, GF: Gap fraction (%), CWD: Coarse woody debris volume ($m^3$/ha), MH: Maximum height (m), SD: Sapling density (n/ha), SIMT: Shannon Index of the merchantable trees, CBAP: Cohort Basal Area Proportion, MTSLF: Mean time since last fire (years).

| **Variable** | **Structural parameter** | **Similarity between field and aerial surveys** | | ***p*-value** |
|---|---|---|---|---|
| | | **Identical** | **Different** | |
| Structural complexity (*n identical = 15; n different = 55*) | TD | 996.66 ± *465.3* | 932.27 ± *349.55* | |
| | BA | 20.61 ± *8.39* | 17.46 ± *6.77* | |
| | BFP | 0.12 ± *0.16* | 0.13 ± *0.23* | |
| | WSP | 1.41 ± *0.7* | 0.93 ± *0.26* | |
| | GF | 52.82 ± *25.29* | 62.96 ± *24.39* | |
| | CWD | 75.57 ± *71.09* | 57.73 ± *45.97* | |
| | MH | 19.51 ± *3.21* | 18.59 ± *2.76* | |
| | SD | 2506.66 ± *2322.58* | 2670.45 ± *1877.11* | |
| | SI | 0.22 ± *0.14* | 0.12 ± *0.12* | <0.05 |
| | CBAP | 0.4 ± *0.36* | 0.62 ± *0.34* | <0.05 |
| | MTSLF | 180.00 ± *65.88* | 202.07 ± *60.76* | |
| Age Structure (*n identical = 39; n different = 31*) | TD | 892.94 ± *355.12* | 1012.9 ± *393.16* | |
| | BA | 18.31 ± *7.28* | 17.9 ± *7.21* | |
| | BFP | 0.16 ± *0.24* | 0.09 ± *0.18* | |
| | WSP | 1.06 ± *0.52* | 1.00 ± *0.3* | |
| | GF | 57.33 ± *27.15* | 64.92 ± *21.31* | |
| | CWD | 66.18 ± *54.81* | 55.72 ± *49.18* | |
| | MH | 19.03 ± *3.03* | 18.48 ± *2.64* | |
| | SD | 2502.56 ± *1991.56* | 2802.41 ± *1947.96* | |
| | SI | 0.18 ± *0.14* | 0.09 ± *0.11* | <0.01 |
| | CBAP | 0.5 ± *0.38* | 0.66 ± *0.3* | |
| | MTSLF | 183.76 ± *60.03* | 214.41 ± *61.3* | <0.05 |

identified as such by the modern survey, while all the even-aged field plots were accurately identified. Overall, the modern aerial survey tended to overestimate the abundance of even-aged stands on the landscape. The field structural attributes that explained the errors in the identification of the structural complexity classes in the modern aerial survey were the Shannon Index of the merchantable trees and the cohort basal area proportion (**Table 5**). For the age structure, the Shannon Index of the merchantable trees and the minimum time since the last fire were the parameters that best explained age structure errors. Sites erroneously identified, for both age structure and structural complexity, had a lower Shannon Index of the merchantable trees but an equivalent balsam fir proportion value, indicating that other species than balsam or black spruce (e.g. jack pine, white birch, aspen or white spruce) may have influenced these results. In addition, the progressive replacement of the first cohort, defined by the cohort basal area proportion, or the stand age, defined by the minimum time since the last fire, had different influence on modern survey accuracy. Indeed, cohort basal area proportion was only significantly different for structural complexity, while the minimum time since the last fire was only significantly different for the age structure. It suggests that these processes have different impacts on stand structure and thus caused different errors in the modern survey. Overall, older monospecific stands dominated by old-growth cohorts were more likely to be inaccurately categorized than younger stands where the first cohort was still dominant and/or where tree diversity was higher.

### *Which boreal old-growth structures are less accurately classified by the modern aerial survey?*

Based on the results of the logistic regression and of the Wilcoxon or Student tests, balsam fir proportion, gap fraction, Shannon Index of the merchantable trees, CBAP and minimum time since the last fire were the main field structural attributes selected to construct the multivariate regression tree. The optimal tree was divided into 5 clusters (**Figure 3**), where CBAP is the first cut-off factor (threshold value = 0.2), balsam fir proportion the second (threshold value = 2.57% for clusters 1-4) and gap fraction the third (threshold value = 49.4% for clusters 1-2 and threshold value = 72.4% for clusters 3-4).

Cluster 1 contained most of the mixed black spruce – balsam old-growth stands and was defined by a high gap fraction. The majority of the merchantable trees belonged to the suppressed crown class. All field plots were old-growth and around half of them were accurately identified as such by the modern aerial survey in this cluster (Overall accuracy = 52.9%, Table 56). Cluster 2 contained the remaining mixed black spruce – balsam old-growth stands, with a lower gap fraction than cluster 1. Again, all field plots were old-growth. Suppressed trees still dominated the canopy but trees from the other layers were more abundant in comparison to cluster 1. This cluster was better identified by the aerial survey as being old-growth (Overall accuracy = 66.7%). Cluster 3 contained a small part of the pure black spruce old-growth stands and was defined by the highest gap fraction among the clusters. The vertical structure of cluster 3 was intermediate between cluster 1 and cluster 2. Less than one-third of the field plots belonging to this cluster were accurately classified by the modern aerial survey (Overall accuracy = 28.6%). Cluster 4 included most of the pure black spruce old-growth stands, with a lower gap fraction compared to cluster 3. In contrast to the previous clusters, trees from the intermediate crown class were dominant in cluster 4, while suppressed and codominant trees were present in similar proportions. Around one fifth of the field plots were accurately classified by the modern aerial survey in this cluster (Overall accuracy = 21.1%). Finally, cluster 5 contained stands at the beginning of old-growth transition, including those containing a small proportion of balsam fir. The vertical structure of cluster 5 differed from those of the previous clusters, as trees belonging to the codominant crown class were more frequent. All the even-aged stands and more than one third of the old-growth stands were accurately identified by the modern aerial survey (Overall accuracy = 46.7%).

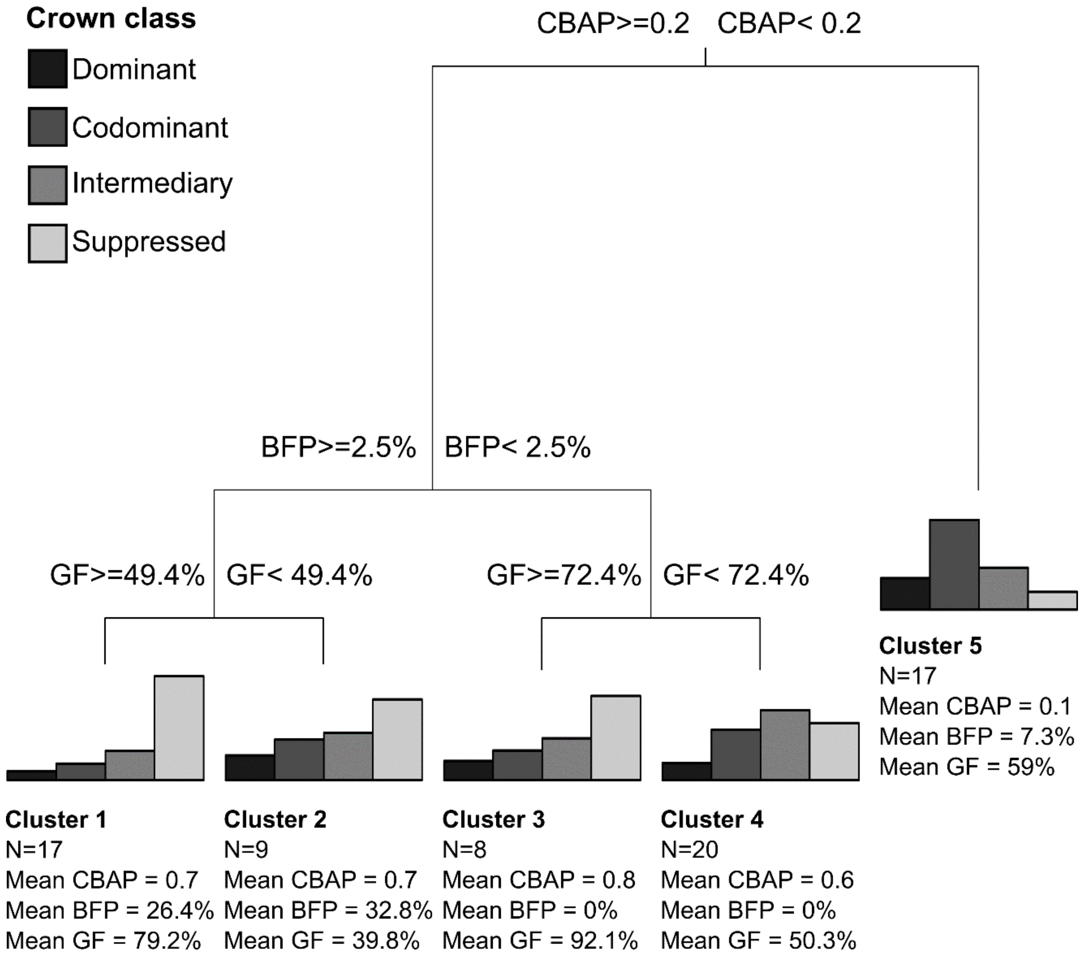

**Figure 3** Dendrogram of the multivariate analysis performed on the distribution of the canopy layers in the field plots. Histogram represent the mean frequency of the canopy layers category in each class. CBAP: Cohort Basal Area Ratio, BFP: Balsam fir proportion (%), GF: Gap fraction (%).

**Table 6** Error-matrixes between the field and modern aerial surveys for the five clusters identified by multivariate analysis.

| | | **Field plots** | | | **Error matrix** | | | |
|---|---|---|---|---|---|---|---|---|
| **Cluster** | **Modern survey old-growth class** | **Even-aged** | **Old-growth** | ***Total*** | **Even-aged** | **Old-growth** | ***Total*** | **Overall accuracy** |
| Cluster 1 | Even-aged | 0 | 8 | *8* | 0.0 | 47.1 | *47.1* | 52.9 |
| | Old-growth | 0 | 9 | *9* | 0.0 | 52.9 | *52.9* | |
| | *Total* | *0* | *17* | *17* | *0.0* | *100.0* | *100.0* | |
| Cluster 2 | Even-aged | 0 | 3 | *3* | 0.0 | 33.3 | *33.3* | 66.7 |
| | Old-growth | 0 | 6 | *6* | 0.0 | 66.7 | *66.7* | |
| | *Total* | *0* | *9* | *9* | *0.0* | *100.0* | *100.0* | |
| Cluster 3 | Even-aged | 0 | 5 | *5* | 0.0 | 71.4 | *71.4* | 28.6 |
| | Old-growth | 0 | 2 | *2* | 0.0 | 28.6 | *28.6* | |
| | *Total* | *0* | *7* | *7* | *0.0* | *100.0* | *100.0* | |
| Cluster 4 | Even-aged | 0 | 15 | *15* | 0.0 | 78.9 | *78.9* | 21.1 |
| | Old-growth | 0 | 4 | *4* | 0.0 | 21.1 | *21.1* | |
| | *Total* | *0* | *19* | *19* | *0.0* | *100.0* | *100.0* | |
| Cluster 5 | Even-aged | 4 | 8 | *12* | 26.7 | 53.3 | *80.0* | 46.7 |
| | Old-growth | 0 | 3 | *3* | 0.0 | 20.0 | *20.0* | |
| | *Total* | *4* | *11* | *15* | *26.7* | *73.3* | *100.0* | |

## Discussion

The results of the preindustrial and modern aerial surveys were often inconsistent. In particular, a large proportion of the undisturbed mature stands that were classified as old-growth in the preindustrial survey were classified as even-aged in the modern survey; clearly there is an error in one of the surveys. These changes occurred primarily in sparse pure black spruce stands. The comparison to field plot data clearly showed that the modern aerial survey underestimated the abundance of old-growth forests on the landscape with its accuracy decreasing with stand age, first cohort replacement and the reduction in tree species diversity. Differences in vertical and horizontal structures among even-aged, monospecific black spruce old-growth and mixed black spruce – balsam fir old-growth stands may have also challenged the accuracy of the modern aerial survey.

### *Aerial surveys underestimate boreal old-growth forest abundance and diversity*

The lack of accuracy in the identification of boreal old-growth forests in the modern aerial survey was unexpected and worrying. This survey was performed during a period where the importance and relative abundance of old-growth forests was well known and the erosion of their abundance on the landscape in Eastern Canada was already identified as a major issue (Kneeshaw and Gauthier 2003). Thus, boreal old-growth forests were a contemporary management issue and we expected that modern survey would provide increased precision on their status and distribution over the landscape. In addition, boreal old-growth forests were probably abundant in the study territory, where the theoretical fire cycle over the last century ranges between 200 and 272 years (Gauthier, Raulier, et al. 2015; Couillard et al. 2016). In Eastern Canadian boreal forests, the onset of the old-growth stage may vary from one stand to another, but almost all stands that have not burned in the last 200 years present a complex vertical and horizontal structure (Martin et al. 2018). Thus, stands with a clearly complex structure should represent at least half of the productive landscape, even if recent fires and logging activities may have decreased their current abundance (**Appendix E**). Yet, the modern aerial survey identified only 5.8% of the productive forests and 19.4% of the productive mature stands as structurally old-growth. According to the low accuracy of the modern aerial survey in the identification of boreal old-growth forests on the study territory, it is therefore likely that most of the boreal old-growth forests were not identified.

Boreal old-growth forests were twice as abundant in the preindustrial vs. the modern aerial survey (respectively 49% and 19.4% of the centroids). This frequency is close to the theoretical old-growth frequency that can be estimated from the landscape disturbance regime (**Appendix E**). Yet, the accuracy of the preindustrial survey cannot be estimated with our field data because of the long time interval between the preindustrial survey and our field survey. The efficacy of the preindustrial aerial survey in identifying old-growth should be assessed with field surveys in future research projects, for example using the temporary and permanent field plots surveyed by the MFWP for each decadal forest survey, as it is possible that this survey was more accurate than the modern. Determining the preindustrial aerial survey error rate would also help to better identify the factors explaining the differences with the modern aerial survey. Moreover, the criteria used to define the old-growth stands changed between the two aerial surveys. In the preindustrial aerial survey, the qualification of structurally complex mature stands was based on the subjective determination of a strong variation in tree heights (Pelletier et al. 2007). In contrast, in the modern aerial survey old-growth stands were identified based on specific canopy cover thresholds of the cohort structure and the variation in tree height (MRNF 2008). As a consequence, these changes in the methodology of photointerpretation of forest structure may have caused a decrease in identifying accurately old-growth forests in our study area.

### *Aerial survey thresholds and indicators are irrelevant for boreal forests*

Stands perceived as old-growth in the preindustrial aerial survey but as even-aged in the modern aerial were mainly sparse pure black spruce forests. Environments favouring pure black spruce stands at the end of succession in this region are often less productive than those favouring mixtures of black spruce and balsam fir (Messaoud et al. 2014; Martin et al. 2018; Portier et al. 2018). Moreover, a sparser canopy may indicate a low stand productivity caused by paludification or low-severity fires (Fenton et al. 2005; Smirnova et al. 2008). As a result, stands that shifted from an old-growth to an even-aged structure between the two surveys were probably defined by relatively low stand heights. Yet, to be classified as irregular, and therefore old-growth, by the modern aerial survey, tree height had to vary by at least 8 m for the irregular structure class or 5m for the bi-cohort (this class however represented only 0.5% of the centroids). Such thresholds are relevant in biomes where trees get taller with age, leading to a complex vertical stratification of old-growth stands (Franklin et al. 2002). However, boreal old-growth forest characteristics often differ from those of old-growth forests from other biomes, because of the harsh climatic conditions that limit tree height and longevity (Bergeron and Harper 2009). Thus, many boreal old-growth forests may be erroneously identified as structurally even-aged because the thresholds used by the modern aerial survey require too large of a height differential.

The difficulty in detecting structurally complex pure black spruce old-growth stands may be reinforced by their poorly stratified vertical structure. Indeed, for most of these stands, codominant, intermediate and suppressed trees represented an equal proportion of the canopy. In contrast, suppressed trees dominated the canopy of mixed black spruce – balsam fir old-growth stands. This stratification may result from balsam fir's greater sensitivity to spruce budworm outbreaks, root rot and windthrow, leading to higher mortality rates in comparison to black spruce (Ruel 2000; Morin et al. 2009). In contrast, the canopy of pure black spruce old-growth stands may have been perceived as vertically homogeneous, and then confounded with an even-aged canopy, resulting in their misclassification as "even-aged" stands. Thus, from an aerial perspective, stand vertical stratification was more visible for mixed black spruce – balsam fir old-growth stands than for pure black spruce.

Identifying pure black spruce old-growth stands can also be challenging because of the possible absence of tree species transition between the even-aged and old-growth stages. Indeed, because of its semi-serotinous cones and its layering ability, black spruce can either act as a pioneer or a late-successional species (Harvey et al. 2002). As a consequence, black spruce stands with no changes in tree species composition since the last stand-replacing disturbance are common in Eastern Canadian boreal forests driven by wildfires as stand-replacing disturbances (Harper et al. 2002; Martin et al. 2018). Consequently, differentiating several black spruce cohorts in old-growth stands is challenging, in particular from aerial photographs. In contrast, the position of the other tree species in forest succession is well defined. Therefore, it may be easier to identify the old-growth stage of stands containing tall and old pioneer species, like aspen, or late-successional species, like balsam fir, in comparison to monospecific black spruce stands.

Distinguishing an old-growth forest from an even-aged is difficult, because there is no clear shift between the two stages (Pesklevits et al. 2011). For the same reason, defining thresholds that discriminate even-aged and old-growth stands is also challenging. The combination of the Weibull's shape parameter and cohort basal area proportion to identify boreal old-growth forests has proven to be efficient (Martin et al. 2018) and represents the same cartographic structural attributes as those used by the modern aerial survey (i.e. increasing vertical complexity and progressive replacement of the first cohort). However, it is possible that field and aerial old-growth stage thresholds did not totally match, especially for the definition of the beginning of the old-growth stage. Consequently, we expected that stands inaccurately identified as even-aged by aerial surveys would have been mostly stands at the beginning of the old-growth transition. Nevertheless, stands at the beginning of the old-growth transition were grouped in the same cluster (Cluster 5). Only 20.5% of the field plots identified as old-growth by the field survey but as even-aged by the modern aerial survey belonged to this cluster. Thus, the discrepancies observed between modern aerial and field surveys were not caused by a bias due to inconsistent old-growth thresholds but by the modern aerial survey inaccuracy, as most of these stands were unambiguously old-growth. Moreover, the field plots were 400m$^2$ in size, while forest polygons often have an area of several hectares. As a result, ground plots may not have been able to capture internal variability within a polygon. However, the polygons of the decadal forest inventories are supposed to represent homogeneous stands in terms of structure and age. In addition, we have mainly identified uneven-aged stands with complex structures in the field plots and very few regular even-aged stands. It seems unlikely that we have mainly sampled small old-growth residual forests within even-aged stands since site selection was random. While it is possible that the structure of old-growth boreal forests can be highly variable within the same stand, we think that the field inventories were able to determine whether the polygons sampled were old-growth or even-aged forests.

## Conclusion and management implication

Boreal old-growth forests structural specificities challenged aerial survey accuracy, causing a significant underestimation of their abundance on the study territory. This error was reinforced by the standardization of Québec's decadal forest survey methodology for all the province. Modern survey thresholds and indicators were thus poorly adapted to boreal old-growth forests common structural attributes, i.e. a low tree height, the lack of clearly delineated canopy strata and the absence of any species transition between the even-aged and the old-growth stage. In contrast, the transition period between the even-aged and the old-growth stage had no influence on aerial survey accuracy, as the majority of the old-growth stands inaccurately identified as even-aged were true old-growth stands.

Pure black spruce old-growth stands were those that were the most confused with even-aged stands by the modern aerial survey. Yet, the majority of Québec's boreal forests become pure black spruce stands at the end of succession. Therefore, the majority of Québec's boreal forests may be erroneously identified as structurally even-aged by the modern aerial survey. Moreover, pure black spruce old-growth stands are not only abundant but also structurally diverse. Thus, the results of our study raise concerns about the capacity of forest management to maintain the preindustrial boreal landscape diversity as most boreal old-growth forests are not well identified by forest inventories.

The efficacy of photographic aerial surveys in identificatying and discriminating of complex forest structures has been questioned previously and the results of our study confirm these concerns. Therefore, new techniques should be used to accurately identify boreal old-growth forests (Chaieb et al. 2015). LiDAR (Light Detection And Ranging) technology is therefore a promising tool for a quick and efficient discrimination of stand structures (Kane et al. 2010; Jayathunga et al. 2018). In a change from the modern (fourth) aerial forest survey, the ongoing fifth decadal forest survey collects both photographic and LIDAR data, opening the way for a better identification of boreal old-growth forests. However, the efficacy of LIDAR-derived metrics to discriminate boreal old-growth and even-aged forests has not yet been demonstrated. As a consequence, future research must be performed to determine if the transition from aerial photographic to LIDAR surveys will improve the identification of boreal old-growth forests in managed landscapes.

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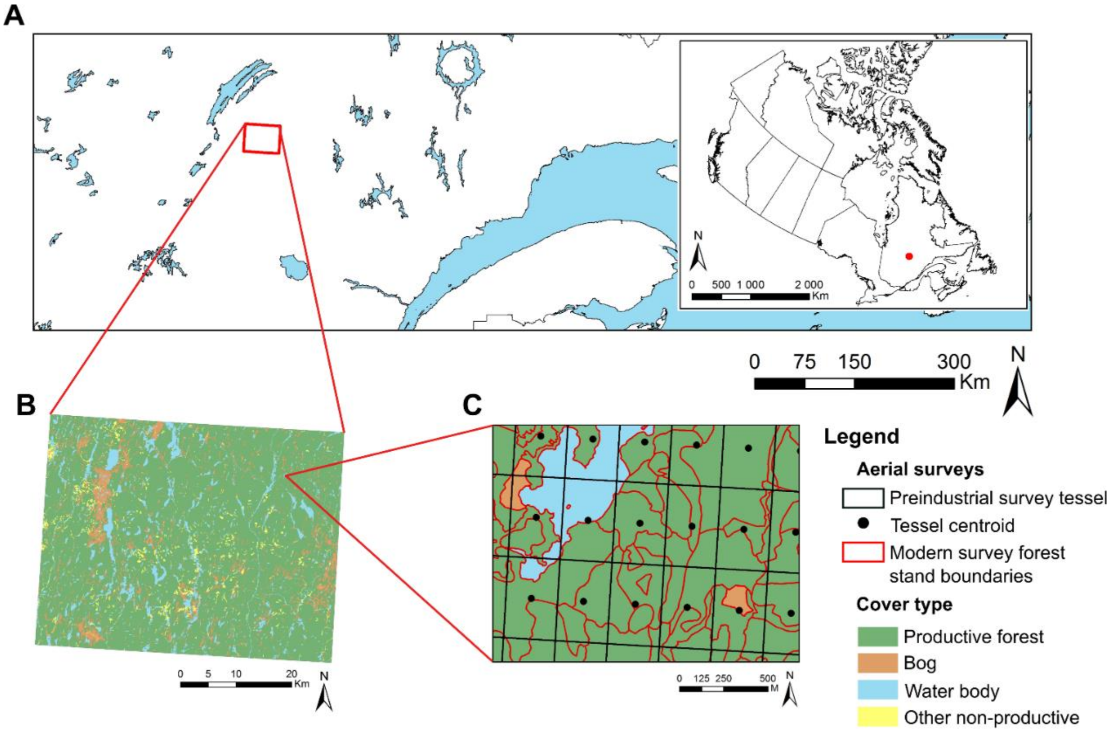
## Supplementary materials



**Appendix A** A: Location of the study territory in the province of Québec. The insert map represents its location in Canada. B: Spatial distribution of the main cover types in the study territory. C: Example of preindustrial aerial survey tessels and modern aerial survey forest stands' boundaries.

[Tapez ici]

| Parameter | Acronym | Unit | Description | Mean | Std.error | Minimum | Maximum |
|---|---|---|---|---|---|---|---|
| Tree density | TD | n/ha | Number of living merchantable stems per hectare | 922.97 | 384.48 | 50.00 | 1875.00 |
| Sapling density | SD | n/ha | Number of living saplings per hectare | 2630.74 | 1933.76 | 275.00 | 10950.00 |
| Basal area | BA | $m^2$/ha | Basal area of the living merchantable trees per hectare | 17.53 | 7.53 | 0.37 | 35.45 |
| Basal fir proportion | BFP | % | Proportion of balsam fir in the basal area | 12.53 | 21.54 | 0.00 | 94.64 |
| Coarse woody debris volume | CWD | $m^3$/ha | Calculated according to the Marshall et al. (2000) formula for linear coarse woody debris sampling: | 58.65 | 52.36 | 0.00 | 197.01 |
| Gap fraction | GF | % | Mean value of the five gap fraction results at each site | 62.82 | 25.42 | 20.88 | 100.00 |
| Maximum height | MH | m | Mean height value of the dominant trees sampled at each site | 18.49 | 3.17 | 7.90 | 24.40 |
| Weibull's shape parameter | WSP | - | Calculated using the Weibull's function of diameter distribution (Bailey and Dell 1973), defined by the following equation for a random variable X:<br>$f(x) = \left(\frac{a}{b}\right) \times \left(\frac{x}{b}\right) \times exp\{-(x/b)^{a}\}; x \geq 0; a>0; b>0$<br>This equation is characterized by the shape parameter $a$, identified in our study as the Weibull's shape parameter (WSP), and the scale parameter $b$.<br>WSP ≥ 1.5 represent a Gaussian distribution of the diameters, 1 ≤ WSP < 1.5 an irregular distribution and WSP<1 a reverse J-shaped distribution | 1.05 | 0.45 | 0.07 | 2.76 |
| Shannon index | SI | - | Calculated according to the Shannon diversity index formula (Shannon and Weaver 1949) with basal area abundance rather than individual abundance | 0.14 | 0.14 | 0.00 | 0.46 |
| Cohort basal area proportion | CBAP | - | Proportion of N+1 trees in the basal area, calculated using the Kneeshaw and Gauthier (2003) formula:<br>$CBAP = \frac{(BA_{N\ \ 1\,trees} + 0.1)}{(BA_{N+1\,trees} + 0.1 + BA_{First\ cohort\ trees})}$<br>Where $BA$ is the basal area. | 0.57 | 0.37 | 0.06 | 1.00 |
| Minimum time since last fire | MTSLF | years | Maximum age value among the ten basal discs | 195.81 | 62.53 | 89.00 | 307.00 |

**Appendix B** Description of the field structural attributes computed from the field surveys and summary statistics.

| Parameter | Class | Description | Survey | Thresholds |
|---|---|---|---|---|
| Preindustrial dominant species | Black spruce | Black spruce constitutes at least 50% of the basal area | Preindustrial | Standing live trees |
| | Balsam fir | Balsam fir constitutes at least 50% of the basal area | | |
| | Jack pine | Jack pine constitutes at least 50% of the basal area | | |
| | Broadleaved species | Broadleaved species constitutes at least 50% of the basal area | | |
| Modern black spruce abundance | ≥25% of the canopy | Black spruce constitutes at least 25% of the canopy | Modern | Dominant and codominant trees (regular stands) or trees higher than 7m (irregular stands) |
| | <25% of the canopy | black spruce constitutes less 25% of the canopy | | |
| Modern balsam fir abundance | ≥25% of the canopy | Balsam fir constitutes at least 25% of the canopy | Modern | Dominant and codominant trees (regular stands) or trees higher than 7m (irregular stands) |
| | <25% of the canopy | Balsam fir constitutes less 25% of the canopy | | |
| Modern jack pine abundance | ≥25% of the canopy | Jack pine constitutes at least 25% of the canopy | Modern | Dominant and codominant trees (regular stands) or trees higher than 7m (irregular stands) |
| | <25% of the canopy | Jack pine constitutes less 25% of the canopy | | |
| Modern broadleaved species abundance | ≥25% of the canopy | Broadleaved species constitutes at least 25% of the canopy | Modern | Dominant and codominant trees (regular stands) or trees higher than 7m (irregular stands) |
| | <25% of the canopy | Broadleaved species constitutes less 25% of the canopy | | |
| Preindustrial tree density | ≥ 80% | Tree canopies cover at least 80% of the stand surface | Preindustrial | All trees beyond the regeneration stage |
| | [60%-80%[ | Tree canopies cover at least 60% and less than 80% of the stand surface | | |
| | [40%-60%[ | Tree canopies cover at least 40% and less than 60% of the stand surface | | |
| | [25%-40%[ | Tree canopies cover at least 25% and less than 40% of the stand surface | | |

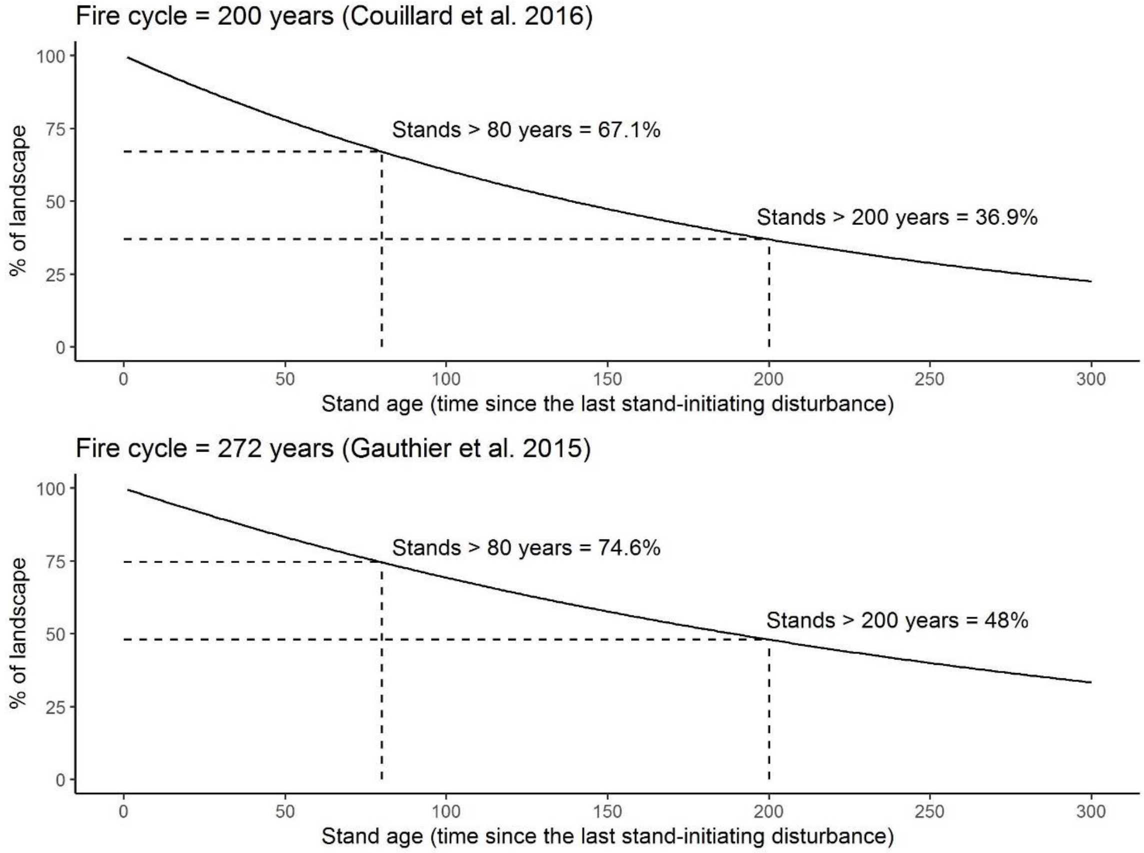
**Appendix C** Description of the cartographic structure attributes computed for the centroids (1/2).

| Parameter | Class | Description | Survey | Thresholds |
|---|---|---|---|---|
| Modern tree density | ≥ 80% | Tree canopies cover at least 80% of the stand surface | Modern | Dominant and codominant trees (regular stands) or trees higher than 7m (irregular stands) |
| | [60%-80%[ | Tree canopies cover at least 60% and less than 80% of the stand surface | | |
| | [40%-60%[ | Tree canopies cover at least 40% and less than 60% of the stand surface | | |
| | [25%-40%[ | Tree canopies cover at least 25% and less than 40% of the stand surface | | |
| Preindustrial tree height | ≥21 m | Mean height of dominant and codominant trees ≥ 21 m | Preindustrial | Dominant and codominant trees |
| | [15-21 m[ | Mean height of dominant and codominant tree between 15 and 21 m | | |
| | [9-15 m[ | Mean height of dominant and codominant tree between 9 and 15 m | | |
| | <9 m | Mean height of dominant and codominant tree < 9 m | | |
| Modern tree height | ≥22 m | Mean height of dominant and codominant trees ≥ 22 m | Modern | Dominant and codominant trees |
| | [17-22 m[ | Mean height of dominant and codominant tree between 17 and 22 m | | |
| | [12-17 m[ | Mean height of dominant and codominant tree between 12 and 17 m | | |
| | [7-12 m[ | Mean height of dominant and codominant tree between 7 and 12 m | | |
| | <7 m | Mean height of dominant and codominant tree < 7 m | | |

**Appendix C** Description of the cartographic structure attributes computed for the centroids (2/2).

| Resid. Df | Resid. Dev | Df | Deviance | Pr(>Chi) | AUC | COD | Parameter | Df | Deviance | Resid. Df | Resid. Dev | Pr(>Chi) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 3161 | 4285.2 | -5 | 474.88 | <0.001 | 0.71 | 0.14 | Mod. balsam fir abund. | 1 | 293.1 | 3160 | 3992.1 | <0.001 |
| | | | | | | | Preindus. tree density | 2 | 156.2 | 3158 | 3835.8 | <0.001 |
| | | | | | | | Modern tree density | 2 | 25.5 | 3156 | 3810.3 | <0.001 |

**Appendix D** Results of the logistic regression final model comparing the frequency of centroids according to their structural evolution between the preindustrial and modern surveys (i.e. *Consistent* or *Inconsistent*).. Mod.: modern, Abund.: abundance, Preindus.: preindustrial.



**Appendix E** Estimated landscape-age structure on the study territory according to the fire cycles estimated by Couillard et al. (2016) and Gauthier et al. (2015) using the Van Wagner (1978) formula.