UNIVERSITÉ DU QUÉBEC À MONTRÉAL

TYPOLOGIE, DYNAMIQUE ET VALEUR DE CONSERVATION DES VIEILLES FORÊTS BORÉALES RÉSINEUSES DE L'EST DU CANADA EN TERRITOIRE AMÉNAGÉ

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AVANT-PROPOS

L'artificialisation des écosystèmes forestiers boréaux que l'on observe depuis la révolution industrielle s'accompagne d'importants enjeux de conservation de la biodiversité et des services écosystémiques. Afin de répondre à ces problématiques, il est nécessaire d'obtenir connaissance fine de l'écologie des peuplements forestiers préindustriels afin de développer des stratégies d'aménagement permettant de s'assurer d'une gestion durable des forêts.

Les vieilles forêts, c'est-à-dire les peuplements multigénérationnels dynamisés par des perturbations naturelles de faible à moyenne intensité, font partie des types de forêt les plus menacés par les activités humaines dans les territoires boréaux, notamment l'exploitation forestière. Elles ont ainsi presque totalement disparu en Europe et la rareté des peuplements résiduels pouvant servir de référence complexifie fortement le developpement de stratégies de gestion permettant de restaurer ces territoires. Dans d'autres pays, comme la Russie ou le Canada, elles sont encore abondantes, bien que souvent en déclin, et peuvent donc encore servir de modèles de référence.

Cette thèse se concentre donc sur les vieilles forêts boréales résineuses du Canada, afin de rester centré sur un écosystème homogène. Elle vise essentiellement à identifier la diversité de structures forestières se cachant derrière le terme général de « vieille forêt » et les processus façonnant cette diversité. De plus, elle a pour objectif de déterminer si la diversité des vieilles forêts boréales est correctement identifiée par les inventaires forestiers aériens et si elle est globalement conservée dans les territoires aménagés.

TABLE DES MATIÈRES

LISTE DES FIGURES

LISTE DES TABLEAUX

LISTE DES ABRÉVIATIONS, DES SIGLES ET DES ACRONYMES

AIC : Akaike information criterion

AUC : Area under the ROC curve

BA: Basal area

BF : Balsam fir

BFP: Balsam fir proportion

BFWB : Balsam fir – white birch

BRL : Broadleaved

BS : Black spruce

BSBF : Black spruce – balsam fir

BSFM : Black spruce – feather moss

CBAP: Cohort Basal Area Proportion

COD : Coefficient of discrimination

CWD: Coarse woody debris

DBH : Diameter at breast height

DMH : Depth of the mineral horizon

DOH : Depth of the organic horizon

GF: Gap fraction

JP : Jack pine

MFFP : Ministère de la Forêt, de la Faune et des Parcs

MH: Maximum height

MRN : Ministère des Ressources Naturelles

MRNF : Ministère des Ressources Naturelles et de la Faune

MTSLF: Minimum time since last fire

ROC : Receiver operating characteristic

SD: Sapling density

SI: Shannon-index

SP : Spruce spp.

TD: Tree density

TSD : Total soil depth

WSP: Weibull’s shape parameter

RÉSUMÉ

La conservation des vieilles forêts, c'est-à-dire les peuplements dynamisés par les perturbations naturelles secondaires, dans les territoires aménagés du biome boréal est désormais un enjeu environnemental majeur. L'efficacité des mesures de gestion prises à leur encontre nécessite néanmoins une bonne connaissance des écosystèmes que l'on regroupe sous le terme « vieille forêt ». L'objectif de cette thèse est donc d'améliorer nos connaissances quant à la diversité, la dynamique et la conservation des vieilles forêts boréales résineuses dans les territoires aménagés de l'Est du Canada.

Cette étude se concentre sur un territoire d'étude de 2200km^2 situé dans le domaine bioclimatique de la pessière noire à mousse du Québec, Canada. Les caractéristiques structurelles de 74 peuplements, matures à surannés, y ont été échantillonnées. Des analyses dendrochronologiques ont aussi été réalisées pour 21 de ces sites. Enfin, nous avons utilisé les données des inventaires forestiers décennaux réalisés par le gouvernement du Québec depuis les années 60 pour observer l'évolution des vieilles forêts dans le territoire d'étude ainsi que l'acuité avec laquelle elles sont identifiées.

Nos résultats montrent que les vieilles forêts boréales sont structurellement très diversifiées. Onze différentes structures ont ainsi pu être identifiées. Cette diversité résulte pour partie de la topographie mais augmente aussi avec le temps depuis la dernière perturbation majeure. La dynamique de perturbation secondaire de ces écosystèmes gagne aussi en complexité au fur et à mesure que la première cohorte, apparue suite à la dernière perturbation majeure, est remplacée par de nouvelles cohortes, renforçant cette diversité structurelle. Au début du processus de transition vers l'état de vieille forêt, les perturbations de sévérité faible dominent mais les perturbations de sévérité modérée gagnent progressivement en importance, jusqu'à atteindre un niveau similaire à celui des perturbations de sévérité faible. Les épidémies de tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana,* Clemens) apparaissent alors comme un élément clé de cette dynamique de perturbations secondaires, indépendamment de leur sévérité.

En comparaison des feux de forêt, l'aménagement forestier a récolté une plus grande proportion de vieilles forêts (se définissant ici par un âge supérieur à 100 ans) sur ce territoire, notamment caractérisées par un volume de bois marchand plus important. L'influence de l'exploitation forestière sur la diversité structurelle du territoire diffère donc de celle du feu. Par ailleurs, le plus récent inventaire photographique aérien réalisé par le gouvernement du Québec sous-estimait fortement l'abondance des vieilles forêts sur le territoire d'étude. La majorité de ces peuplements, se définissant sur le terrain par une structure complexe, étaient identifiés comme des peuplements équiens (c'est-à-dire structurellement simples) par l'inventaire aérien. Des seuils inadaptés à la forêt boréale ainsi que l'absence d'éléments de vieilles forêts particulièrement visibles par télédétection ou suivant une observation superficielle du peuplement peuvent expliquer ces résultats.

Une fois le stade de vieille forêt atteint, les peuplements forestiers boréaux continuent donc de suivre une dynamique complexe, ce qui peut mener à de nombreux changements structuraux dans le temps. La diversité des vieilles forêts boréales doit donc être reconnue dans l'aménagement forestier, car impliquant la présence de nombreux types d'habitats nécessaires à la biodiversité. Nos résultats montrent cependant que les peuplements récoltés en priorité sont les vieilles forêts avec la plus forte valeur marchande. Ignorer cette diversité – par exemple en se retreignant à un simple pourcentage de vieilles forêts à conserver, qu'importe leur type – pourrait donc mener à une réduction de la diversité structurelle des vieilles forêts en territoire aménagé, causant à terme une perte d'habitat. Dans l'état actuel des choses, les inventaires photographiques aériens ne permettent pas de reconnaître la diversité des vieilles forêts, ce qui empêche la mise en place de stratégies efficaces.

Intégrer de manière durable les vieilles forêts boréales dans l'aménagement forestier demande par conséquent non-seulement la reconnaissance de la richesse et de la complexité de ces écosystèmes, mais aussi le développement d'outils permettant d'assurer l'identification des nombreuses formes sous lesquelles elles peuvent se présenter.

Mots clés : Aménagement écosystémique, forêt surannée, succession, conservation, paysage préindustriel

ABSTRACT

Maintaining old-growth forests, i.e. stands driven by gap-dynamics, in managed boreal landscapes is a major environmental issue. The efficacy of old-growth forests conservation strategies depends however on an adequate knowledge about these ecosystems. The objective of this thesis is therefore to improve our knowledge about the diversity, the dynamics and the conservation values of boreal old-growth forests in manged landscapes.

This study focuses on a 2200km^2 territory situated in Québec's black spruce – feathermoss bioclimatic domain, Canada. We sampled the structural characteristics of 74 stands that were mature to very old. We also performed dendrochronological analysis on 21 of these sites. Finally, we also used Québec's decadal forest surveys data sampled since the 1960's to observe the evolution of old-growth forest characteristics on the study territory, as well as the accuracy of these surveys in identifying old-growth stands.

According to our results, boreal old-growth forests are structurally diversified. 11 different old-growth forests structures have been identified. This diversity is in part a result of topography but also of time since the last stand-replacing disturbance. Secondary disturbances dynamics increase in complexity while the first cohort, which appeared following the last stand-replacing disturbance, is replaced by new cohorts. At the beginning of the transition process toward the old-growth stage, a low severity defines most of the secondary disturbances but moderate severity disturbances progressively gain in importance. When the true old-growth stage is reached, low and moderate severity disturbances are equal in importance in stand dynamics. Most of these disturbances seems to result from spruce budworm (*Choristoneura fumiferana,* Clemens) outbreaks, independently of disturbance severity.

In comparison to forest fires, most of the stands logged on the study territory were old-growth stands (here defined by an age superior to 100 years) characterized by higher merchantable wood volume. Logging activities have therefore an influence on landscape structural diversity which differs from that of fire. Moreover, the most recent photographic aerial survey performed by Québec's government significantly underestimated old-growth forests abundance on this territory. Most of these stands, defined by a complex structure based on field surveys, were identified as even-aged (i.e. structurally simple) by the aerial survey. Unsuitable thresholds for boreal forests as well as the absence of particularly visible old-growth attributes were the main factors that may explain the low accuracy of aerial surveys.

The dynamics of boreal old-growth forests is complex, especially once the true old-growth stage reached. For this reason, the structure of old-growth stands may significantly change over time. Boreal old-growth forest structural diversity must be explicitly acknowledged by forest managers, because it implies the presence of different habitats among old-growth stands and therefore different species. However, logging activities cut in priority old-growth forests with the highest economic value, as indicated by our results. Ignoring this diversity (e.g. by only defining a given percentage of old-growth forests that must be maintained in managed landscapes, regardless of their structure) could therefore lead to the erosion of boreal old-growth forest diversity, causing biodiversity issues because of the disappearance of specific habitats. In addition, orthographic forest surveys are currently not accurate enough to identify boreal old-growth forests and discriminate their structures, hence limiting the development of efficient management strategies.

The integration of boreal old-growth forests in sustainable forest management therefore requires first the acknowledgement of the diversity and the complexity of these ecosystems and second, the development of accurate tools capable of identifying all the forms of boreal old-growth forests.

Keywords : Ecosystem-based management, overmature forest, succession, conservation, preindustrial landscape

CHAPITRE I

INTRODUCTION

1.1 Contexte

Depuis la révolution industrielle, l'empreinte anthropique sur la planète augmente de manière exponentielle. Les activités humaines ont désormais un impact suffisamment important sur la biosphère pour devenir une force géologique majeure (Steffen et al. 2015; Waters et al. 2016). Il en résulte de nombreux déséquilibres à l'échelle mondiale, dont les exemples les plus notables sont la sixième extinction de masse (Dirzo et al. 2014) et le changement climatique (IPCC 2018). Ces changements globaux affectent l'ensemble des biomes et des écosystèmes, y compris les écosystèmes forestiers. Ceux-ci sont notamment sujets à une déforestation, une artificialisation, une fragmentation et un rajeunissement à grande échelle (Kuuluvainen 2002; Achard et al. 2009; Gauthier et al. 2015a) . Ces changements mettent non seulement en péril la biodiversité forestière mais aussi les nombreux services écosystémiques associés, tels la séquestration du carbone atmosphérique ou la purification de l'air et de l'eau (Maser et Sedell 1994). En plus d'un préjudice éthique (Batavia et Nelson 2017), la disparition de ces espèces et de ces services auront probablement des conséquences économiques et sociales particulièrement néfastes (Burton et al. 2010; Gauthier et al. 2015a). La conciliation des enjeux environnementaux en plus des besoins socio-économiques est ainsi devenue l'un des paradigmes dominants de la gestion forestière. Le Sommet de la Terre de Rio de Janeiro en 1992 peut alors être considéré comme une date clef, permettant une sensibilisation internationale aux objectifs de gestion durable des forêts (Montreal Process Working Group 1995).

Dans le même temps, l'intérêt pour le fonctionnement des forêts dites « naturelles » s'est développé de manière sans cesse accrue, car vues comme un référend pour établir des stratégies de gestion durable (Puettmann et al. 2009). Afin de maintenir la biodiversité et les services écosystémiques des forêts, il a ainsi été proposé que l'aménagement forestier devait s'inspirer de la dynamique de perturbation naturelle (Attiwill 1994; Kuuluvainen 2002; Gauthier et al. 2008) ou que les peuplements aménagés devaient contenir des éléments structuraux des forêts naturelles (Burton et al. 1999; Bauhus et al. 2009). Le concept de « forêt naturelle » est toutefois particulièrement vague, mais il peut le plus souvent être compris par opposition aux forêts aménagées selon le dualisme « homme/nature » (Batavia et Nelson 2016; Batavia et Nelson 2017). De nombreux autres termes ont par ailleurs longtemps été utilisés, avec comme idée qu'ils étaient des synonymes de « forêt naturelle », par exemple forêts primaires, anciennes, vierges, matures, naturelles, surannées, originelles, intactes ou encore virginales. Néanmoins, chacun de ces termes représente un concept écologique différent et une meilleure clarification de la terminologie est progressivement apparue dans le courant du XXe siècle (Frelich et Reich 2003; Wirth et al. 2009). Le concept de « vieille forêt » (*old-growth forest*) fut alors l'un de ceux ayant le plus attiré l'attention de la communauté scientifique, des gestionnaires et du grand public dans ce contexte de changements globaux (Frelich et Reich 2003; Wirth et al. 2009; Pesklevits et al. 2011).

1.2 État des connaissances

1.2.1 Définitions

Le concept de « vieille forêt » est relativement récent en écologie, mais les recherches traitant de ces écosystèmes n'ont fait qu'augmenter depuis la seconde moitié du XXe siècle (Wirth et al. 2009). Définir ce qu'est une vieille forêt, et en contrepartie ce qui ne l'est pas, est néanmoins particulièrement complexe. Il existe, de fait, de très nombreuses de définitions de vieilles forêts, pouvant être regroupées en six classes majoritaires (Frelich et Reich 2003; Kimmins 2003; Hilbert et Wiensczyk 2007; Wirth et al. 2009) :

- Définition structurelle : peuplement ayant atteint un certain âge ; présence de nombreux arbres vieux et de fort diamètre ; fort volume de bois mort ; forte complexité verticale et horizontale ; présence d'arbres de tous âges…
- Définition dynamique : peuplement sous dynamique des trouées ; peuplement ayant atteint la phase finale de succession ; âge du peuplement supérieur à l'intervalle de retour des perturbations primaires ; âge des arbres dépassant leur espérance de vie moyenne…
- Définition biogéochimique : productivité primaire nette égale ou inférieur à zéro ; réseau trophique atteignant un seuil donné de complexité ; présence de la totalité des stades de dégradation du bois mort…
- Définition économique : forêt ayant dépassé l'âge optimum d'exploitabilité
- Définition esthétique : forêt impressionnante ; invite à l'humilité et à la spiritualité
- Autre type de définition : non-perturbée par les humains ; couvre une surface minimum

Chacune de ces définitions possède des limites particulières. Les principales critiques qui leur sont adressées sont en général leur caractère arbitraire, la difficulté à intégrer certains de ces seuils dans la gestion courante ou encore l'existence de contre-exemples qui limitent leur universalité (Kimmins 2003; Wirth et al. 2009; Pesklevits et al. 2011). Il est donc désormais admis qu'une définition générale universelle n'est ni possible, ni forcément souhaitable. Au contraire, les définitions des vieilles forêts doivent s'adapter au contexte écologique de la région étudiée (Frelich et Reich 2003; Pesklevits et al. 2011). Il peut donc exister une multiplicité de définitions, restreintes à une échelle locale. Pour une définition plus générale mais aussi plus limitée, on retient alors couramment la définition de Hunter (1989) : une vieille forêt est une forêt relativement vieille et peu perturbée par les humains (*"old-growth forests are relatively old and relatively undisturbed by humans")*.

Durant de nombreuses années, les travaux traitant des vieilles forêts se sont souvent restreints au dualisme « forêt jeune/vieille forêt ». Les vieilles forêts étaient ainsi majoritairement étudiées par opposition aux « forêts jeunes » (c'est-à-dire n'ayant pas encore atteint le stade de vieille forêt), impliquant que chacun de ces groupes représente en lui-même un ensemble homogène. Ainsi, si les caractéristiques propres aux vieilles forêts dans les différents biomes sont désormais relativement bien connues, il reste encore une grande part d'incertitude quant à l'hétérogénéité interne des vieilles forêts. Oliver et Larson (1996) ou Franklin et al. (2002) ont proposé différents modèles décrivant la transition vers l'état de vieille forêt, impliquant des différences entre les vieilles forêts en transition (c'est-à-dire celles contenant encore des individus de la cohorte apparue suite à la dernière perturbation initiale; c'est-à-dire la dernière perturbation à avoir réinitialisé le processus de succession forestière) et les vieilles forêts dites « vraies » (il ne reste plus aucun individu appartenant à la cohorte apparue suite à la dernière perturbation initiale). Néanmoins, bien qu'étant plus détaillés qu'une simple séparation entre forêt jeune et vieille forêt, ces modèles cessent de faire une différence entre les peuplements une fois le stade de vieille forêt vraie atteint. Ceci peut notamment être dû à la difficulté de placer un peuplement sur une chronoséquence à partir du moment où il ne reste plus aucun des arbres apparus suite à la dernière perturbation initiale (Garet et al. 2012; Portier et al. 2018). Cette question est pourtant cruciale car des différences de composition et de structure entre les peuplements impliquent des différences quant à leur biodiversité et leurs fonctions écologiques (Janssen et al. 2011; Schowalter 2017; Boudreault et al. 2018). De la même manière, des différences de composition et de structure impliquent des variations quant à la valeur économique des vieilles forêts. Ceci sous-entend alors que la pression anthropique peut ainsi varier d'un type de vieille forêt à l'autre, l'exploitation forestière étant avant tout motivée par des intérêts financiers (Perry 1998; Puettmann et al. 2009; Halme et al. 2013). Il est pourtant admis depuis plus d'une quarantaine d'années que même rendus au dernier stade de succession, les forêts restent des écosystèmes dynamiques (Dix et Swan 1971). Le concept de « climax », c'est-à-dire la phase finale et statique de la succession forestière (Clements 1916), est désormais majoritairement abandonné car les forêts n'atteignent jamais un point où elles restent ensuite totalement stables (Kuuluvainen 2002). En effet, les perturbations naturelles secondaires se manifestent sous une forte diversité de nature, de sévérité, d'intensité, de spécificité, de taille et de temporalité (Shorohova et al. 2011; Kneeshaw et al. 2011; De Grandpré et al. 2018). Les vieilles forêts étant principalement dynamisées par les perturbations secondaires, c'est-à-dire des perturbations ne réinitilisant pas la succession forestière (Oliver et Larson 1996; Shorohova et al. 2011; Kneeshaw et al. 2011), il est donc probable que cette diversité des perturbations induit une forte hétérogénéité de structure et de composition de ces écosystèmes, qui changent dans le temps. Au cours des dernières années, divers modèles de successions mettant en avant la diversité structurelle et la complexité de la dynamique des vieilles forêts ont été proposés (Reilly et al. 2015; Halpin et Lorimer 2016; Meigs et al. 2017).

1.2.2 Les vieilles forêts dans le biome boréal

Dans les biomes tempérés et tropicaux, la notion de vieille forêt est relativement instinctive en raison de la présence récurrente d'arbres de forte dimension, un élément souvent inconsciemment associé à l'idée de naturalité et d'ancienneté (Alexander 2001; Mosseler et al. 2003; Cooper 2006). Dans le biome boréal, il a été au contraire plus difficile de convaincre les gestionnaires et le grand public de la présence et de l'importance de ces écosystèmes dans les paysages forestiers. Ceci s'explique en premier lieu par les dimensions plus modestes qu'atteignent les arbres des forêts boréales, y compris ceux vieux de plusieurs siècles (Bergeron et Harper 2009; Kneeshaw et al. 2018). Dans le contexte de la forêt boréale, le paramètre le plus souvent retenu pour définir le début du stade de vieille forêt est l'apparition d'une dynamique des trouées, où les arbres meurent seuls ou par petits groupes en raison de perturbations naturelles secondaires (chablis, épidémies…) et sont remplacées ou maintenues par des espèces tolérantes à l'ombre (Kneeshaw et Gauthier 2003; Wirth et al. 2009; Shorohova et al. 2011). Le passage à l'état de vieille forêt est donc un processus graduel et peu visible, limitant toute séparation discrète entre forêts « jeunes » et vieilles forêts (Bragg 2002; Pesklevits et al. 2011). Il se peut aussi que la transition vers l'état de vieille forêt se fasse sans qu'il y ait changement d'espèce. Par exemple, l'épinette noire (*Picea mariana* (Mill.)), l'essence dominante dans l'Est de la forêt boréale canadienne, est aussi bien capable de jouer le rôle d'espèce pionnière que celui d'espèce de fin de succession (Harvey et al. 2002; Lecomte et Bergeron 2005). Il manque donc le plus souvent des éléments structuraux simples et visibles permettant aux gestionnaires et au grand public d'identifier facilement les vieilles forêts dans le biome boréal.

De plus, les feux de forêts jouent un rôle important dans la dynamique de perturbation naturelle des forêts boréales (Johnson 1992; Cyr et al. 2009; Shorohova et al. 2011). En raison du caractère impressionnant de ce type de perturbation, il a donc été longtemps assumé que les forêts boréales étaient dans leur grande majorité brûlées avant de pouvoir atteindre le stade de vieille forêt (Cogbill 1985; Johnson 1992). Pourtant, il a depuis été démontré que les feux sont des perturbations très hétérogènes en termes de fréquence, de taille, d'intensité, de sévérité ou de saisonnalité, surtout à l'échelle extrarégionale. Ainsi, dans certaines régions, les incendies forestiers se résument majoritairement à des feux de surface, causant une mortalité faible (Shorohova et al. 2009; Kuuluvainen et Aakala 2011; Shorohova et al. 2011). Dans d'autres, ils se définissent au contraire par des feux de couronne, causant une mortalité presque totale (Bergeron et al. 2004; Kneeshaw et al. 2011; Shorohova et al. 2011). Les vieilles forêts boréales sont ainsi abondantes dans les paysages dominés par les feux de surfaces car ces perturbations agissent comme une perturbation secondaire et non comme une perturbation initiale (Shorohova et al. 2009; Kuuluvainen et Aakala 2011). De plus, dans les territoires dominés par des feux de couronne, les vieilles forêts restent abondantes en raison des fortes variations de cycle de feux que l'on peut observer d'une région à l'autre (Bergeron et al., 2002, 2004; Bouchard et al. 2008; Bergeron et Harper 2009). Si l'on observe bien certaines régions définies par un cycle de feu très court, c'est-à-dire inférieur à la longévité des arbres, de nombreuses régions présentent au contraire des cycles de feu bien plus long (Gauthier et al. 2015b). De plus, les feux de couronne brûlent les peuplements indifféremment de leur âge, créant des paysages dont la structure d'âge suit la forme d'un J-inversé (Van Wagner 1978). Ceci implique que même dans un paysage se définissant par un cycle de feu court, des vieilles forêts seront toujours présentes, bien que ce soit en faible proportion (Belleau et al. 2007; Kneeshaw et al. 2018). Ainsi, les vieilles forêts sont des écosystèmes-clefs des paysages forestiers boréaux.

Jusqu'à la fin de la Seconde Guerre Mondiale, l'exploitation forestière dans les paysages boréaux se résumait majoritairement à des coupes de faible intensité, souvent réalisées à proximité des rivières pour s'assurer d'un transport facile du bois. Toutefois, à partir de la seconde moitié du XXe siècle, les progrès technologiques de la société industrielle ont permis la production d'outils permettant l'exploitation mécanique à large échelle des forêts boréales (Esseen et al. 1997; Östlund et al. 1997; Boucher et al. 2017). Les coupes totales sont très rentables à court terme, opérationnellement aisées à réaliser et simples à intégrer dans les plans d'aménagement forestier. Pour ces raisons, elles sont devenues le traitement majoritaire réalisé en forêt boréale (McRae et al. 2001; Tahvonen et Rämö 2016; Kneeshaw et al. 2018). Afin de justifier leur utilisation, les gestionnaires forestiers ont considéré que les coupes totales avaient les mêmes effets sur les paysages boréaux que les feux de forêts, en se basant sur l'idée que les paysages forestiers naturels sont principalement constitués de forêts équiennes (Landres et al. 1999; Kuuluvainen 2009; Bergeron et Harper 2009) Or, les travaux récents sur la reconstitution historique des régimes de feux montrent clairement que la structure d'âge des paysages forestiers est passablement plus variée et que les forêts à structure équienne ne constituent qu'une proportion du couvert forestier boréal sous régimes naturels de feux (Bergeron et al. 2004, 2006, Gauthier et al. 2008; Grondin et al. 2018). Par ailleurs, et au contraire des feux de forêt, les coupes forestières sont soumises à des impératifs économiques et à des contraintes techniques (Perry 1998; Puettmann et al. 2009). Leur distribution dans l'espace n'est donc pas aléatoire mais suit des patrons contagieux (Boucher et al. 2017). Il en résulte alors une très forte fragmentation des paysages exploités (Haeussler et Kneeshaw 2003; Schmiegelow et Monkkonen 2002). De plus, pour que leur exploitation soit rentable, il est nécessaire que les peuplements récoltés se définissent par un volume minimum de bois. Pour cette raison, ce sont les peuplements matures et vieux qui sont prioritairement récoltés (Östlund et al. 1997; Kuuluvainen 2009; Boucher et al. 2015). Afin de maximiser les volumes récoltés, la révolution forestière dans les paysages exploités est souvent bien inférieure au cycle de feu ou de perturbation initiale naturelle. Ceci aggrave le rajeunissement en empêchant le recrutement de nouveaux peuplements dépassant l'âge de rotation (Bergeron et al. 2002; Drapeau et al. 2009; Kuuluvainen 2009). Enfin, à l'échelle du peuplement, la coupe totale agit différemment du feu, par exemple en exportant le bois mort ou en sélectionnant les arbres survivants en raison de leur valeur économique. Les peuplements de seconde venue ont ainsi des caractéristiques biologiques et dynamiques différentes de ceux se régénérant suite à un feu (Haeussler et Kneeshaw 2003; Kuuluvainen et Gauthier 2018).

Les vieilles forêts constituent les peuplements forestiers qui souffrent le plus de l'écart entre les stratégies d'aménagement basées sur les coupes totales et la dynamique des perturbations naturelles. En Scandinavie, ces écosystèmes sont presque entièrement disparus, alors qu'ils sont naturellement dominants en raison de la rareté des perturbations naturelles primaires dans cette région (Östlund et al. 1997; Halme et al. 2013). La majorité des vieilles forêts scandinaves se retrouvent désormais restreintes dans une région montagneuse située à l'extrême nord de la Suède et de la Finlande, débordant légèrement sur la Norvège et la Russie (Kuuluvainen et al. 2017). Ce rajeunissement du paysage a causé une érosion et une fragmentation des habitats liés aux vieilles forêts, affectant la biodiversité (Berg et al. 1994; Esseen et al. 1997; Drapeau et al. 2000, 2003, 2009; Imbeau et al. 2001; Schmiegelow et Monkkonen 2002; Cadieux et Drapeau 2017). A titre d'exemple, le bois mort est un élément très présent dans les vieilles forêts et son abondance a par conséquent fortement baissé dans les territoires aménagés scandinaves. Or, près d'un quart des espèces forestières dépendent du bois mort et sont donc désormais directement menacées par les changements profonds apportés aux paysages forestiers (Siitonen 2001; Tikkanen et al. 2006). Au contraire de la Scandinavie, les vieilles forêts sont encore relativement abondantes en Russie et au Canada, principalement en raison de leurs superficies plus vastes et d'un aménagement forestier plus récent (Shorohova et al. 2011; Bergeron et Harper 2009). Leur abondance et la biodiversité qu'elles abritent pourraient néanmoins devenir tout autant menacées que les vieilles forêts scandinaves et pourraient elles aussi presque totalement disparaître des paysages exploités si aucune modification n'est apportée à la manière dont les paysages boréaux sont exploités (Imbeau et al. 2001; Fall et al. 2004; Bergeron et al. 2017; Grondin et al. 2018).

En raison des menaces découlant de l'aménagement forestier à échelle industrielle, la protection ou la restauration des vieilles forêts boréales sont désormais des enjeux de gestion majeurs (Kuuluvainen 2002; Gauthier et al. 2008; Kneeshaw et al. 2018). L'efficacité des stratégies d'aménagement des vieilles forêts repose sur la qualité de nos connaissances quant à leur diversité structurelle et à leur dynamique des vieilles forêts dans un territoire donné. Si les spécificités des vieilles forêts boréales ou leur abondance dans les paysages préindustriels sont bien connues, elles sont encore souvent perçues comme un ensemble homogène et statique une fois l'état de vieille forêt atteint. Ces connaissances limitées des vieilles forêts peuvent compromettre l'efficacité des stratégies de gestion mises en place pour leur protection. En effet, si sous le terme de « vieilles forêts » se cachent en réalité une multitude de types de peuplements aux caractéristiques structurelles variées, il n'est pas certain que cette diversité

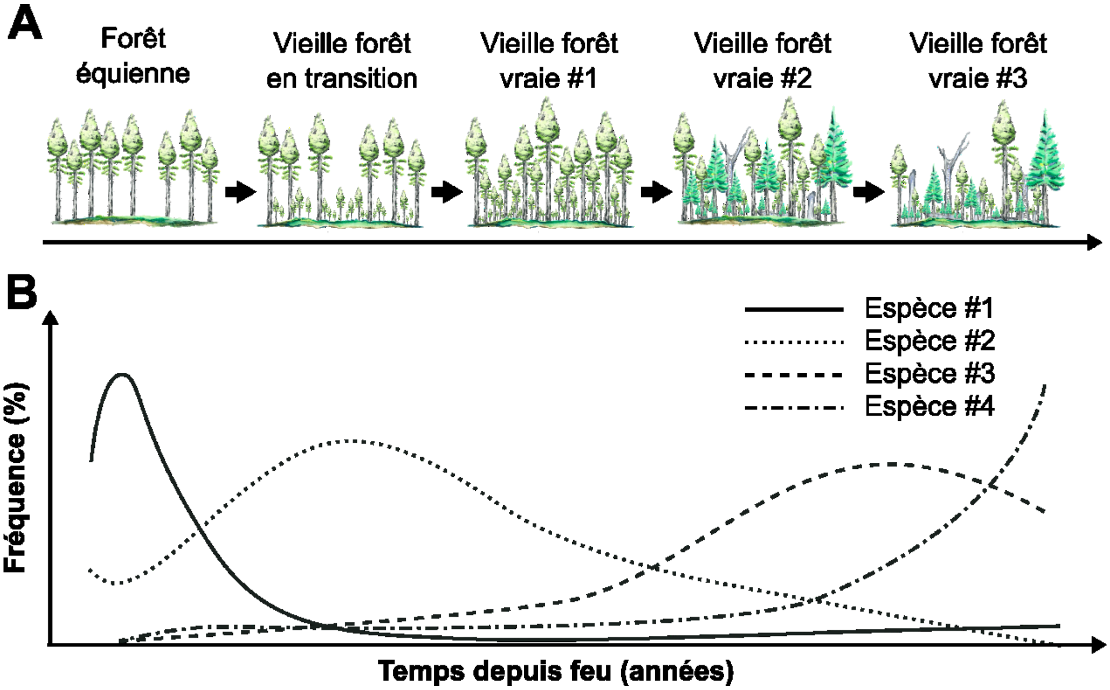

Figure 1-1 Figure conceptuelle représentant (A) un modèle d'évolution structurelle théorique d'une vieille forêt boréale de l'Est Canadien et (B) les changements de composition de 4 espèces théoriques en fonction de ces changements structuraux. Une concentration de l'exploitation forestière sur la structure « Vieille forêt vraie #1 » mènerait par conséquent à un déclin des structures « Vieille forêt vraie #2 » et « Vieille forêt vraie #3 », réduisant ainsi la disponibilité en habitats pour les espèces #3 et #4 qui leurs sont associées. Aquarelles par Valentina Buttò.

de structures puisse être efficacement conservée si elle n'est pas explicitement reconnue. Ainsi, dans les territoires aménagés, il est possible que les vieilles forêts dont les caractéristiques structurelles sont les plus intéressantes sur le plan économique soient les premières à être récoltées. Par conséquent, même si une certaine proportion de vieilles forêts est conservé dans le paysage, en l'occurrence les vieilles forêts à plus faible volume marchand, elle pourrait ne pas être représentative de toute leur diversité structurelle. Certaines espèces dépendant de conditions de vieilles forêts spécifiques, notamment celles à plus fort volume marchand, pourraient alors s'en trouver affectées. De plus, les liens dynamiques entre les vieilles forêts étant inconnus, il est possible que la suppression par la récolte de certains types de forêts ait à moyen-terme une influence négative sur les types structuraux restants (Figure 1-1). Mieux comprendre cette diversité et cette dynamique des vieilles forêts ouvre la voie à de nouvelles pratiques de gestion permettant de s'assurer d'un équilibre entre les enjeux écologiques et les enjeux socio-économiques.

1.2.3 L'Est Canadien, un laboratoire d'étude des vieilles forêts boréales

La dynamique de perturbation naturelle et les traits écologiques des espèces forestières changent fortement d'une région à l'autre du biome boréal (Kneeshaw et al. 2011; Shorohova et al. 2011). Afin de s'assurer que la diversité structurelle et la dynamique observée s'inscrive dans un contexte homogène, il est donc important d'étudier ces éléments à une échelle spatiale relativement restreinte. Dans le cas contraire, il est probable que toute hétérogénéité observée soit principalement causée par des spécificités infrarégionales. De plus, afin de capter au mieux la représentativité préindustrielle des vieilles forêts, il est nécessaire de se concentrer sur des territoires encore peu perturbés où ces écosystèmes sont naturellement abondants. La forêt boréale de l'Est Canadien est ainsi un territoire idéal pour améliorer notre compréhension à une échelle fine des vieilles forêts. De plus, de nombreuses études portant sur ce sujet y ont déjà été réalisées, offrant une base scientifique solide. Néanmoins, beaucoup de ces recherches ont été réalisées sur la ceinture d'argile, une vaste (180 000 km^2) formation géologique résultant du drainage d'un ancien lac glaciaire située à la frontière entre l'Ontario et le Québec (Bergeron 2000; Harper et al. 2002; Harper et al. 2003; Cyr et al. 2005; Harper et al. 2005; Lecomte et Bergeron 2005; Simard et al. 2007; Belleau et al. 2011; Fenton et Bergeron 2011). Ce type de formation est peu représentatif de la forêt boréale du Québec, où les dépôts glaciaires et fluvioglaciaires dominent. La texture argileuse du sol et le faible relief limitent de plus fortement le drainage des peuplements forestiers situés sur la ceinture d'argile, ce qui cause à terme leur paludification (Fenton et al. 2005; Simard et al. 2007). Sur des stations suffisamment drainées, situées sur des dépôts glaciaires et fluvioglaciaires, on observe au contraire une absence de paludification et les peuplements restent ainsi productifs au cours des siècles, voire des millénaires (Garet et al. 2009; Pollock et Payette 2010; Ward et al. 2014). De plus, les vieilles forêts boréales ont souvent été présentées comme étant des peuplements sur le déclin, ce qui servait ensuite à justifier l'utilisation massive des coupes totales en suivant une rotation inférieure à l'âge d'initiation de la dynamique des trouées (Lichstein et al. 2009). La concentration de la recherche sur les structures et les dynamiques des vieilles forêts dans un contexte environnemental propice à la paludification pose donc non-seulement un problème de représentativité, mais pourrait aussi renforcer des préjugés négatifs sur ces écosystèmes, alors que le déclin (dans le sens de l'ouverture progressive de peuplement jusqu'à l'état de tourbière forestière) représente l'exception plutôt que la règle (Wirth et Lichstein 2009). Si les forêts boréales de l'Est Canadien sont un terrain idéal pour étudier la dynamique et la diversité des vieilles forêts boréales, il est donc important de s'assurer que ces recherches se déroulent dans un environnement représentatif de la majorité de ce territoire.

1.3 Objectifs et hypothèses

Le premier objectif général de la thèse est d'améliorer nos connaissances quant à la diversité et à la dynamique des vieilles forêts de l'Est de Canada situés sur des dépôts glaciaires ou fluvioglaciaires. Le second objectif est d'évaluer la valeur de conservation des différents types de vieilles forêts dans les territoires aménagés. Au Québec, la forêt boréale peut se diviser en deux domaines bioclimatique, séparés selon un gradient nord-sud : la forêt boréale mixte (sapinière à bouleau blanc) et la forêt boréale coniférienne (pessière à mousse) (Saucier et al. 1998). Ils se définissent par certains points communs mais aussi par des dynamiques de perturbation et de succession spécifiques. Dans le cadre de ce projet de recherche, il est par contre préférable de se concentrer sur un seul de ces domaines bioclimatiques afin d'en réaliser une étude exhaustive. Je me suis concentré sur l'étude d'un territoire de 2200km^2 situé dans le sous-domaine de la pessière noire à mousses de l'Est du Québec, Canada (Figure 1-2). Les analyses qui y ont été réalisées combinent inventaires de terrain, analyses dendrochronologiques et comparaisons des résultats des inventaires forestiers provinciaux des époques préindustrielles et modernes.

Mon premier objectif spécifique est d'établir si les vieilles forêts boréales de l'Est Canadien sont des peuplements structurellement hétérogènes, y compris le stade de vieilles forêts vraies atteintes. Mes hypothèses sont les suivantes : 1) les vieilles forêts boréales de l'Est Canadien peuvent se diviser en plusieurs structures, chacune définie par des caractéristiques spécifiques, 2) chacune de ces structures est liée à des caractéristiques environnementales particulières, et 3) il est possible de distribuer ces structures de vieilles forêts selon un modèle de succession structurelle suivant des gradients temporels et environnementaux.

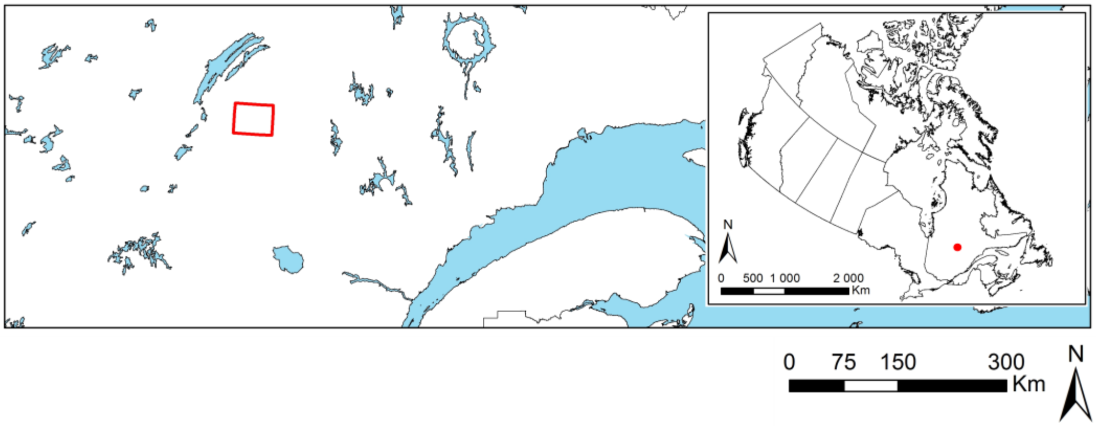

Figure 1-2 Situation du territoire d'étude du doctorat (rectangle rouge) dans la province du Québec. L'insert indique son emplacement dans le Canada (point rouge).

Mon second objectif est de déterminer si les vieilles forêts sont dynamisées par des perturbations de différentes temporalité et sévérité. Mes hypothèses sont : 1) les perturbations de sévérité faible et modérée présentent des patrons temporels différents et 2) les perturbations de sévérité modérée sont plus abondantes dans les vieilles forêts vraies et favorisent différents composants de la régénération en comparaison des perturbations de sévérité faible.

Mon troisième objectif est de vérifier si, avant perturbation, les peuplements coupés partageaient des caractéristiques structurelles et abiotiques similaires à ceux brûlés. Je cherche donc ici à comparer l'impact des coupes sur la diversité structurelle des paysages aménagés en comparaison de la dynamique de feu. Mon hypothèse est la suivante : 1) en comparaison du feu, la coupe forestière perturbe des peuplements définis par un volume supérieur de bois marchand.

Mon quatrième objectif vise à déterminer si les vieilles forêts boréales sont correctement identifiées comme tels par les inventaires photographiques aériens, c'est-à-dire la méthode d'inventaire dominante dans la forêt boréale du Québec. Mes hypothèses sont les suivantes : 1) les résultats des inventaires photographiques aériens sont cohérents dans le temps et 2) les inventaires aériens les plus récents arrivent efficacement à identifier les différents types de vieilles forêts boréales.

1.4 Approches méthodologiques

Le territoire d'étude couvre une superficie de 2200km^2 et est dominé par des dépôts glaciaires et fluvioglaciaires. L'exploitation forestière y a commencé en 1991 mais est restée faible jusqu'en 2000, où les niveaux de récolte ont ensuite augmenté. Les vieilles forêts y sont donc encore abondantes et relativement accessibles en raison du réseau de desserte forestière. Plusieurs études du Ministère de la Forêt, de la Faune et des Parcs ont été réalisées sur ce territoire (Grondin et al. 2012; Couillard et al. 2016), permettant de donner une meilleure perspective à nos résultats.

Nous avons inventorié les caractéristiques structurelles de 74 sites entre 2014 et 2016. Ces sites sont distribués selon un gradient stationnel, allant de la pessière pure sur dépôt de surface organique aux sapinières à bouleau blanc, et un gradient temporel, allant des forêts équiennes matures aux vieilles forêts vraies (*sensu.* Oliver et Larson 1996), afin d'obtenir un échantillon représentatif de la diversité du territoire. Au sein de 21 des 74 sites étudiés, nous avons aussi récolté entre 18 et 51 rondelles de pieds provenant de tiges échantillonnées pour la réalisation d'analyses dendrochronologiques, permettant de reconstruire la dynamique de perturbation de ces peuplements. Nous, nous avons utilisés les cartes d'inventaires forestiers des premiers, seconds et quatrièmes inventaires décennaux réalisés par la province du Québec pour comparer les caractéristiques structurelles et abiotiques des peuplements coupés à ceux brûlés. La nature des perturbations de forte intensité (feu sévère ou coupe forestière) a été déterminée en utilisant les cartes de coupe et de feu du Ministère de la Forêt, de la Faune et des Parcs. Enfin, nous avons aussi utilisé les résultats du quatrième inventaire forestier décennal pour déterminer si les peuplements identifiés sur le terrain comme étant des vieilles forêts étaient bien classifiés comme telles par cet inventaire.

1.5 Structure de la thèse

Cette thèse de doctorat se divise en six chapitres, comprenant l'introduction de la thèse dans le premier, la présentation des résultats obtenus sous forme d'articles scientifiques dans les quatre suivants et enfin une conclusion générale. Parmi ces six chapitres, le second a été publié dans le journal *Forest Ecology and Management*; le troisième est accepté pour publication par le journal *Annals of Forest Science*; le quatrième est accepté pour publication par le journal *Forest Ecology and Management*; le cinquième chapitre est accepté pour publication au *Canadian Journal of Forest Research*. L'introducation et la conclusion générale n'ont quant à eux pas été rédigés dans un objectif de publication.

Chapitre II : Diversité structurelle et dynamique des vieilles forêts boréales de l'Est du Canada

Ce chapitre porte sur la diversité structurelle des vieilles forêts boréales du l'Est du Canada et leur discrimination en fonction du stade de transition (forêt équienne, vieille forêt en transition et vieille forêt vraie) et des conditions stationnelles. Les données structurelles et les caractéristiques stationnelles de 71 peuplements ont été échantillonnés entre 2015 et 2016. Il a alors été possible de séparer ces peuplements en 11 structures spécifiques, se différenciant notamment en fonction de leur volume de débris ligneux au sol, de la proportion de sapin baumier dans la surface terrière, de la surface terrière et du degré d'ouverture de la canopée. Le temps depuis feu et la pente sont les deux facteurs environnementaux et temporels qui discriminent le plus ces structures. Deux de ces structures correspondent à des forêts équiennes, trois à des vieilles forêts en transition et sept à des vieilles forêts vraies. Les vieilles forêts boréales ne sont donc pas des peuplements homogènes, mais montrent au contraire une forte diversité, particulièrement chez les vieilles forêts vraies. Ces résultats suggèrent que la structure des forêts boréales peut fortement changer dans le temps, y compris une fois le stade de vieille forêt vraie atteint. Pour conserver la diversité des vieilles forêts dans les paysages aménagés, raisonner seulement en termes de superficie de vieilles forêts à maintenir en territoire aménagé est insuffisant. Il est nécessaire considérer également la variabilité, la représentativité et la dynamique de leurs structures.

Chapitre III : La diversité de sévérité des perturbations naturelles secondaires façonne la diversité des vieilles forêts boréales

Ce chapitre porte sur la dynamique des perturbations naturelles secondaires dans les vieilles forêts de l'Est du Canada. Nous avons échantillonné 18 à 51 rondelles de pieds dans 21 peuplements parmi les 74 inventoriés au total dans le territoire d'étude. Les résultats des analyses dendrochronologiques obtenus à partir de ces rondelles montrent que les vieilles forêts de l'Est du Canada sont dynamisées par une combinaison de perturbations secondaires de sévérités faibles et modérée. L'intensité de ces perturbations variait fortement dans le temps, notamment pour les perturbations de sévérité modérée. Nous avons identifié huit pics de reprises de croissance, dont la majorité coïncidaient avec des épidémies de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana,* Clemens). Il était néanmoins possible d'observer presque constamment des reprises de croissance dans les peuplements étudiés au cours des derniers siècles. Les vieilles forêts en transition étaient dominées par les perturbations de faible sévérité alors que les deux classes de perturbations avaient une importance similaire dans la dynamique des vieilles forêts vraies. Ces résultats soulignent non-seulement le dynamisme des vieilles forêts boréales mais aussi leur résilience. Par ailleurs, ces variations de sévérité des perturbations naturelles secondaires semblent être un important moteur de la diversité structurelle des vieilles forêts.

Chapitre IV – Les pratiques d'aménagement forestier ont réduit la diversité structurelle des vieilles forêts boréales résiduelles de l'Est Canadien.

Ce chapitre vise à déterminer si la structure des peuplements exploités diffère de ceux brûlés. Nous avons pour cela comparé les résultats de deux inventaires forestiers réalisés sur le territoire d'étude en 1983, soit 8 ans avant le début des activités d'exploitation forestière (inventaire préindustriel), et en 2007, soit 16 ans après (inventaire moderne). Les caractéristiques structurelles et abiotiques des peuplements exploités étaient significativement différentes de ceux brûlés. Plus précisément, les peuplements exploités étaient plus vieux, plus denses, moins bien drainés et contenaient une plus forte proportion d'épinette noire que les peuplements brûlés. Ces différentes caractéristiques peuvent être considérées comme étant des indicateurs du volume de bois marchand, et impliquent donc un volume supérieur dans les peuplements récoltés en comparaison de ceux brûlés. L'exploitation forestière vise ainsi en priorité des structures de forêts spécifiques, définie par une plus forte valeur financière, et réduit ainsi la diversité structurelle du paysage.

Chapitre V – La diversité structurelle des vieilles forêts boréales limite la fiabilité des inventaires photographiques aériens

Ce chapitre porte sur l'étude de la fiabilité des inventaires photographiques aériens quant à l'identification des vieilles forêts dans les paysages boréaux Québécois. Nous avons comparé les résultats de deux inventaires aériens réalisés en 1968 (inventaire préindustriel) et en 2007 (inventaire récent) sur un territoire de 2200km^2. Nous avons aussi comparé les résultats de l'inventaire récent avec ceux obtenus à partir de 74 placettes de terrain échantillonnés entre 2014 et 2016. Les résultats des deux inventaires aériens étaient très incohérents : la majorité des peuplements identifiés comme « vieilles forêts » par l'inventaire préindustriel et non-perturbés par la suite étaient classés comme « équiens » par l'inventaire récent. La majorité des placettes identifiées sur le terrain comme étant des vieilles forêts étaient aussi classées « équiens » par l'inventaire récent. Le manque d'attributs de vieilles forêts évidents (par ex. des arbres de très grande taille) ainsi que l'utilisation de critères inadaptés étaient les principaux éléments expliquant ces erreurs. Il est ainsi possible que la majorité des vieilles forêts boréales du Québec ne soient pas correctement identifiées, limitant alors l'efficacité des stratégies conservation de la loi sur l'aménagement durable du territoire forestier actuellement en vigueur au Québec.

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CHAPITRE II

STRUCTURAL DIVERSITY AND DYNAMICS OF BOREAL OLD-GROWTH FORESTS CASE STUDY IN EASTERN CANADA

PUBLISHED RESEARCH PAPER

Title: Structural diversity and dynamics of boreal old-growth forests case study in Eastern Canada

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2.1 Abstract

Old-growth stands are considered as key components of boreal forest diversity and their preservation is largely integrated into management plans. However, while the differences between old-growth and young forests have largely been studied, little is known about the diversity of boreal old-growth forests. In managed landscapes, the efficacy of old-growth conservation plans may be reduced depending on how these old-growth forests are considered: as a single, homogeneous and steady-state forest type or as multiple, diverse and dynamic forest types. To fulfil this gap, our objectives were: (1) to create a typology of old-growth boreal structures; (2) to observe how these structures are influenced by environmental and temporal parameters; and (3) to elaborate a succession model of old-growth structural dynamics along temporal and environmental gradients. Seventy-one mature and overmature stands were sampled within a 2200 km^2 territory situated in Eastern Canada. Cluster analysis divided the sampled stands into two even-aged types, three transition old-growth types and six true old-growth types. Slope, minimum time since last fire and organic horizon depth were the three environmental and temporal parameters influencing the old-growth structures. Paludification-related productivity decline was present in only one old-growth forest type, while the other sites remained productive. These results allowed the creation of three succession models of the dynamics of old-growth stands in the boreal forest of eastern Canada. Boreal stands can undergo numerous structural changes once the old-growth succession process is initiated. An increase in structural diversity when the true old-growth stage is reached, coupled with a variety of secondary disturbance characteristics, favours multiple pathways of structural evolution of these ecosystems over time. Therefore, forest management planning should incorporate this complexity to improve the preservation of old-growth forests in managed territories.

2.2 Résumé

Les vieilles forêts boréales sont considérées comme des éléments-clés de la biodiversité forestière boréale et leur préservation est un objectif couramment intégré dans les stratégies d’aménagement. Toutefois, alors que les différences entre jeunes et vieilles forêts ont été largement étudiées, nous avons peu de connaissances quant à la diversité interne des vieilles forêts. Dans les territoires aménagés, l’efficacité des mesures de gestion visant à mieux intégrer les vieilles forêts peut être remise en question en fonction de la manière dont ces écosystèmes sont perçus, c’est-à-dire comme des écosystèmes homogènes et stables ou comme des écosystèmes diversifiés et dynamiques. Pour combler cette lacune, nos objectifs étaient : (1) créer une typologie structurelle des vieilles forêts boréales ; (2) observer comment ces structures sont influencées par des paramètres environnementaux et temporels ; et (3) élaborer un modèle de succession de la dynamique structurelle des vieilles forêts le long des gradients temporels et environnementaux. Soixante et onze peuplements matures et surannés ont été échantillonnés dans un territoire de 2200 km^2 situé dans l'Est du

Canada. L'analyse par groupements a divisé les peuplements échantillonnés en deux types de forêts équiennes, trois types de vieilles forêts en transition et six types de vieilles forêts vraies. La pente, le temps minimal écoulé depuis le dernier feu et la profondeur de l'horizon organique sont les trois paramètres environnementaux et temporels qui ont influencé les structures des vieilles forêts. La baisse de productivité liée à la paludification n'était présente que dans un seul type de vieille forêt, tandis que les autres sites demeuraient productifs. Ces résultats ont permis de créer trois modèles de succession de la dynamique des vieilles forêts dans la forêt boréale de l'Est du Canada. Les peuplements boréaux peuvent subir de nombreux changements structurels une fois que le processus de succession des vieilles forêts est amorcé. Une augmentation de la diversité structurelle lorsque le stade de vieille forêt vraie est atteint, associée à des perturbations secondaires aux caractéristiques (nature, sévérité) diversifiées, favorise le développement de multiples chemins d'évolution structurelle dans le temps. Par conséquent, la planification de l'aménagement forestier devrait tenir compte de cette complexité afin d'améliorer la préservation des vieilles forêts dans les territoires aménagés.

2.3 Introduction

In forest ecosystems, the old-growth stage can mainly be defined as stands driven by gap-dynamics, with tree mortality caused by secondary disturbances (Hilbert and Wiensczyk 2007; Wirth et al. 2009; Shorohova et al. 2011). In the boreal biome, old-growth forests represent a significant proportion of the natural landscape, regardless of the differences in disturbance dynamic and species traits among the boreal regions (Östlund et al. 1997; Cyr et al. 2009; Shorohova et al. 2009). Even in territories characterized by short fire cycles, old-growth forests are present due to the random distribution of fire (Bergeron et al. 2002; Bouchard et al. 2008; Cyr et al. 2009). These ecosystems are considered as key habitats of the boreal biome because of their specific structural attributes and their relative stability in comparison to younger stands driven by stand-replacing disturbances (Esseen et al. 1997; Kimmins 2003; Fenton and Bergeron 2011). In managed territories, the choice of harvesting system tends to be determined by the system’s short-term profitability and its capacity to generate the maximum possible volume (Haeussler and Kneeshaw 2003), leading to an upper limit of forest rotation, which is generally earlier than the initiation of gap dynamics (Östlund et al. 1997; Bergeron et al. 2002). Furthermore, in some boreal regions, natural disturbances such as fire, windthrow or insect outbreak still occur and compound the impacts of forest harvesting (Armstrong 1999; Bergeron et al. 2006). Consequently, many boreal landscapes are now rejuvenated, simplified and fragmented (Östlund et al. 1997; Etheridge et al. 2006; Boucher et al. 2015). As a result, in heavily managed boreal territories, a significant portion of the erosion of forest biodiversity is linked to the rejuvenation of the forest landscape (Berg et al. 1994; Esseen et al. 1997; Siitonen 2001). In territories where forests are mainly harvested for the first time and where the knowledge about local biodiversity is still scarce, similar losses are expected (Cyr et al. 2009).

Old-growth forests consequently represent an important issue in forest management, with different planning processes aimed at minimizing the loss of old-growth forests and reducing the impacts when it is harvested (Mosseler et al. 2003; Le Goff et al. 2010). Emphasis has been placed on management models based on the natural disturbance regime (Kuuluvainen 2002; Gauthier et al. 2009) or on the imitation of stand scale natural processes (Vanha-Majamaa et al. 2007; Kuuluvainen 2009). However, these models require a complete understanding of boreal forest natural dynamics at all temporal and spatial scales to be efficient (Kneeshaw and Gauthier 2003; Kuuluvainen 2009; Halme et al. 2013). Each boreal region presents specific characteristics because of particular combinations of climatic factors, disturbance dynamics and species traits (Kneeshaw et al. 2011; Shorohova et al. 2011). Hence, a fine scale understanding of the old-growth dynamics in each boreal region is necessary for efficient management.

Eastern Canada boreal forests fall into this paradigm and a more detailed understanding of old-growth forests is needed. Indeed, most management strategies in this territory consider old-growth forests as a homogeneous group, contrasted uniquely to even-aged stands (Brassard and Chen 2006; Bergeron and Harper 2009). Studies about their diversity and dynamics have focused on the transition processes from even-aged to old-growth forest, typically defined by canopy break-up, the presence of gap dynamics and the progressive replacement of the first cohort (Bergeron and Harper 2009). Once this transition is complete, old-growth forests tend to be viewed as structurally undifferentiated (Nguyen et al. 2002; Harvey et al. 2002). Structural evolution has been observed, however, in boreal old-growth forests undergoing paludification (Lecomte et al. 2006; Bergeron and Harper 2009), a process that is associated with certain soil types and climatic conditions (Lavoie et al. 2005). However, when other soil types and climates are examined, more complex dynamics of old-growth boreal stands can be expected (De Grandpré et al. 2008; Gauthier et al. 2010), as productivity declines due to paludification are associated with specific abiotic conditions (Pollock and Payette 2010; Girard et al. 2014; Ward et al. 2014).

Therefore, the analysis of Eastern Canadian boreal old-growth forest structural diversity and the factors explaining its distribution across the landscape is a pertinent case study of a common old-growth forest management problem. A management strategy that aims to maintain old-growth forests, yet which considers them as homogeneous entities, cannot preserve all types of old-growth forest. This recurring issue can be expressed as follows: in a given ecological context, are the old-growth forests a homogeneous and steady-state forest type or multiple, diverse and dynamic forest types? Our study aims to fill this knowledge gap for Eastern Canada by identifying the diversity of old-growth forest structures and their dynamics across a boreal landscape. Specifically, our objectives are: (1) to define a typology of boreal old-growth forests based on their structural attributes; (2) to observe whether the groups created by the typology can be related to specific environmental characteristics; and (3) to create a succession model of old-growth structural dynamics along both temporal and environmental gradients.

2.4 Methods

2.4.1 Study territory

The study site covers a 2200 km^2 area of public land along the southern edge of Lake Mistassini (72°52’36’’ W, 50°18’50’’ N) (Figure 2-1). The area is crossed by the Mistassini, the Ouasiemsca and the Nestaocano rivers. The study site is part of the western subdomain of the black spruce (*Picea mariana* (Mill.))–feather moss bioclimatic domain (Saucier et al. 1998) and belongs to the physiographic region of the Nestaocano River Hills. The topography is essentially characterized by gentle hills and an altitude range from 350 to 750 m. Thick glacial tills are the dominant surface deposits. Rivers and streams are often surrounded by sand deposits or vast bogs. Mean annual temperature ranges from -2.5 to 0.0 °C, annual rainfall (rain and snow) from 700 to 1000 mm and growing season length from 120 to 155 days. Black spruce and balsam fir (*Abies balsamea* (L.) Mill.) are the dominant tree species, and 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*) (Bergeron et al. 1998). Timber exploitation in the region began in 1992 and continued at a relatively low level until 2000 when harvest levels increased. This region was chosen for study because it encompasses the spectrum of environmental diversity of the western black spruce–feather moss bioclimatic domain, from poorly-drained valley bottoms situated on organic deposits to well-drained till slopes.

2.4.2 Sampling

Based on the Québec’s Ministry of Forests, Wildlife and Parks (MFWP) ecological classification, this territory can be divided into 19 environmental types; six of these represent over 72% of the total area. They can be defined by the following Potential vegetation/Slope/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 (Blouin and Berger 2004). Because they cover the environmental diversity of the study territory, we selected sites within these six environmental types, with an objective of each having equal sampling intensity. According to Oliver and Larson (1996), old-growth forests can be divided

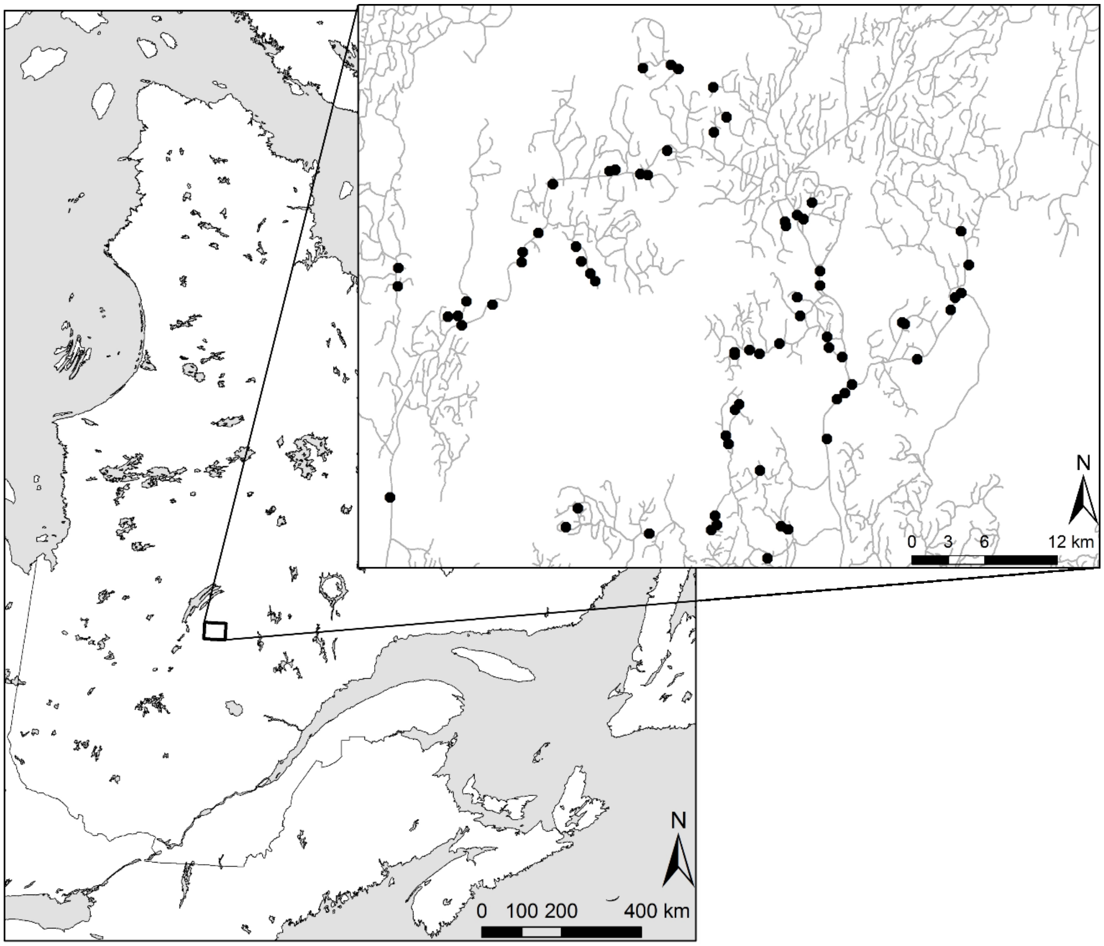

Figure 2-1 Map of the study territory. The distribution of the sampled stands is indicated by the black dots on the inset map. The grey lines represent the network of forestry roads.

into two stages: transition old-growth (gap dynamics have started, however the stand is still dominated by first cohort trees) and true old-growth (all the trees from the first cohort have disappeared). Following this definition, we attempted to sample the complete successional sequence from mature stands (stands approaching the age of canopy break-up) to true old-growth forests. However, we faced limitations during our site selection. The first limitation is that the dominant boreal tree species in the study area are relatively short-lived (Burns and Honkala 1990), making it impossible to estimate stand ages older than 200 years without using radiocarbon dating (Fenton and Bergeron 2011; Garet et al. 2012). The second is the absence of clear and constant age thresholds between the transition processes, making it impossible to define age classes based on a single transition process. Therefore based on the literature (Uhlig et al. 2001; Bergeron and Harper 2009; Gauthier et al. 2010), we decided to divide our sample stands into three age groups, each one dominated by a single transition process: 80-100 years (maturing), 100–200 years (canopy break-up and beginning of the gap dynamic), >200 years (first cohort disappearance).

A first survey was realized in order to assess the age of the site, throughout core sampling of five dominant and codominant trees per sites. Then, seventy-one sites were sampled based on stratified random sampling of forest inventory potential vegetation type and stand age, depending on accessibility. As the study territory is a managed area, the 80-100 years class was the least abundant (12 sites sampled, with at least one site per environmental type), as this class is the most often harvested (Bouchard and Garet 2014). However, gap-dynamics do not start exactly 100 years after the fire (Bouchard et al. 2008; Lecomte and Bergeron 2006), so we assumed that numerous sites in the 100-200 years were class were still even-aged, compensating the lack of sites in the 80-100 years class.

At each site, the centre of the plot was systematically placed 125m beyond the stand edge in order to limit edge effects and to avoid bias. Soil and topographic parameters were determined by digging a soil profile at the plot centre and measuring topographic variables with a clinometer. Living trees having a diameter at breast height (dbh) ⩾9 cm (merchantable trees) were sampled in a 400m^2 square plot (20 × 20m), the standard plot size in the Québec forest survey (MFFP 2016). For each individual tree, we noted dbh, vitality (alive, senescent or dead) and position in the canopy (dominant, codominant, intermediary or oppressed), the two last parameters being defined according to the MFWP typology (MRN 2013). We then identified and measured the dbh of all living trees having a dbh <9 cm and a height >1.30m (saplings) found in two 100 m^2 subplots within the 400 m^2 plot. Gap fraction, the ratio between gap length and total transect length (Runkle 1982, Battles et al. 1996), was also measured along five 25 m long transects starting from the centre of the 400 m^2 plot. Gaps were defined as all sections of the transect where the canopy was below the 2/3 height of the dominant trees (Pham et al. 2004) and having a gap length superior to 2 m. This second criterion was included to avoid confusion between actual gaps and the natural separation between tree crowns in these forests. Downed coarse woody debris (CWD) diameter, where the CWD intersected the transect line, and species was determined along four 20 m long transects following the edge of the 400 m^2 plot, a methodology inspired by Clark et al. (1998). We considered only CWD having a diameter ⩾9 cm at the transect intersection and not buried at a depth >15 cm; CWD buried below this depth was ignored as it was difficult to sample. When a piece of CWD crossed two transects, any second encounter was skipped to avoid double-counting. To determine the minimum stand age, we collected a disc from each base of ten merchantable trees; we sampled a similar number of trees per layer (dominant, codominant, intermediary and oppressed) for each site. 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.

2.4.3 Data analysis

Discs were air-dried and sanded with progressively finer grade sandpaper. Tree rings were counted along two radii for each disc and the maximum value was considered as the minimum age of the tree. Strong growth-release or growth-reduction events were identified by visual observation and the ring representing the growth-change threshold was determined. The ten rings before and after this threshold were measured with a precision of 0.01 mm manual Henson micrometer (Fred C. Henson, Mission Viejo, Calif, USA) or a LINTAB measurement table (LINTAB™, Rinntech, Heidelberg, Germany) along the two radii. Tree ring data were computed using the TSAP-WIN program (Rinntech, Heidelberg, Germany). If the mean change of the two growth measurements was >50%, it was considered as a significant release or reduction event (Black and Abrams 2003; Fraver and White 2005). These data and the age distribution of the sampled stems were used to determine if these trees belonged to the first or to subsequent cohorts (N+1 cohorts). We considered that all trees belonged to the first cohort when the difference between the youngest and the oldest tree did not exceed 30 years, as this threshold represents the beginning of seed production for black spruce and balsam fir (Burns and Honkala 1990; Viglas et al. 2013), the main late successional species. All the individuals exceeding this 30 years threshold were considered as belonging to the N+1 cohorts. Individuals belonging to the 0-30 years group were considered as first cohort trees as long as there was no evidence of juvenile suppression or only one tree remained in this group. If one of these criteria was fulfilled, all the trees were considered as belonging to the N+1 cohorts. 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, and were not classified as first cohort or N+1 cohort trees.

Ten structural parameters and five environmental and temporal parameters were obtained from the sampled data and used for the analysis (Table 2-1). These ten structural parameters were considered adequate to describe (i) vertical and horizontal variation in the stands (Oliver and Larson 1996; Boucher et al. 2003; Bergeron and Harper 2009), (ii) mortality events and regeneration efficiency (Oliver and Larson 1996; Desponts et al. 2004; Pham et al. 2004), (iii) changes in productivity (Harper et al. 2003; St-Denis et al. 2010), (iv) replacement of shade intolerant species by shade tolerant ones (Bergeron 2000; De Grandpré et al. 2000; Kneeshaw and Gauthier 2003) (v) transition dynamics (Bergeron 2000; Bergeron and Harper 2009; Gauthier et al. 2010), (vi) development of the paludification process (Simard et al. 2007; Ward et al. 2014) and (vii) influence of soil and topographic characteristics on secondary disturbance dynamics and forest succession (Ruel 2000; Gauthier et al. 2010; Messaoud et al. 2014). Snags (i.e., standing deadwood) basal area or density have not been included among the parameters because preliminary studies have shown that they are redundant with CWD results. The Weibull's shape parameter and the CBAP were calculated according to the formulas described in table 2-1. The calculation of the Weibull's shape parameter

Table 2-1 Description of the structural, environmental and temporal parameters used in this study.

Type	Parameter	Acronym	Unit	Description
Structural parameters	Tree density	TD	n/ha	Number of living merchantable stems per hectare
	Sapling density	SD	n/ha	Number of living saplings per hectare
	Basal area	BA	m^2/ha	Basal area of the living merchantable trees per hectare
	Basal fir proportion	BFP	%	Proportion of balsam fir in the basal area
	Coarse woody debris volume	CWD	m^3/ha	Calculated according to the Marshall et al. (2000) formula for linear coarse woody debris sampling:
	Gap fraction	GF	%	Mean value of the five gap fraction results at each site
	Maximum height	MH	m	Mean height value of the dominant trees sampled at each site
	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: $f(x) = \left(\frac{a}{b}\right) \times \left(\frac{x}{b}\right) \times exp\{-(x/b)^a\}; x \geq 0; a>0; b>0$ 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. 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
	Shannon index	SI	-	Calculated according to the Shannon diversity index formula (Shannon and Weaver 1949) with basal area abundance rather than individual abundance
	Cohort basal area proportion	CBAP	-	Proportion of N+1 trees in the basal area, calculated using the Kneeshaw and Gauthier (2003) formula: $CBAP = \frac{(BA_{N\quad 1\,trees} + 0.1)}{(BA_{N+1\,trees} + 0.1 + BA_{First\ cohort\ trees})}$ Where BA is the basal area.
Environmental and temporal parameters	Minimum time since last fire	MTSLF	years	Maximum age value among the ten basal discs
	Slope	SL	%	Mean slope value along the 400 m^2 square plot
	Depth of the organic horizon	DOH	cm	Mean depth of the organic horizon along the soil profile
	Depth of the mineral horizon	DMH	cm	Mean depth of the mineral horizon along the soil profile
	Total soil depth	TSD	cm	Mean total depth of the soil along the soil profile

was performed using the EasyFit 5.5 Professional distribution fitting software (Mathwave Technologies). For each site, saplings and merchantable stems were grouped in 2cm diameter class in order to improve the fitting function. Statistical analyses were completed using R-software, version 3.3.1 (R Development Core Team 2016) using the *vegan* (Oksanen et al. 2017), *cluster* (Maechler et al. 2017), *agricolae* (de Mendiburu 2017), *FactoMiner* (Le et al. 2008) and *lmtest* (Zeileis and Hothorn 2002) packages applying a *p*-threshold of 0.05.

For our first objective of defining a typology, principal component analysis (PCA) was performed using the structural parameters of the 71 sites. The strength of the relationship between each variable and the PCA axis was determined by Pearson's correlation. We then performed a Ward's linkage clustering (Ward 1963) using Euclidean distances to determine homogeneous forest types. The parameters used for the clustering were the structural parameters, but scaled to equalize their variance. The optimal number of forest types was determined using average silhouette widths and fusion-level values (Rousseeuw 1987; Borcard et al. 2011). We considered three sites per forest type as a minimum number to provide a relevant ecological analysis. Once the forest types were defined, among-type differences based on their structural, environmental and temporal parameters were determined by Kruskall-Wallis ANOVA by ranks followed by post hoc multiple comparisons of the treatments for the significant results (Fisher's least significant difference). The old-growth stage of each forest type was determined using two of the structural parameters: Weibull's shape parameter (WSP) and cohort basal area proportion (CBAP). WSP represents the diameter distribution of the living trees, from a normal to a reverse J distribution (Bailey and Dell 1973), and CBAP indicates the proportion of N+1 cohort trees in the stand basal area (Kneeshaw and Gauthier 2003). The combination of these two parameters was considered as an efficient indicator of the gap-dynamics in the studied stands, as they describe both the increasing structural complexity and the progressive replacement of first cohort trees expected during the old-growth transition process (Kneeshaw and Gauthier 2003; Brassard and Chen 2006; Hilbert and Wiensczyk 2007). Even-aged stands are defined here as those having a normal diameter distribution. Old-growth stands have an irregular distribution, but this distribution is rarely a true reverse J, especially in black spruce stands (Boucher et al. 2003; Fraver et al. 2008). As such, we used a WSP threshold of 1.5, with WSP values >1.5 representing a normal distribution and WSP values <1.5 reflecting an irregular distribution (Bailey and Dell 1973). Transition old-growth stands should have CBAP values >0.3 (Kneeshaw and Gauthier 2003; Brassard and Chen 2006), representing the beginning of the first cohort replacement, while true old-growth stands should have a CBAP value of 1 (total replacement of the first cohort, Oliver and Larson 1996). Consequently, even-aged structures were defined by a WSP ⩾1.5 and a CBAP <0.3, true old-growth structures had WSP and CBAP values of <1.5 and 1, respectively, and transition old-growth structures were represented by all other WSP-CBAP combinations. In this study, structurally even-aged stands are not defined as being old-growth, although with a

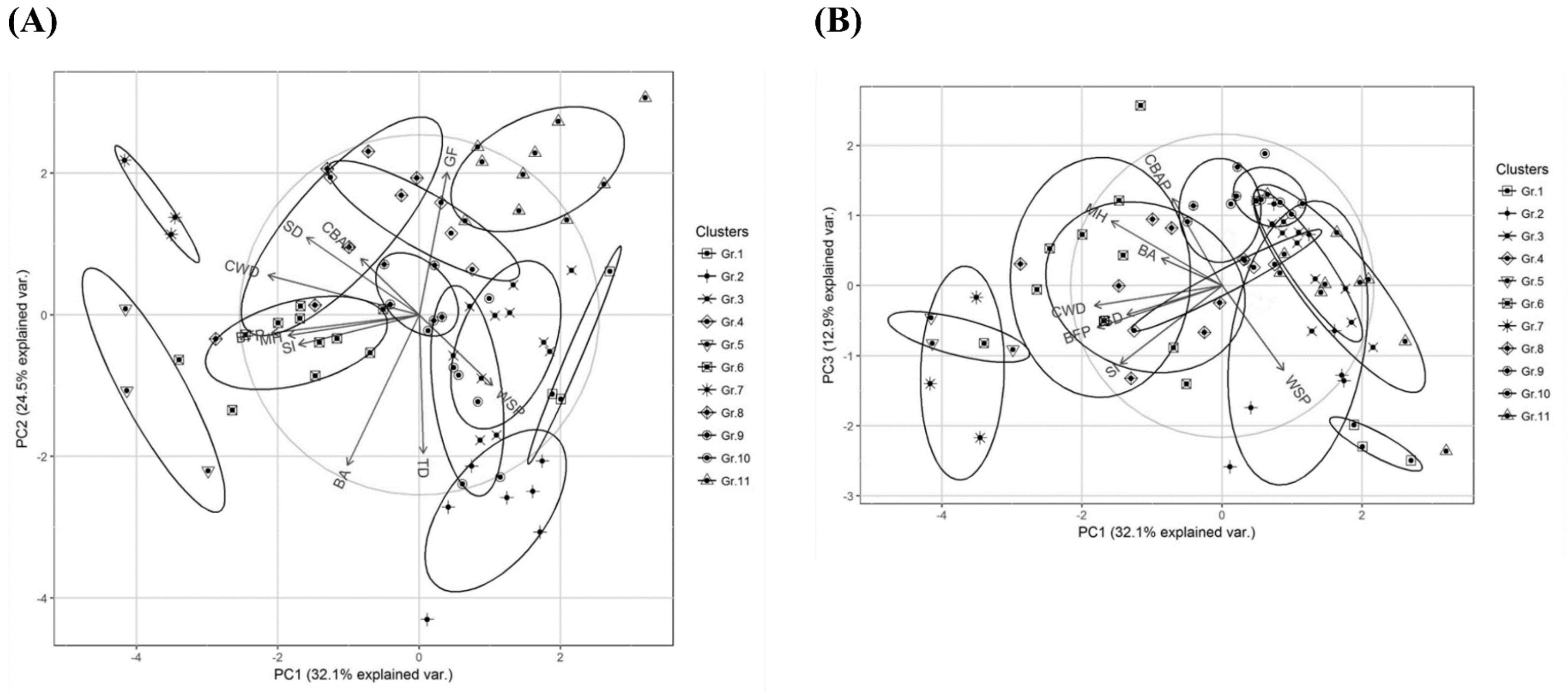

Figure 2-2 Principal component analysis (PCA) and clustering of the 71 study sites. (a) The biplot of the first and the second axes of the PCA (PC1 and PC2). (b) The biplot of the first and the third axes (PC1 and PC3). Sites belonging to the same cluster are identified by specific symbols surrounding a black dot. Ellipses illustrate cluster distributions along the PCA axes at a 95% confidence interval around the centroid. Parameters having a significant correlation with an axis are illustrated on the diagram. For codes see Table 2-1. (Gr.: group).

mean time since the last fire at over 100 years they would have been considered as old-growth in some studies (e.g. Bergeron and Harper 2009).

For our second objective of determining the relationships between forest types and environmental variables, we performed a simple linear regression. Structural parameters of the different forest types were used as dependent variables, and temporal and environmental parameters were the independent variables. Only those independent variables presenting significant differences between forest types and showing no intercorrelations were used. Model assumptions were tested and if they were not fulfilled, the dependant variable was transformed. When transformations were not adequate, the model was considered to be invalid. Finally, our third objective of constructing a successional model was developed using the significantly different parameters of the previous analysis.

2.5 Results and discussion

2.5.1 Typology of old-growth forests

The first three axes of the PCA explained 69.5% of the total variance of the sites (Figure 2-2). All the structural parameters had a significant influence along at least one of the three axes, but seven of them were significant along two or more axes, which emphasizes the intricate interactions between the structural parameters shaping old-growth boreal forests in Eastern Canada. The identification of 11 forest types by cluster analysis underlines this entanglement of boreal oldest structures, as most types overlap to some degree on the PCA biplots. These results illustrate how oldest forest structures are shaped by secondary disturbances that vary in scale, nature and intensity, leading to progressive differentiations rather than abrupt ones (Kneeshaw and Burton 1998; Mosseler et al. 2003). However, the significant results of the Kruskall-Wallis test for all the structural parameters between the forest types (Table 2-2) highlight their specificities, as despite overlap among forest types, each is defined by a set of distinct characteristics.

This diversity of structures can be difficult to visualize, therefore a typology was constructed based on the two most important parameters for each PCA axis: CWD and balsam fir proportion (BFP) for axis 1, basal area (BA) and gap fraction (GF) for axis 2 and CBAP and WSP for axis 3 (Figure 2-3). The importance of the CWD volume and the presence of late-successional species such as balsam fir is consistent with the results of previous studies where these parameters were considered as key elements of old-growth structures (Brassard and Chen 2006; Hilbert and Wiensczyk 2007). Similarly, BA and GF reflect the openness of the canopy, which can be caused by several factors inherent to boreal old-growth dynamics: gap dynamics, secondary

Table 2-2 Mean and standard error (in italics) of the structural parameters for the 11 old-growth forest types defined by hierarchical clustering. Different letters indicate significant differences between forest types at a p value of $\leqslant$0.05. For parameter codes, see Table 2-1.

Parameter	Group 1 (n = 3)	Group 2 (n = 7)	Group 3 (n = 11)	Group 4 (n = 4)	Group 5 (n = 3)	Group 6 (n = 11)	Group 7 (n = 3)	Group 8 (n = 8)	Group 9 (n = 5)	Group 10 (n = 7)	Group 11 (n = 10)
TD	783.33 bd	1517.85 a	977.27 b	618.75 cd	900 bc	868.18 bc	891.66 bc	778.57 cd	745 cd	1457.14 a	502.5 d
	142.15	*282.36*	*255.79*	*104.83*	*330.71*	*230.24*	*104.08*	*310.04*	*44.72*	*244.4*	*248.17*
SD	750 d	1389.28 d	1636.36 cd	2787.5 bc	4150 ab	2972.72 b	9450 a	3796.42 ab	1935 cd	1882.14 cd	2497.5 bc
	468.37	*1027.62*	*690.95*	*1654.47*	*482.83*	*1151.97*	*1307.66*	*962.68*	*1567.3*	*880.42*	*1325.67*
BA	11.6 cd	27.67 a	16.38 b	15.18 bc	27.45 a	21.51 a	14.9 bc	15 bc	15.75 bc	21.93 a	6.95 d
	1.93	*6.43*	*4.88*	*1.44*	*4.81*	*5.38*	*1.91*	*7.68*	*1.67*	*4.73*	*3.3*
BFP	0 e	7.46 be	0.24 de	0.97 bd	81.29 a	21.87 a	54.96 a	22.53 a	1.78 b	1.4 bc	0.11 ce
	0	*14.94*	*0.75*	*1.62*	*11.87*	*8.15*	*5.1*	*26.53*	*1.96*	*1.96*	*0.27*
CWD	3.78 f	11.2 f	26.49 e	107.76 ab	144.4 ab	106.24 ab	154.77 a	70.28 bc	52.31 cd	33.11 de	25.96 ef
	3.66	*12.61*	*13.77*	*60.58*	*72.47*	*40.01*	*62.94*	*12.55*	*16.42*	*21.77*	*28.56*
GF	60.41 bc	38.73 d	52.57 bc	94 a	35.38 d	46.36 cd	72.73 ab	95.16 a	48.16 cd	53.95 bc	93.43 a
	34.28	*16.4*	*15.33*	*12*	*12.61*	*13.04*	*14.83*	*7.33*	*15.24*	*11.99*	*10.15*
MH	13.93 e	16.22 de	17.84 bd	20.17 ab	21.76 a	21.36 a	19.7 ac	20.42 a	19.64 abc	17.81 cd	15.02 e
	0.55	*2.43*	*2.89*	*0.85*	*1.15*	*2.29*	*2.22*	*2.18*	*1.91*	*1.41*	*2.8*
WSP	1.82 a	1.54 ab	1.04 bc	0.78 d	0.78 d	0.8 d	0.88 cd	0.94 cd	0.8 d	1.15 ac	0.98 cd
	0.16	*0.66*	*0.2*	*0.12*	*0.17*	*0.48*	*0.12*	*0.17*	*0.06*	*0.22*	*0.19*
SI	0.24 ab	0.17 bc	0.02 e	0.03 de	0.28 ab	0.27 ab	0.31 a	0.24 ab	0.12 cd	0.03 de	0.01 e
	0.06	*0.14*	*0.05*	*0.06*	*0*	*0.11*	*0.05*	*0.08*	*0.1*	*0.04*	*0.03*
CBAP	0.08 e	0.11 e	0.32 e	0.17 e	0.46 de	0.61 cd	0.82 ac	0.86 ab	0.91 ab	0.95 a	0.65 bd
	0	*0.09*	*0.16*	*0.1*	*0.35*	*0.29*	*0.3*	*0.18*	*0.09*	*0.09*	*0.37*

disturbances or paludification (Oliver and Larson 1996; Pham et al. 2004; Fenton and Bergeron 2011). These four parameters are sufficient to divide our forest types into distinct structural paths, and they are consequently key factors for describing the structural diversity of old-growth boreal forests.

Despite this, CBAP and WSP remain important indicators of old-growth stages and provide insight into the position of the forest types along the old-growth succession process. The forest types having the highest mean CBAP values contained numerous stands with a CBAP value of 1, (true old-growth forests, Oliver and Larson 1996), but none of our forest types had a mean CBAP of 1. The Eastern Canadian boreal forest is characterized by relatively small changes in stand composition during succession. Indeed, black spruce is both pioneer and a late successional species and shade-intolerant broadleaved species, such as paper birch, are also found at low densities in old-growth stands (Bergeron 2000; Harvey et al. 2002; Gauthier et al. 2010). Similarly, in our forest types, no important changes in stand composition can be observed over time (Appendix A). Then, it seems that the first cohort complete disappearance may not induce significant structural changes. True old-growth structures in Eastern Canadian boreal stands could be reached even when the first cohort has not totally disappeared. In addition, the cohort of oldest trees is harder to identify in uneven-aged structures and this implies a possible CBAP underestimation for the oldest stands. For these reasons, we decreased the CBAP threshold from 1 to 0.6, twice the transition old-growth threshold (Kneeshaw and Gauthier 2003; Brassard and Chen 2006). Thus, we now include stands where the first cohort trees represent a minor part of the living basal area. According to this classification, two of our forest types were even-aged, three were transition old-growth and six were true old-growth. As such, our results offer an efficient alternative to the common perception of old-growth boreal forests being homogeneous entities.

The presence of forest types representing even-aged structures was expected as the initiation of gap dynamics can occur over a wide age range, especially in black spruce–dominated stands (De Grandpré et al. 2000; Uhlig et al. 2001). These even-aged forest types also present a mean MTSLF superior to 100 years, making them old-growth forests according to age-based definitions for Québec's boreal forest (Bergeron and Harper 2009; Cyr et al. 2009), a threshold however based on the age of exploitation of boreal forests in Quebec. These results are another example of the complexity in consistently defining old-growth forests among and within regions (Wirth et al. 2009; Pesklevits et al. 2011). Group 1 represents open jack pine–black spruce mixtures typical of regularly burned areas (Smirnova et al. 2008) while Group 2 includes dense pure black spruce stands, black spruce–jack pine mixtures and black spruce–balsam fir–white birch mixtures (Appendix A). Therefore, despite their differences in tree composition, even-aged stands are regrouped into two specific structures, apparently discriminated by stand-replacing disturbance dynamics.

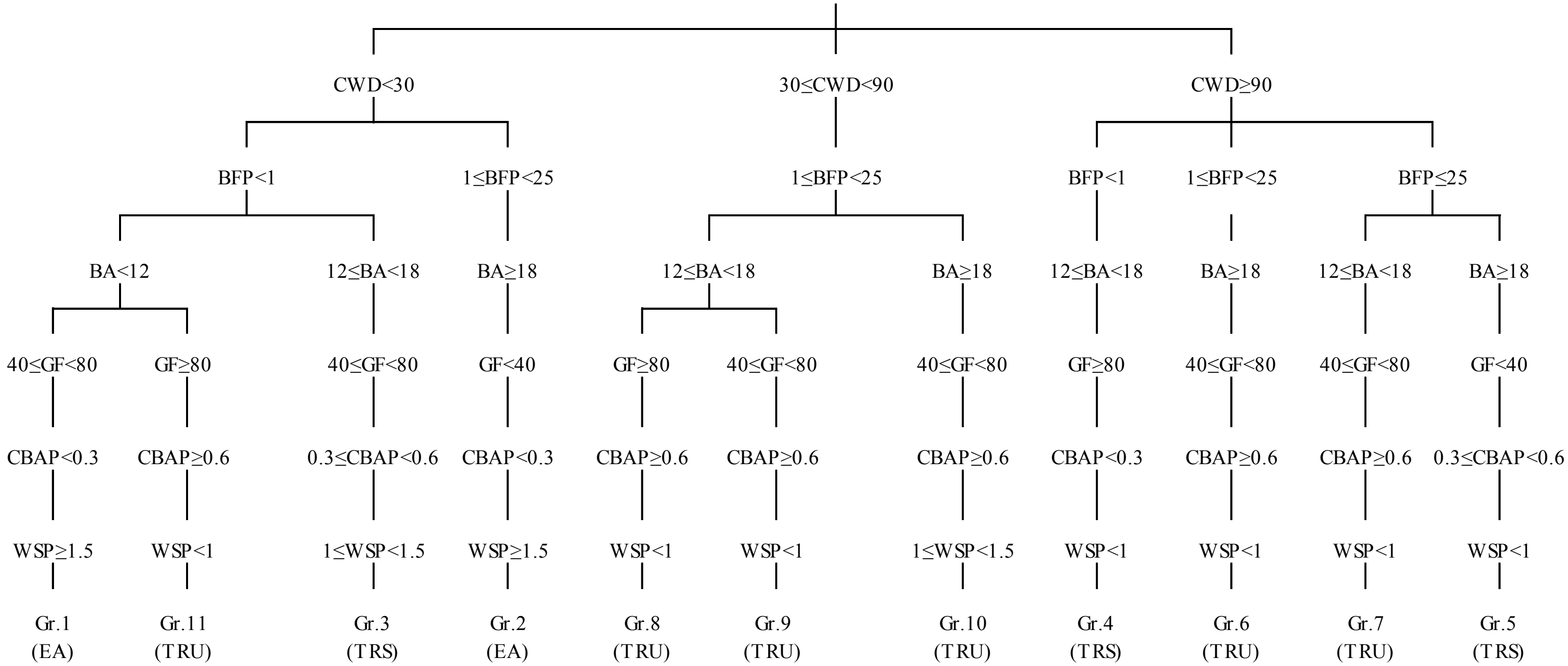

Figure 2-3 Typology of the old-growth forest types based on structural attributes. The old-growth stage of each forest type is presented under their names in parentheses: EA (even-aged), TRS (transition old-growth) and TRU (true old-growth). CWD: coarse woody debris, BFP: balsam fir proportion, BA: basal area, GF: gap fraction, CBAP: cohort basal area proportion, WSP: Weibull's shape parameter, Gr.: group).

In contrast, transition old-growth and true old-growth structures are highly variable, confirming that old-growth forests are a key element of landscape structural heterogeneity (Franklin et al. 2002; Harper et al. 2002; Hendrickson 2003). Moreover, in comparison to the even-aged or transition old-growth stages, true old-growth stages present the highest number of specific structures. Structural diversity is expected to increase in the absence of stand replacing disturbance (Franklin et al. 2002). Our results support this observation for boreal stands in Eastern Canada, as structural richness increased along the old-growth transition process.

2.5.2 Influence of environmental and temporal parameters on old-growth structures

Among the environmental and temporal parameters examined, minimum time since last fire (MTSLF), slope and depth of the organic horizon differed significantly among the forest types (Table 2-3). MTSLF values ranged from 104 to 254 years (Group1 and Group 9), slope from 2.20 to 32.3% (Group 11 and Group 5) and depth of the organic horizon to 11.0 to 47.2 cm (Group 5 and Group 11). As forests are dynamic systems, MTSLF is a key element of boreal forest dynamics, especially during the transition to old-growth where strong structural changes happen within a century (Brassard and Chen 2006; Bergeron and Harper 2009). Slope favours the development of balsam fir in the black spruce–feather moss bioclimatic domain, this species is more present on steep and well-drained sites (Messaoud et al. 2007; Gauthier et al. 2010; Côté 2013). In addition, the higher susceptibility of balsam fir to windthrow compared to black spruce and the competitiveness of balsam fir regeneration in the resulting gaps creates a positive feedback of windthrow occurrence, leading to a shift in natural disturbance dynamics (Ruel 2000; Girard et al. 2014). Finally, the depth of the organic horizon is a limiting factor for balsam fir development, and the decrease in productivity caused by the thickening of the organic layer leads to canopy opening and low density structures (Messaoud et al. 2007; Simard et al. 2007; St-Denis et al. 2010). However, the depth of the organic horizon is influenced both by MTSLF and slope (Fenton et al. 2005; Laamrani et al. 2014). Therefore, these last parameters are the principal environmental and temporal factors influencing old-growth structures, while the depth of the organic horizon is the result of their interaction.

Table 2-3 Mean and standard error (in italics) of the environmental parameters of the 11 old-growth forest types defined by hierarchical clustering. Different letters indicate significant differences between forest types at a p value of $\leqslant 0.05$. For parameter codes, see Table 2-1.

Parameter	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6	Group 7	Group 8	Group 9	Group 10	Group 11
MTSLF	104 d	114.42 d	170.45 c	215.25 ab	160.66 cd	177.54 bc	188.33 ac	245.28 a	253.8 a	248.71 a	220.9 ab
	19.15	*23.22*	*51.75*	*9.42*	*50.14*	*18.1*	*50.14*	*49.16*	*45.45*	*50.84*	*71.24*
SL	4.33 de	7.42 de	6.36 ce	10.75 bd	32.33 a	14.18 ac	18.66 ab	14.14 ac	5.8 de	6.85 ce	2.2 e
	7.5	*12.34*	*3.9*	*9.21*	*3.05*	*9.56*	*5.03*	*10.57*	*7.66*	*5.58*	*4.58*
DOH	26.66 bd	20.28 cd	35.09 ab	33.25 ac	11 d	24 bd	29 ad	35.85 ab	29.6 ac	31.85 ac	47.2 a
	20.2	*9.49*	*15.2*	*19.55*	*4.58*	*11.61*	*15.09*	*15.74*	*13.95*	*12.58*	*18.34*
DMH	4.33	9.42	10.18	8	15.33	20.36	16.66	7.28	9	12.85	4
	7.5	*9.98*	*10.08*	*6,00*	*13.57*	*18.73*	*16.5*	*11.02*	*7.31*	*14.41*	*6.59*
TSD	31	29.71	45.27	41.25	26.33	44.36	45.66	43.14	38.6	44.71	51.2
	17.69	*12.89*	*9.88*	*17.7*	*14.97*	*15.53*	*14.01*	*11.81*	*10.85*	*12.13*	*13.7*

Regression analysis highlighted the influence of MTSLF and slope on the structural attributes, explaining in part the differences between the forest types (Table 2-4). Slope significantly influenced two structural attributes: balsam fir proportion (positive) and gap fraction (negative). These results may be explained by the more suitable conditions offered by the steepest sites for balsam fir due to better soil drainage (Côté 2013). On less pronounced slopes balsam fir is less present because of frequent fire recurrence or paludification (Messaoud et al. 2007; Smirnova et al. 2008; St-Denis et al. 2010). However, carbon-14 reconstructions of fire dynamics over the study area indicate that the fire cycle is shorter at the bottom of the valley (i.e., where the slope is low) than on the hills (i.e., where the slope is higher) (Couillard et al. 2016). Differences in stand-replacing disturbance dynamics according to the topography in the study area can therefore help explain the higher abundance of balsam fir in the steepest areas. MTSLF had a significant influence on four parameters: coarse woody debris (positive), Weibull's shape parameter (negative), cohort basal area proportion (positive) and maximum height (positive). These results illustrate the progressive accumulation of deadwood during the old-growth transition process (Sturtevant et al. 1997; Clark et al. 1998), the structural stand complexification because of the replacement of the first cohort (Oliver and Larson 1996; Wirth et al. 2009) and the linear relationship between age and black spruce height (Robichaud and Methven 1993). Moreover, slope and MTSLF influence different structural parameters although without significant interactions between them (Table 2-4). Because of the specific effects of MTSLF and slope on the diversity of old-growth structures, old-growth forests must be defined using both temporal and environmental parameters.

2.5.3 Structural dynamics of boreal old-growth forests

We created three succession models of boreal old-growth succession, distinguished by the degree of slope: gentle slopes, medium slopes and steep slopes) (Figure 2-4). As all even-aged forest types were found in the gentle slope succession model, the types of even-aged stands that would have been at the initial stages of the other models were determined by examining the transition stand characteristics and the species composition of their coarse woody debris (Appendix B). However, these stands are purely theoretical and cannot be include in our typology, their purpose is therefore to simply clarify the succession models. The medium slope succession model starts with an even-aged black spruce stand situated on medium slopes while the high slope succession model begins with an even-aged broadleaved–black spruce–balsam fir mixture situated on steep slopes. The absence of even-aged stands on the steepest sites is consistent with previous suggestions that gap dynamics begin earlier in these conditions, potentially because of their higher sensitivity to secondary disturbance (Uhlig et al. 2001; Gauthier et al. 2010). Among the transition old-growth forests, Group 5 is specific to the steep slope succession model, but Group 3 and Group 4 can be found in both gentle and medium slope succession models. These last two forest types represent moderate (Group 3) and a strong (Group 4) canopy break-up. Group 4 appears to represent a specific case found in black spruce stands, where canopy break-up starts at an older age (MTSLF >200 years) or when transition old-growth stands are affected by an abnormally strong secondary disturbance. This results in an important punctual rather than gradual mortality event that may occur due to the susceptibility of a stand dominated by old, tall and even-aged black spruce to stem breakage and windthrow (Robichaud and Methven 1993; Pothier et al. 1995).

Table 2-4 Results of the regression analysis of the environmental and the temporal and structural parameters. The models that did not fulfil the assumptions are represented by the symbol "-" in the model results. Significance is represented by the following symbols: n.s. (not significant), * (p value $\leqslant 0.05$), ** (p value $\leqslant 0.01$), *** (p value $\leqslant 0.001$). Coefficient of the independent variable is presented only when the results were significant. Parameter codes are found in Table 2-1.

Structural parameter	Model result			Coefficient of the independent variables		
	F	R^2	significance	SL	MTSLF	SL × MTSLF
TD	2.15	0.09	n.s.			
SD	3.18	0.12	*			
BA	4.36	0.16	**			
BFP	14.88	0.40	***	0.02*		
CWD	14.72	0.40	***		$4.13e^{-03}$***	
WSP	7.77	0.27	***		$-8.03e^{-04}$**	
GF	5.78	0.21	***	0.01*		
MH	13.75	0.38	***		0.02**	
CBAP	25.9	0.54	**		$3.96e^{-03}$***	
SI	-	-	-			

Once the true old-growth stage is reached, stand structures are still considered as dynamic, since diverse secondary disturbances and the effective regeneration of black spruce and balsam fir under a canopy in non-paludified contexts keep structural types changing through time (Pham et al. 2004; McCarthy and Weetman 2006; Girard et al. 2014). In contrast, the dynamics of paludified stands inhibit any transition toward another true old-growth structure as tree regeneration is suppressed in the absence of fire (Fenton et al. 2005; Fenton and Bergeron 2011).

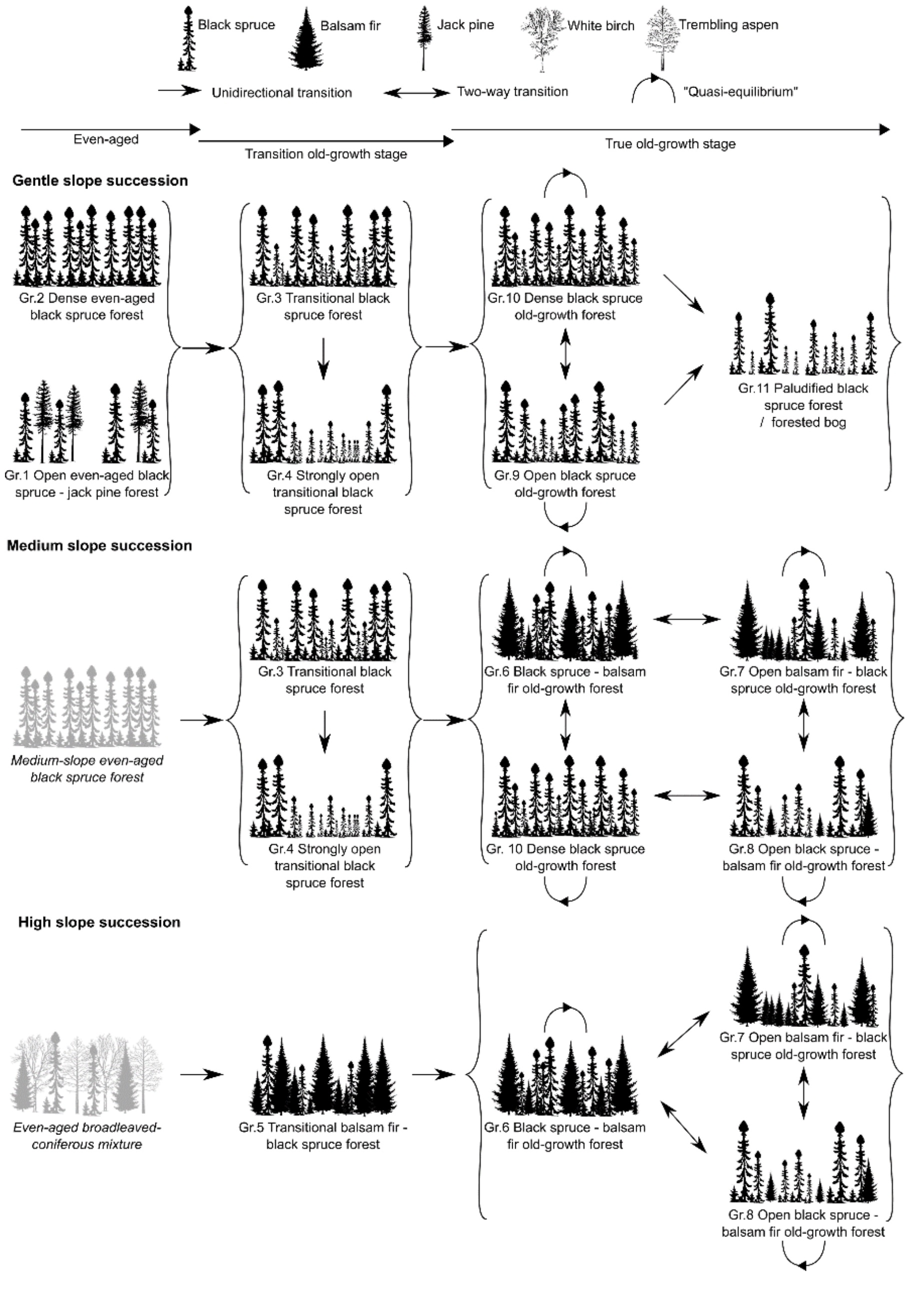

Figure 2-4 Ecological models of the successional dynamics of old-growth boreal forests in the study region. Brackets regroup old-growth forest types (Gr. = Group) passing through the same transition process. Grey stands without group identification and a name written in italic represent theoretical even-aged structures starting the medium slope and high slope succession. The five silhouettes at the top of the figure are reproduced with permission from Natural Resources Canada, Canadian Forest Service, https://tidcf.nrcan.gc.ca/en/trees, 2017.

Among our forest types, Group 11 is considered as representing forested bogs and paludified forests because of its strong depth of the organic horizon and gap fraction coupled with low basal area and maximum height values. Consequently, this is the only true old-growth structure connected to the others by a unidirectional link. All other true old-growth structures can evolve along a coarse woody debris/balsam fir proportion and basal area/gap fraction gradient or maintain a relatively homogeneous structure, depending on secondary disturbance dynamics. Slope then defines which structure can be connected to another, all of them covering two succession models except for Gr.9 and Gr.11, which are specific to gentle slope succession. Consequently, true boreal old-growth forests in Eastern Canada present a variety of structures and compositions, mainly determined by topography and secondary disturbance dynamics.

Eastern white cedar (*Thuja occidentalis* L.) and white spruce (*Picea glauca* (Moench) Voss), the two other late-successional species in Eastern Canada (Harvey et al. 2002), are almost absent in our study territory, probably because they are more related to mixedwood boreal forests than to coniferous boreal forests (e.g., Bergeron 2000). Eastern white cedar or white spruce has been sampled in two stands, one defined by the Group 6 structure and the other by the Group 7 structure. In addition, Eastern Canada is not a totally homogeneous territory, presenting particular geomorphologic properties, such as the Clay-Belt region dominated by clay soils rather than tills (Harper et al. 2003; Lecomte and Bergeron 2005; Bergeron and Harper 2009), or particular climatic conditions, such as the moist maritime climates at the eastern edge of Canada (Bouchard and Pothier 2011; Kneeshaw et al. 2011). The identified structures are consequently unlikely to represent all the structural diversity of Eastern Canadian boreal old-growth forests but represent a regional subset of the whole. At a larger scale, these structures cannot be generalized to territories defined by other climatic conditions, disturbance dynamics and species traits (Shorohova et al. 2008; Kneeshaw et al. 2011; Shorohova et al. 2011). Despite this, black spruce dominated stands or black spruce – balsam fir mixtures are the main late-successional forest formations in Eastern Canadian boreal forest (De Grandpré et al. 2000; Bouchard et al. 2008; Gauthier et al. 2010), and our work therefore provides a pertinent analysis of the boreal old-growth diversity and internal dynamics in Eastern Canada. Furthermore, our study underlines the importance in identifying the structural richness of boreal old-growth forests at a fine scale, as these complex ecosystems should not be considered as a uniform entity, even in a seemingly homogeneous landscape.

2.6 Implications for management

Different propositions have been made to better preserve old-growth forests or their structural attributes under forest management. The most common proposals involve conservation, using partial cuts, extending forest rotations or reducing harvesting rate (Bauhus et al. 2009; Ruel et al. 2013; Bouchard and Garet 2014). Our study could help researchers and managers to identify various type of old-growth in order to develop management practices adapted to old-growth forest conservation. Our results suggest that true old-growth structures exist before all the first cohort dies, and that old-growth stands can stay productive on till soils. Thus, extending forest rotations can be an efficient management solution, especially when considering that temporal continuity is an important component for old-growth forest biodiversity (Spies 2004; Schmiegelow and Monkkonen 2002; Fenton and Bergeron 2011). Partial cuts are often considered effective for conserving old-growth elements in managed stands as they can be applied with different objectives and different retention levels (Harvey et al. 2002; Bauhus et al. 2009; Kuuluvainen 2009). Their adaptability could allow the application of these treatments to maintain the main structural features of old-growth stands or to create similar structural transitions that are highlighted by our study.

When considering the structural characteristics of the forest types identified by our study, we observe strong variations in tree density, basal area and maximum height, implying important differences in wood volume and quality. One of the main limits for a broader development of alternatives to clearcutting is their economic viability (Ruel et al. 2013; Bose et al. 2014; Tahvonen and Rämö 2016), and these discrepancies in economic value may restrict their application for all the old-growth structures. An additional limit is the differences in technical applicability of alternative treatments depending on the stand characteristics. For instance, partial cuts can negatively affect stand structures, by aggravating a preexisting paludification process or causing strong windthrow mortality (Ruel et al. 2013; Bose et al. 2014). Nevertheless, the responsibility of the abundant use of clearcutting in the erosion of old-growth stands and the homogenization of the landscape has been largely admitted (Östlund et al. 1998; Boucher and Grondin 2012; Haeussler and Kneeshaw 2013). In addition, in a clearcutting dominated scenario, it is likely that the remnant old-growth stands will be those with a lesser economic value because of a priorization of short-term profitability (Haeussler and Kneeshaw 2003; Ruel et al. 2013). These two last points are contradictory with the aims of natural base-management, where remnant stands in a managed territory must be representative of the preindustrial forest (Kuuluvainen 2002; Gauthier et al. 2009). Therefore, despite the limits previously observed for clearcutting alternatives, a shift must be done in the management of boreal old-growth forests. The preservation of the structural diversity in managed territories should require a particular attention and the development of less intensive treatments adapted to stand specificities should be prioritized. By providing a structural differentiation of boreal old-growth forests in Eastern Canada, our study present reliable guidelines for a better preservation of the structural diversity of old-growth forests in managed landscapes. On a larger scale, it demonstrates that the recognition of the structural diversity and dynamic of boreal old-growth forests is a prior issue for an efficient preservation of these ecosystems.

2.7 Conclusion

Boreal old-growth forests in Eastern Canada do not represent uniform stands but rather reflect a diversity of structures and variable amounts of black spruce and balsam fir. This distribution of old-growth structures across the landscape is partially determined by temporal and environmental conditions, with slope and minimum time since the last fire as the principal determinants defining the possible structural trajectories of an aging stand. Moreover, even when the true old-growth stage is reached, old-growth boreal forests remain dynamic, as structural changes occur dictated by secondary disturbance characteristics and stand attributes. Therefore, the diversity and the dynamics of boreal old-growth forests must be integrated into forest management planning to ensure an efficient preservation of the range of structural attributes of these ecosystems in timber harvested landscapes. Among the principal parameters differentiating old-growth structures, the proportion of balsam fir and gap fraction could be identified from cartographic surveys, but further studies need to be undertaken to determine the effectiveness of such an approach. Furthermore, the transition processes between true old-growth structural types remain unknown, and complementary work should be completed to better understand the dynamics of these ecosystems.

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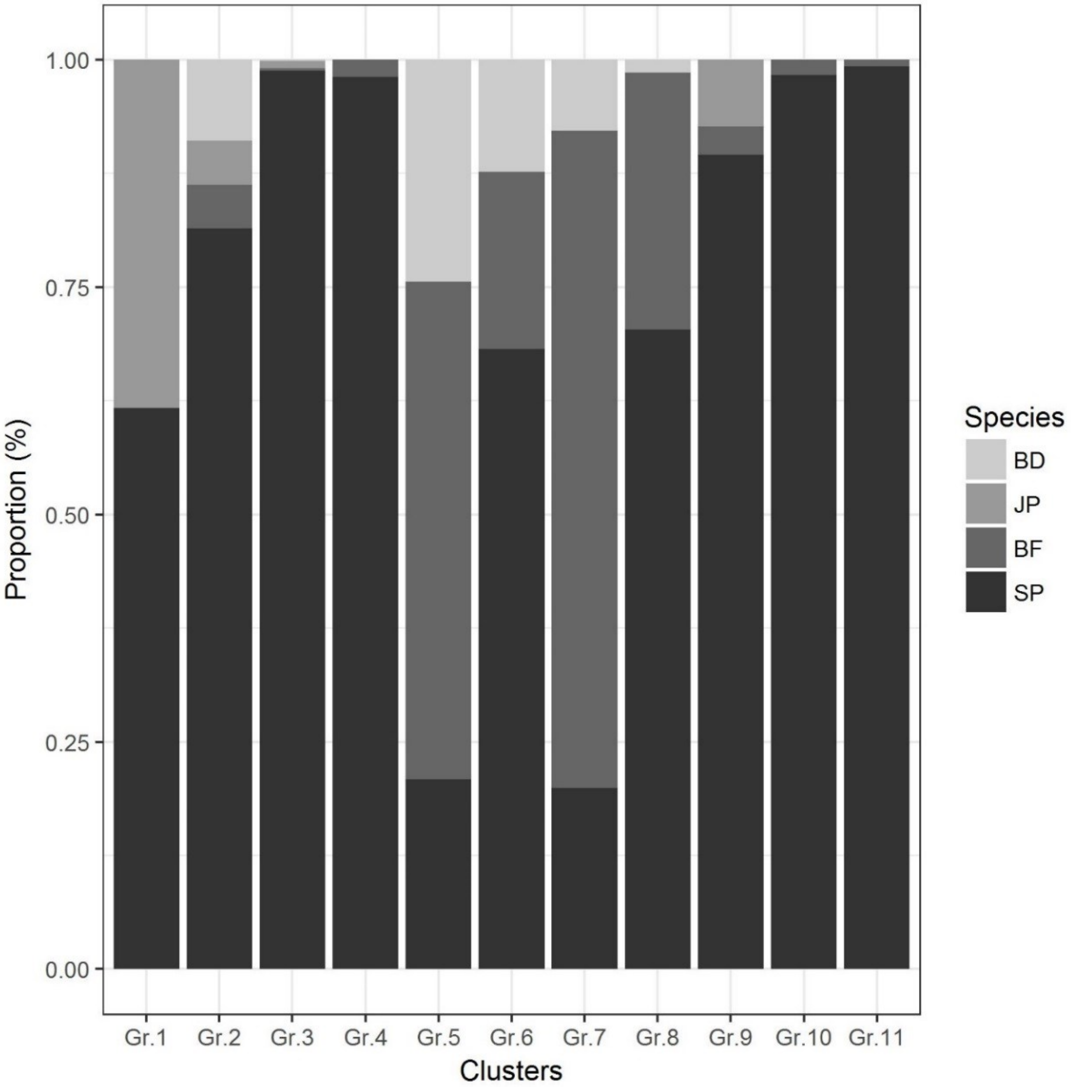
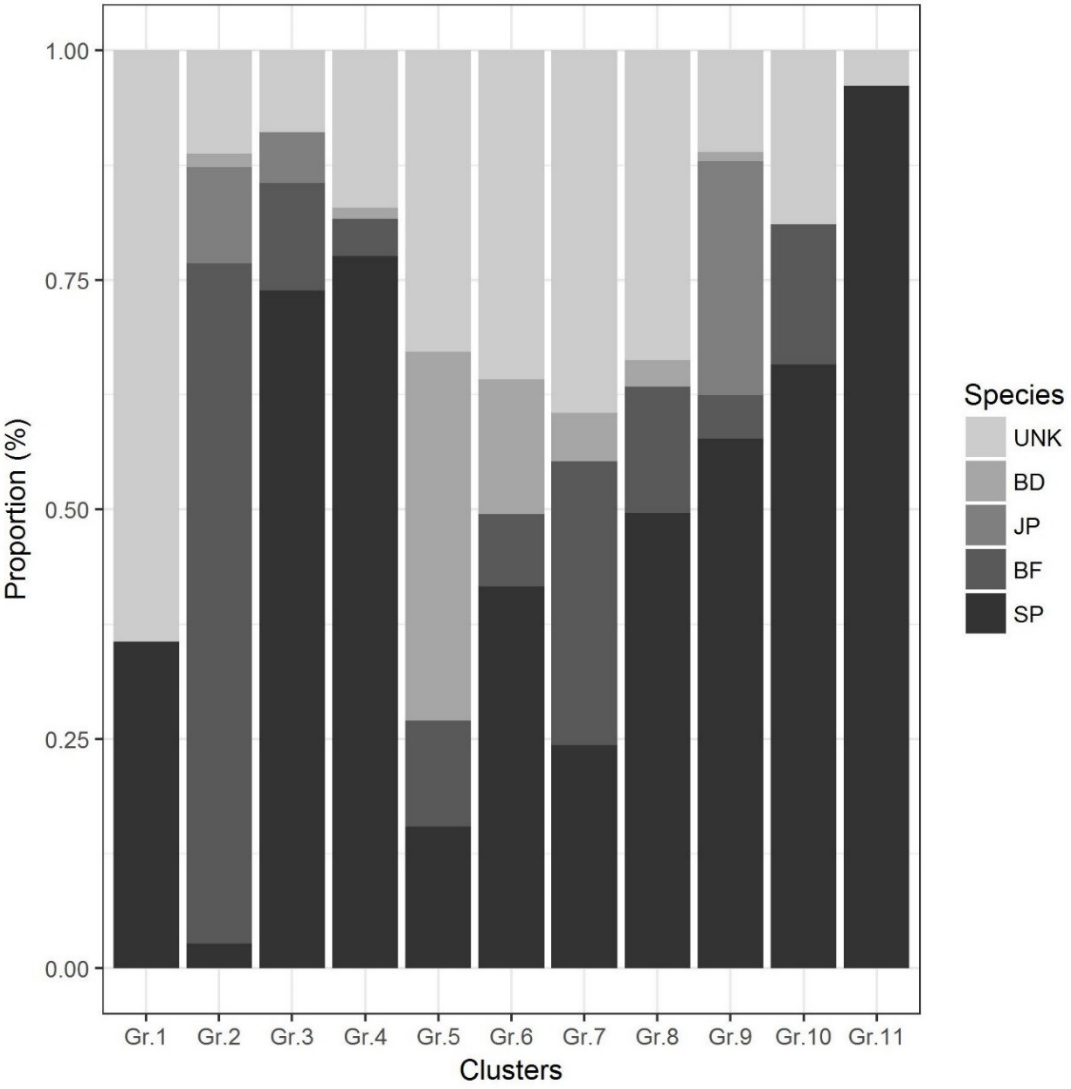
2.10 Supplementary material

Appendix A. Mean basal area proportion of the tree species for each forest type as defined by the hierarchical cluster analysis. SP = black and white spruce, BF = balsam fir, JP = jack pine and BD = broadleaved species.



Appendix B. Mean coarse woody debris volume proportion of the tree species for each forest type as defined by the hierarchical cluster analysis. SP = black and white spruce, BF = balsam fir, JP = jack pine, BD = broadleaved species and UNK = unknown species.



CHAPITRE III

SECONDARY DISTURBANCES OF LOW AND MODERATE SEVERITY DRIVE THE DYNAMICS OF EASTERN CANADIEN BOREAL OLD-GROWTH FORESTS

Accepted research paper

Title: Secondary disturbances of low and moderate severity drive the dynamics of eastern Canadian boreal old-growth forests

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Declaration of interests: none

Running head: Eastern Canadian boreal old-growth forests dynamics is driven both by low and moderate severity secondary disturbances. Each severity is defined by particular disturbance agents and temporal patterns. They have both specific influence on stand dynamics and structure, shaping therefore the diversity of boreal old-growth forests.

Keywords: Low severity, moderate severity, natural disturbance, succession, spruce budworm, windthrow

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3.1 Abstract

Context: A regular succession of low-severity disturbances are seen as determining the dynamics of the old-growth stage (gap dynamics); however, recent studies suggest that moderate-severity secondary disturbances also play an important role in the dynamics of eastern Canadian boreal forests.

Aim: This study aims to determine if eastern Canadian boreal old-growth forests are driven by a combination of low- and moderate-severity secondary disturbances.

Methods: We reconstructed the 200-year disturbance history of 20 boreal old-growth stands using dendrochronological analysis. We discriminated low- from moderate-severity disturbances based on their respective influence on mean stand growth (i.e. low-severity: no change in mean stand growth; moderate-severity: abrupt growth-release in the mean stand growth).

Results: The secondary disturbance regime of eastern Canadian boreal old-growth forests varies highly over time, reflected by disturbance peaks in the chronological record. Most peaks occurred during spruce budworm outbreaks related to both low- and moderate-severity disturbances. Between each peak, low-severity disturbances dominate. Each level of disturbance severity has specific consequences for stand dynamics.

Conclusion: Both low and moderate secondary disturbances are drivers of forest dynamics in eastern Canadian boreal old-growth stands and shape the structural diversity of these stands. The complexity of these dynamics should be recognized in management planning to ensure the efficiency of old-growth forest conservation policies.

3.2 Résumé

Contexte : On considère qu'une succession régulière de perturbations de faible sévérité détermine la dynamique des vieilles forêts (dynamique des trouées) ; cependant, des études récentes suggèrent que les perturbations secondaires de sévérité modérée jouent également un rôle important dans la dynamique des forêts boréales de l'Est du Canada.

Objectif : Cette étude vise à déterminer si les vieilles forêts boréales de l'Est du Canada sont dynamisées par une combinaison de perturbations secondaires de sévérités faibles et modérées.

Méthodes : Nous avons reconstitué l'historique de perturbation sur les 200 dernières années de 20 vieilles forêts boréales à l'aide d'analyses dendrochronologiques. Nous avons fait la distinction entre les perturbations sévérité faible et celles de sévérité modérée en fonction de leur influence respective sur la croissance moyenne des peuplements (c.-à-d. faible sévérité : aucun changement de la croissance moyenne des peuplements ; sévérité modérée : reprise de croissance abrupte de la croissance moyenne).

Résultats : Le régime de perturbations secondaires des vieilles forêts boréales de l'Est du Canada varie considérablement au fil du temps, comme en témoignent les pics de perturbations observés dans les données dendrochronologiques. La plupart des pics se sont produits pendant les épidémies de tordeuse des bourgeons de l'épinette, résultant aussi bien des perturbations de sévérités faibles ou modérées. Entre chaque pic, les perturbations de faible sévérité dominent. Chaque classe de sévérité a des conséquences spécifiques sur la dynamique du peuplement.

Conclusion : Les perturbations secondaires de sévérités faibles et modérées sont les moteurs de la dynamique forestière dans les vieilles forêts boréales de l'Est du Canada et façonnent la diversité structurelle de ces peuplements. La complexité de cette dynamique devrait être reconnue dans la planification de l'aménagement pour assurer l'efficacité des politiques de conservation des vieilles forêts.

3.3 Introduction

Recognition of the prominence of boreal old-growth stands, here defined as stands driven by secondary disturbances, represented a major paradigm shift in boreal forest ecology (Kneeshaw and Gauthier 2003; Kuuluvainen 2009). Prior to this shift, the assumptions held that old-growth forests were almost absent in boreal landscapes because of relatively frequent forest fires; and that some boreal forest stands did not remain stable in an old-growth phase, but they rather became open peatlands in the absence of fire (Bergeron and Harper 2009; Wirth and Lichstein 2009). Nonetheless, old-growth forests are abundant in the boreal landscape, even in territories where the fire cycle is relatively short; this pattern reflects the random distribution of fires across all age classes (Bergeron et al. 2001). In addition, the distinctive structural attributes and ecological continuity of old-growth stands imply the presence of specific habitats that are absent from younger stands (Drapeau et al. 2002; Drapeau et al. 2003; Fenton and Bergeron 2008; Boudreault et al. 2018). For these reasons, boreal old-growth forests are now recognized as key components of boreal landscapes.

Since the mid-20th century, intensive industrial forest harvesting has expanded markedly across the boreal landscape. In territories that are characterized by severe crown fires, such as the boreal forests in Eastern Canada, the harvested surface area can approximate 75% of the burned surface area during the same period (Bouchard and Pothier 2011; Boucher et al. 2017). Furthermore, in landscapes driven by low-severity surface fires and where fire mitigation is very efficient, logging has almost become the only type of severe-intensity disturbance (Östlund et al. 1997). Clearcutting systems are by far the most common harvesting method in the boreal forest biome. This approach is most profitable for forest companies, and the effects of clearcutting are assumed to be equivalent to those from fire (Bergeron et al. 2001). However, fire burns trees of all age classes, while logging primarily affects mature and old forests, thereby rejuvenating the landscape (Östlund et al. 1997; Fall et al. 2004; Bergeron et al. 2006). In addition, the short-term rotation of clearcutting systems accelerates this rejuvenation by inhibiting the establishment of new mature or old stands (Bergeron et al. 2002; Kuuluvainen 2009). The result is a markedly diminished abundance of boreal old-growth forests in managed territories over the last century. The consequential environmental effects include a decline of floral, faunal, and fungal forest species associated with abundant dead wood of diverse decay stages (Siitonen 2001).

Alternative management models have emerged over the two last decades to counter the loss of old-growth stands in managed landscapes. These new approaches copy the natural disturbance regimes of the different managed regions (Bergeron and Harvey 1997; Harvey et al. 2002; Kuuluvainen 2002; Grandpré et al. 2009) or imitate stand-scale natural processes (Vanha-Majamaa et al. 2007; Kuuluvainen 2009). The efficacy of these models, however, depends of an accurate understanding of disturbance regimes in a given area; however, each boreal region differs in terms of climatic factors, disturbance dynamics, and species' traits (Kneeshaw et al. 2011; Shorohova et al. 2011). As such, local-scale studies are necessary to assess whether a particular management strategy is or can be adapted to the local characteristics of a landscape.

The main drivers of secondary disturbance in eastern Canadian boreal forests are spruce budworm (SBW - Choristoneura fumiferana (Clem.)) outbreaks and windthrow events (Bouchard et al. 2006; Kerharo 2013; De Grandpré et al. 2018). Other disturbances that drive mortality in these forests include jack pine budworm (Choristoneura pinus pinus) and forest tent caterpillar (Malacosoma disstria) (Jan and Volney 1988; Bergeron and Charron 1994). However, as the main boreal hosts of these two defoliating insects are pioneer species (Nealis and Lomic 1994; Cooke and Lorenzetti 2006), their influence on old-growth dynamics are negligible.

The disturbance regimes of Fennoscandian boreal forests are relatively well understood and involve a mix of low-, moderate-, and high-severity disturbances, i.e. disturbances causing a mortality gradient ranging from low (one tree or a few affected trees) to high (stand-replacing) (Kuuluvainen and Aakala 2011; Hart 2018). In contrast, the perception of dynamics within eastern Canadian boreal forests remains relatively simplistic, dividing the disturbance regime into low-severity secondary disturbances and high-severity stand-replacing disturbances (Bergeron and Harper 2009; Shorohova et al. 2011). Nonetheless, previous studies have highlighted that secondary disturbance dynamics in regional boreal old-growth forests vary in their severity, nature, and spatial distribution (Kneeshaw and Bergeron 1998; Pham et al. 2004; Aakala et al. 2007). It is likely that disturbances of moderate severity play an important role in the overall landscape disturbance regime, in particular because of the dynamics of the SBW (Kneeshaw et al. 2009; Shorohova et al. 2011).

Similarly, the structural diversity of eastern Canadian boreal forests suggests that these ecosystems are driven by both low- and moderate-severity disturbances (Martin et al. 2018). However, the transition toward an old-growth stage is a progressive process where late-successional species replace progressively the cohort that appeared following the last stand-replacing disturbance (Harper et al. 2005; Lecomte et al. 2006; Gauthier et al. 2010). It supposes that disturbances of moderate severity gain progressively in importance at the later stages of the old-growth succession process. Furthermore, differences in the severity of secondary disturbances also imply differences in the post-disturbance regeneration dynamics (Kneeshaw and Bergeron 1998; Montoro Girona et al. 2018). It is therefore likely that the secondary disturbance regime of eastern Canadian boreal forests is more complex than is currently portrayed.

Our study aims to determine if the secondary disturbance regime of eastern Canadian boreal stands is driven by various types of secondary disturbance. We hypothesized that (1) low- and moderate-severity disturbances present different temporal patterns and that (2) moderate-severity disturbances are more abundant in old-growth stands and favour different components of the regeneration layer. The innovative nature of our research lies in using dendrochronological data for analysing disturbances of low and moderate severity over the two last centuries in forests at different stages of the old-growth succession. Thus, our study is not restricted to the effects of the most recent secondary disturbances, but we will observe their long-term patterns of secondary disturbance and their influence on old-growth stand dynamics. Consequently, our research contributes to the increasing body of literature discussing the complexity of secondary disturbance regimes in boreal landscapes by reconstructing the disturbance history of a part of eastern Canadian boreal old-growth forests.

3.4 Methods

3.4.1 Study territory

The study was conducted in a 2200 km2 area of public lands, located south-east of Lake Mistassini, Quebec (72° 52′ 36″ W, 50° 18′ 50″ N) (Figure 3-1). This area lies within the black spruce (*Picea mariana* (Mill.)) ‑ feather moss bioclimatic domain, the dominant boreal forest domain in Eastern Canada. Regional topography is characterized by gentle hills having an altitude ranging from 350 to 750 m asl. Thick glacial till dominates the surficial deposits, and sand deposits or vast bogs often surround waterways. Mean annual temperature ranges from -2.5 to 0.0 °C, annual rainfall (rain and snow) is 900–1100 mm, and the growing season lasts 140–150 days (Robitaille and Saucier 1998). Black spruce and balsam fir (*Abies balsamea* (L.) Mill.)

are the dominant tree species. We selected this study area as it encompasses the environmental diversity of the black spruce–feather moss bioclimatic domain, from poorly drained valley bottoms situated on organic deposits to well-drained till slopes. We also selected this area as timber exploitation began in 1991, initially at low levels until 2000 when harvest levels increased. Consequently, old-growth stands remain abundant and relatively accessible.

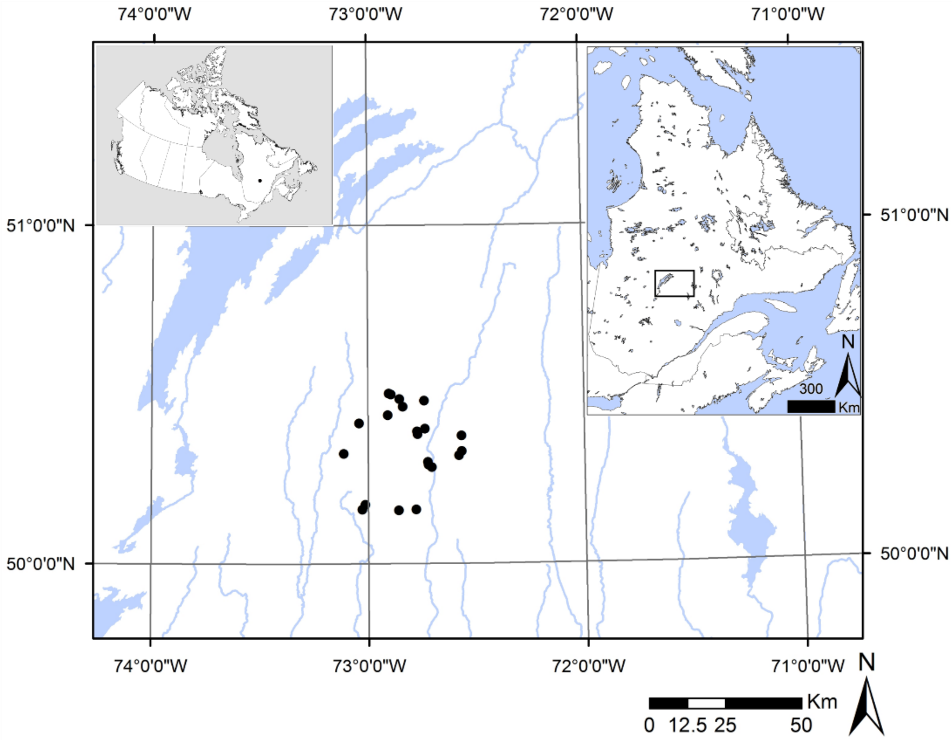


Figure 3-1 Map of the study area. Black dots represent the sample sites, blue lines and polygons represent rivers and standing waterbodies, respectively. The inset maps indicate the position of the study area map in Canada (left) and in the province of Quebec (right).

3.4.2 Sampling

Based on the nomenclature of the Quebec Ministry of Forests, Wildlife, and Parks (MFWP), the study area is divided into 19 environmental forest types. Six of these, however, cover 72% of the forest area. Given the environmental diversity of the study area, we focused our sampling within these six environmental forest types. Moreover, to encompass the complete old-growth successional sequence, we aimed to have an equal representation of sites belonging to mature, transition old-growth, and true old-growth phases. According to the literature for this ecosystem type (Uhlig et al. 2001; Bergeron and Harper 2009; Gauthier et al. 2010), the likely age classes associated with each phase are 80–100 years for even-aged mature stands, 100–200 years for transition old-growth, and >200 years for true old-growth.

We estimated the minimum age of 42 sites in a preliminary survey by sampling two cores at the base of five dominant and codominant trees at each site. Then, we performed a stratified random sampling to sample sites from each environmental type and age class. Twenty-one (21) sites were sampled during the summer and autumn of 2014 and 2015. We inventoried at least one site per environmental type and age class, except for the "Black spruce–feather moss on low slope, till deposit, and subhydric drainage" type, as we did not find a site within the 100–200 year age class (Appendix A).

We sampled coniferous basal discs in the same 20 × 20 m plots sampled by Martin et al. (2018), with the goal of obtaining 30 living and dead stems having a diameter at breast height (dbh) ⩾9 cm (merchantable stems). We kept discs that showed stem decay if the rot was partial and the analysis of most of the tree rings remained possible. When it was impossible to sample a minimum of 30 stems per site, we sampled trees near the plot edge or saplings within the plot, depending on the site characteristics.

Discs were air-dried and mechanically sanded for tree-ring measurements. Then, we measured tree rings along two radii to the nearest 0.01 mm. These ring-width series were corrected by a combination of visual cross-dating and the use of the COFECHA computer program (Holmes 1983). We rejected accurately dated series having a poor statistical fit with the average curve of the disc due to growth anomalies. Similarly, we removed a disc from the final dataset when one of the two series measured on the basal disc correlated poorly with the mean stand chronology. We obtained 1550 accurately dated dendrochronological series, belonging to 775 trees.

3.4.3 Data preparation

We determined the diameter distribution of merchantable stems (dbh >9 cm) and saplings (height ⩾1.3 m and a dbh <9 cm) in each plot following Martin et al. (2018) and using Weibull's equation (Bailey and Dell 1973). A Weibull's shape parameter (WSP) ⩾1.5 indicates a normal diameter distribution, and a WSP <1.5 indicates an irregular diameter distribution. We also calculated the cohort basal area proportion (CBAP) for each site using the formula of Kneeshaw and Gauthier (2003):

$$CBAP = \frac{(BA_{N+1\ trees} + 0.1)}{(BA_{N+1\ trees} + BA_{First\ cohort\ trees} + 0.1)}$$

where BA is the basal area. We identified first cohort trees, N+1 trees, and the old-growth stage of each plot following Martin et al. (2018). Stands were defined as even-aged if WSP ⩾1.5 and CBAP <0.3, true old-growth when WSP <1.5 and CBAP >0.6, and transition old-growth for all other conditions. We selected this methodology due to the increasing acknowledgement of the complexity of forest succession, including that of boreal forests (Cumming et al. 2000; McCarthy and Weetman 2006; Smirnova et al. 2008). Therefore, combining the CBAP and the WSP improves the discrimination of the different stages of old-growth succession while recognizing both the intrinsic progressive nature of the transition toward the old-growth stage and alternative successional pathways. Among the 21 sites sampled, 1 was identified as even-aged, 10 as transition old-growth, and 10 as true old-growth (Appendix B). We therefore removed the even-aged site from further analysis. In addition, the number of trees sampled was almost equivalent between the two old-growth stages for CE 1800–2000 period; however, the number was very low for both old-growth stages prior to CE 1800. For this reason, analyses focused on the CE 1800–2000 period (Appendix C).

Abrupt and persistent growth changes (%GC) are an effective proxy for indicating the occurrence of a secondary disturbance and thus override short- and long-term growth patterns associated with climate (Nowacki and Abrams 1997; Fraver and White 2005). We identified these growth changes by comparing sequential 10-yr ring widths via the formula of Nowacki and Abrams (1997):

$$\%GC = \{(M_2 - M_1)/M_1\} \times 100$$

where M1 is the mean ring width for the first 10-year period, and M2 is the mean ring width for the subsequent 10-year period. We classified growth changes by intensity based on the classes defined by Nowacki and Abrams (1997): major (%GC ≥50%) and minor (%GC = 25%–50%). These thresholds are well adapted to boreal forests, where tree growth is generally low (Tremblay et al. 2011). We calculated %GC for each tree, using the mean value of the two raw ring-width series measured for each tree (tree chronology), and for each species per stand, using the mean value of all raw ring-width series measured for each species in the plot (mean plot chronology). We chose to separate tree species due to the different dynamics and strategies vis-à-vis disturbances for black spruce and balsam fir. Relative to black spruce, balsam fir is more sensitive to SBW outbreaks, windthrow events, and root rot (Basham 1991; Ruel 2000; Morin et al. 2009); however, balsam fir regeneration is more competitive than that of black spruce when a canopy opening occurs following a disturbance (Doucet and Boily 1995; Messier et al. 1999). As a result, the abundance of balsam fir in an eastern Canadian old-growth stand may vary markedly over time (Pham et al. 2004; De Grandpré et al. 2009). Therefore, merging the results of both species in mixed stands could have biased the results. We determined growth releases from mean plot chronologies only when ≥ 10 trees constituted the chronology to ensure that the chronologies were representative of the stand’s dynamics.

Discriminating low- from moderate-severity disturbances is challenging, as the threshold between the levels of low and moderate is often unclear (Hart and Kleinman 2018). The most common solution is to use size thresholds, either defined arbitrarily or related to stand characteristics (McCarthy 2001; Reyes and Kneeshaw 2008; Hart and Kleinman 2018). However, such methods cannot be used with dendrochronological data, as information related to the disturbances themselves is generally missing. Yet, tree growth releases are reliable indicators of disturbance dynamics and thus for canopy and tree population turnover (Nowacki and Abrams 1997; Szewczyk et al. 2011; Khakimulina et al. 2016); this makes them a relevant proxy for the disturbance regime. To determine the severity of a secondary disturbance, we considered that a low-severity disturbance would induce individual tree growth release but would not influence mean plot growth, i.e., no growth release in the mean plot chronology, as only a small fraction of the trees is disturbed. This scenario implies few changes in the stand canopy and age structure. In contrast, a disturbance of moderate severity will disturb a larger proportion of trees, leading to important changes in stand structure. In turn, this provokes a greater number of growth releases that will influence mean plot growth. As such, we defined low-severity disturbances as disturbances lacking a significant influence on post-disturbance stand growth because of low overstorey mortality. Moderate-severity disturbances are disturbances that significantly and positively influence post-disturbance stand growth because of moderate overstorey mortality.

To link the two scales (tree and plot) and determine if each release observed between CE 1800 and 2000 on an individual tree was part of a secondary disturbance of low or moderate severity, we compared the occurrence of tree growth releases to releases of the corresponding stand and species. We used stand growth release—identified on the mean plot chronologies—to define windows within which individual tree growth release could be considered as resulting from a moderate-severity disturbance. For a given stand, all individual tree growth releases that occurred in the nine years before or the nine years after an observed stand growth release were classified as moderate-severity secondary disturbance releases, i.e., the individual tree releases contributed to growth release at the plot scale. If not, they were classified as low-severity secondary disturbance releases, i.e., the individual tree releases did not contribute to any growth change at the plot scale. We selected a nine-year threshold as Nowacki and Abrams (1997) applied a ten-year window to identify growth releases. Hence, all individual tree growth releases that occurred nine years before or after a stand growth release may have contributed to this release. As such, our methodology accounts for potential lags that can be observed between disturbance and growth releases, as well as lags between disturbance and tree mortality (Worrall et al. 2005; De Grandpré et al. 2018). To distinguish between strong juvenile growth after a stand-replacing disturbance and growth release due to low- or moderate-severity secondary disturbance, we only considered growth releases that occurred 40 years after the minimal year of stand establishment. This 40-year threshold corresponds to the end of the marked juvenile post-fire recruitment period in even-aged stands (Rossi et al. 2009) as well as the beginning of gap dynamics under particular conditions (Cumming et al. 2000). Finally, we only retained growth releases for each site and year when the number of trees sampled was ≥10, i.e., we did not determine stand growth release when this condition was not fulfilled.

3.4.4 Statistical analysis

To test our first hypothesis—that low- and moderate-severity secondary disturbances differ in their temporal patterns—we identified for each site and each year the percentage of trees being in a state of growth release and the severity of the secondary disturbance (low or moderate). This method provides an improved description of the stand dynamics to using only the absolute number of trees. Tree and sapling density in eastern Canadian old-growth boreal forests may vary markedly between stands, independent of old-growth stage (Martin et al. 2018). In contrast, the frequency of trees in growth release puts into perspective results extracted from the dendrochronological series at the stand scale, and it is therefore a more suitable descriptor. We then applied a locally weighted regression scatterplot (loess) smoothing with a 10% span (Trexler and Travis 1993) for various classes of secondary disturbance severity—low and moderate severity combined, low severity only, and moderate severity only—to observe the presence of release peaks and their co-occurrence between stands. By smoothing the annually observed growth releases for all stands, we expect that this methodology will neutralize potential lags in growth releases that can be observed from one stand to another following a single disturbance event. In addition, we compared the occurrence of these peaks with the chronologies of Morin and Laprise (1990) and Krause (1997), who identified the SBW outbreaks over the last three centuries at sites near our study area. We considered that the occurrence of a release peak during a SBW outbreak period implied that this insect was the main disturbance agent explaining this peak.

For testing our second hypothesis—that low- and moderate-severity secondary disturbances have different effects on the subsequent stand dynamics—we first used logistic regression to compare stand, tree, and release characteristics related to each identified tree growth release for the transition and true old-growth stands. Secondary disturbance severity (low/moderate) was the binary dependent variable, and the following parameters were the independent variables: release intensity (minor/major), old-growth stage (transition/true old-growth), species, and diameter class at release. We applied a likelihood ratio test and residual equidispersion to assess model validity. In addition, we checked model predictive ability using the area under the receiver operating characteristic curve (AUC) method (Zweig and Campbell 1993) and Tjur's coefficient of discrimination (COD; Tjur (2009)). An AUC value >0.7 and a COD >0.2 represents an excellent predictive ability. In addition, we determined for each disturbance severity the mean percentage of trees presenting growth releases per decade and per site to observe the variation in disturbance history and severity between the study sites. We compared these values by combining old-growth stage and release type using a Kruskall-Wallis test followed by a pairwise Wilcoxon test.

We used R-software, version 3.3.1 (R Core Team 2016) for all statistical analyses, running the *ROCR* (Sing et al. 2005), *DescTools* (Signorell 2017), and *ggplot2* (Wickham 2016) packages. We selected a threshold of $p < 0.05$ to establish significance.

3.5 Results

3.5.1 Temporal pattern of low- and moderate- severity secondary disturbances

Considering low- and moderate-severity disturbances together during the CE 1800–2000 period, the proportion of trees having growth releases in the studied stands varies greatly from year to year; nonetheless, eight peaks emerge (Figure 3-2). Six of these peaks occurred during SBW epidemics. In addition, there is no period where tree growth releases are absent, except in the oldest portion of the chronology; therefore, secondary disturbances of variable severity represent a continuous element in the studied old-growth stands over the two last centuries.

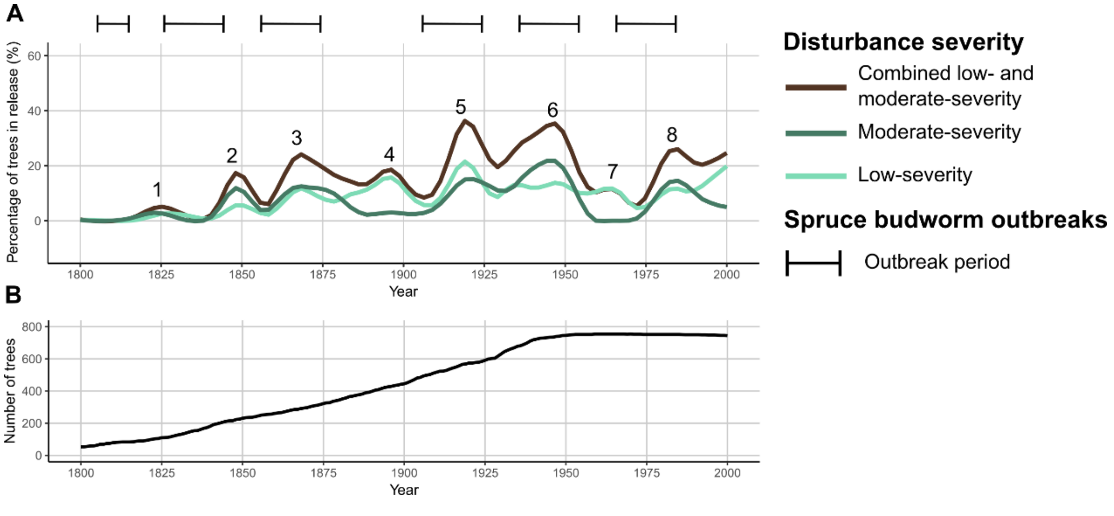


Figure 3-2 (A) Loess smoothing of the percentage of trees having growth release events per decade grouped by secondary disturbance severity: combined low and moderate severity (brown curve), moderate severity (dark green curve), and low severity (light green curve). Numbers identify the eight peaks, and hooks indicate spruce budworm outbreaks. Spruce budworm outbreaks are based on Morin and Laprise (1990) and Krause (1997). (B) Number of trees that make up the developed tree-ring chronology for the period CE 1800–2000.

Relative to the moderate-severity disturbances, the frequency of tree growth releases linked to low-severity disturbances vary much less from year to year. Nevertheless, we still observe the eight previously identified peaks, although they tend to be less pronounced. In contrast, the percentage of trees having growth release related to disturbances of moderate severity varies widely over time; this relative abundance alternates between periods where this proportion is equal or greater to the proportion of trees with growth release resulting from low-severity disturbance and periods where the proportion is near zero.

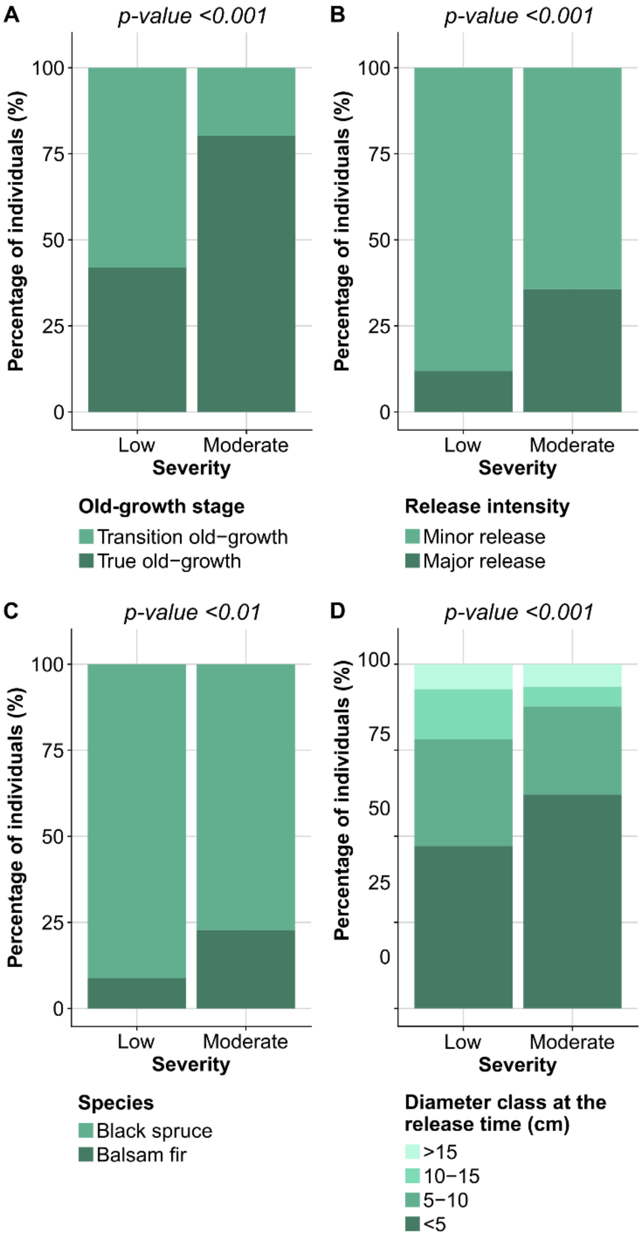
The relative contribution of secondary disturbances of low and moderate severity to the disturbance peaks varies between peaks. Moderate-severity disturbances contributed to six of the eight identified peaks (peaks 1, 2, 3, 5, 6, 8); five occur during SBW outbreaks. The contribution from moderate-severity disturbances is generally equal to that of low-severity disturbances, except for peaks 2 and 6, where moderate-severity disturbances contribute much more. In contrast, peaks 4 and 7 are due solely to low-severity disturbances and occur outside periods of SBW outbreaks. Therefore, both low- and moderate-severity disturbances drive the secondary disturbance regime of boreal old-growth forests; however, given as they often overlap, the implication is that both can result from the same disturbance agents.

3.5.2 Dynamics of old-growth stages

Table 3-1 Results of the logistic regression model comparing the characteristics of the growth releases according to the disturbance severity. AIC: Akaike information criterion; AUC: area under the receiver operating characteristics curve; COD: Tjur’s coefficient of discrimination.

Resid. Df	**Resid. Dev.**	**Df**	**Deviance**	**Pr(>Chi)**	**AIC**	**AUC**	**COD**	**Parameter**	**Df**	**Deviance**	**Resid. Df**	**Resid. Dev.**	**Pr(>Chisq)**
1612	2110.6	-6	-340.69	<0.001	1783.9	0.76	0.2	Old-growth stage	1	233.232	1611	1877.3	<0.001
								Release intensity	1	69.162	1609	1797.5	<0.001
								Diameter class at the release	3	27.627	1606	1769.9	<0.001
								Species	1	10.666	1610	1866.7	<0.01

The four parameters analysed via logistic regression—old-growth stage, release intensity, tree species, and diameter class at release—differed significantly between the levels of disturbance severity (Table 3-1). The logistic regression model presents an excellent predictive value, as evidenced by the significant log-likelihood test ($p < 0.001$), the strong AUC value (0.76), and the high COD (0.2).



of the

Figure 3-3 Class distribution and *p*-values of the four parameters analysed in the logistic regression as a function of the severity of secondary disturbance (low or moderate); (A) old-growth stage, (B) release intensity, (C) species, and (D) diameter class at release. The *p*-values above each bar represent the significance of the specific parameter based on the logistic regression model (see Table 2).

For both levels of disturbance severity, trees that show growth releases are mainly small (tree diameter at the moment of release <10 cm) (Figure 3-3). Despite their small size, most trees having a diameter at release of <10 cm are old (>50 years, Appendix D). Thus, most observed releases are due to suppressed trees that benefit from an opening of the canopy. Yet, these trees were generally smaller and younger in moderate-severity disturbances than in low-severity disturbances. Furthermore, the frequency of release observed for balsam fir is higher in moderate than in low-severity disturbances, even if black spruce is the dominant species for both disturbance severity. Similarly, the frequency of major growth release is higher in moderate than in low-severity disturbances; however, minor releases are the dominant release type for both types of disturbance. Therefore, the characteristics of the gap fillers differ depending on disturbance severity. The distribution of growth releases resulting from low- and moderate-severity disturbances also varies between the different old-growth stages.

The mean decadal percentage of trees having growth releases due to low-severity disturbances did not differ between old-growth stages, but there were fewer trees showing a growth release from moderate-severity disturbances in the transition old-growth than in true old-growth (Figure 3-4). Interestingly, in true old-growth, the mean decadal percentage of trees having low-severity disturbance–induced growth release was similar to that of trees having moderate severity disturbance–induced growth release. Therefore, the dynamics due to disturbances low severity are similar between the transition and true old-growth forests. Furthermore, stand dynamics related to disturbances of moderate severity are at a similar level to that of low-severity disturbances in true old-growth forests. Consequently, the balance between low- and moderate-severity disturbances changed with the disappearance of the first cohort.

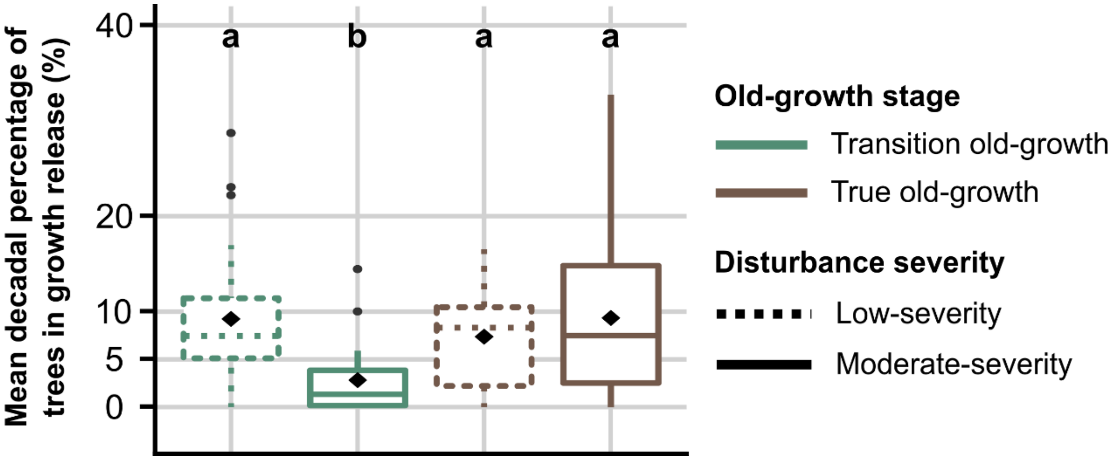


Figure 3-4 Box plot of the stand mean decadal percentage of trees experiencing growth release based on old-growth stage and disturbance severity. Diamonds represent mean values and letters identify significant differences.

3.6 Discussion

In Eastern Canada, both low- and moderate-severity secondary disturbances drive the dynamics within boreal old-growth forests; however, the disturbances occur in both analogous and non-analogous temporal patterns. Secondary disturbances occur continuously across the landscape. Their severity, however, is not constant over time; severity increased during eight distinct peaks over the last 200 years. Six of these eight peaks coincided with SBW outbreaks. Low- and moderate-severity disturbances also influence gap-filler characteristics, e.g., species and age, and vary between the different old-growth stages.

3.6.1 Mixed severity secondary disturbances drive the dynamics of boreal old-growth forests

We found that in addition to low-severity disturbances, moderate-severity disturbances are a distinct component of boreal old-growth forests dynamics in Eastern Canada, as hypothesized by Shorohova et al. (2011) and Martin et al. (2018). Our results add to the literature highlighting the dynamism of boreal old-growth forests in this region (Kneeshaw and Bergeron 1998; Pham et al. 2004; Aakala et al. 2007) and underline that boreal old-growth forests are not declining ecosystems but rather remain productive and dynamic over centuries in the absence of stand-replacing disturbance (Garet et al. 2009; Pollock and Payette 2010; Ward et al. 2014). This dynamism is driven by recurrent mortality events. Our study therefore underlines the long-term resistance and resilience of these ecosystems (*sensu.* Perry and Amaranthus (1997) given that most of the studied stands experienced secondary disturbances of varying severity over the past two centuries. The percentage of trees that experienced growth release was, however, lower in the 19th century relative to the 20th century. Black spruce and balsam fir longevity is relatively low (often <200 years), and slow-growing trees tend to live longer than fast-growing ones (Laberge et al. 2000; Larson 2001). It is therefore likely that only a small fraction of the trees that benefited from 19th-century disturbances survived until the present. Nevertheless, the release patterns for both disturbance types were similar throughout both centuries. This similarity implies that the studied stands were driven by comparable disturbance dynamics during the CE 1800–2000 period, although these dynamics were less obvious in the 19th century.

Moderate-severity disturbances occurred mainly during previously identified SBW outbreaks in the southern portion of the region (Morin and Laprise 1990; Krause 1997). In the eastern Canadian boreal forest, SBW is the main agent of large secondary disturbance (Morin et al. 2009; Shorohova et al. 2011). Previous studies have demonstrated the importance of SBW outbreaks for the dynamics of boreal old-growth forests situated in the main SBW distribution range (Kneeshaw and Bergeron 1998; Pham et al. 2004; Aakala et al. 2007). However, our study sites are currently at the northern edge of SBW distribution; thus, SBW outbreaks should have a limited influence on the disturbance regime of our study stands (Gray 2008). Recent reconstructions of the spatial patterns of SBW outbreaks in Quebec over the 20th century (Navarro et al. 2018) also indicate that our study stands lie outside of SBW hotspots. Nonetheless, we observed a strong influence of this disturbance agent over the two last centuries within our study area; this observation highlights the importance of SBW in landscape dynamics, even at the northern limit of its normal range. SBW outbreaks are cyclical events having a 30-year periodicity (Morin et al. 2009). Moderate-severity disturbances from SBW outbreaks follow the same temporal cycle. Furthermore, mortality caused by SBW is highly variable between stands during an outbreak; the effects vary from a moderate thinning of suppressed trees to a significant mortality of canopy trees (Lesieur et al. 2002; Kneeshaw et al. 2009; Morin et al. 2009). 2009). Similarly, the identified SBW outbreak peaks in our study provoked disturbances of both low and moderate severity, indicating differences in mortality between stands during a single outbreak. This complex pattern of disturbance may also be explained by our study stands being at the northern range of SBW distribution, thereby resulting in SBW-related damage to be more limited relative to areas further south (Bergeron et al. 1995; MacLean and Andersen 2008; Kneeshaw et al. 2009). Thus, SBW is an important driver of the secondary disturbance regime in our study area; its influence is cyclical and varies in severity between stands and during a SBW outbreak.

Secondary disturbances of low severity occurred almost continuously throughout our 200-year chronology. This pattern contrasts with that of secondary disturbances of moderate severity that occurred more sporadically. This continuous low-severity disturbance implies a background mortality throughout the study area. The causes of this background mortality include windthrow, fungal rot and tree senescence, but these events occur more randomly and cause a lower degree of mortality at the landscape scale than do SBW outbreaks (Kerharo 2013; Waldron et al. 2013; Girard et al. 2014). However, two of the eight identified peaks occurred outside SBW outbreaks and were dominated by low-severity disturbances. It is possible that these two peaks resulted from particular climatic events that caused simultaneous low-severity windthrow events across the landscape. In eastern Canadian boreal forests, the secondary disturbance regime is a complex process that comprises a constant background mortality punctuated by moderate-severity disturbances.

3.6.2 Influence of the mixed severity secondary disturbance regime on forest structure and succession

We observed moderate-severity disturbances mainly in true old-growth stands, and these disturbances favoured smaller trees in the regeneration layer. The difference in disturbance severity between the transition (low severity) and the true old-growth stages (moderate severity) may be partially due to the divergence in the structural attributes of old-growth stands. Older and taller black spruce and balsam fir are more prone to windthrow than younger and smaller trees (Viereck and Johnson 1990; Robichaud and Methven 1993; Girard et al. 2014). Similarly, balsam fir is very sensitive to SBW-induced defoliation, thereby resulting in important peaks of balsam fir mortality (Kneeshaw et al. 2009; Morin et al. 2009; Garet et al. 2012). In contrast, SBW outbreak–induced mortality is generally low for black spruce (Lesieur et al. 2002; Garet et al. 2012). As such, the abundance of balsam fir often fluctuates within old-growth stands (Pham et al. 2004; Grandpré et al. 2009). However, old-growth stands are characterized by a greater abundance of balsam fir and taller and older individual trees (Martin et al. 2018); these characteristics render them potentially more sensitive to secondary disturbances than younger stands.

The characteristics of the trees that fill the canopy openings differ based on the severity of the secondary disturbance. For both low- and moderate-severity disturbances, growth release intensity is generally minor; this pattern confirms that what we identified as disturbances of moderate severity are real and not artefacts created by a small number of major releases. Rather, the large and abrupt canopy openings favoured the growth of a significant fraction of the understorey. In contrast, low-severity secondary disturbances likely created only small canopy openings, favouring the growth of a small number of understorey trees. In a context of a limited opening of the canopy, i.e., low-severity disturbance, the older and taller trees in the regeneration layer are more competitive than the smallest and youngest trees. In contrast, as moderate-severity disturbances affect a greater proportion of the canopy, even the smaller trees in the regeneration layer benefit from this important increase in light availability. Furthermore, the tallest trees of the regeneration layer are more likely to be killed by a moderate-severity disturbance as SBW outbreaks or windthrow events are often “top-to-down” disturbances, first killing the tallest trees and then affecting the smaller trees as disturbance severity increases (De Grandpré et al. 2018). This mortality pattern therefore favours the smallest trees. As such, the differences in disturbance severity have specific impacts on the horizontal and vertical structure of a stand as well as the subsequent stand dynamics; low-severity disturbances lead to a progressive and small-scale replacement of the killed trees by the oldest and tallest suppressed trees. In contrast, moderate-severity disturbances lead to a quick and larger-scale replacement of the killed trees, mainly by the youngest and smallest suppressed trees.

The disturbance regime within this study territory is similar to that observed by Kuuluvainen et al. (2014) and Khakimulina et al. (2016) in northern European Russia; they observed low-severity disturbances and punctual moderate-severity disturbances as a result of insect outbreaks. In both studies, low-severity disturbances created gaps, i.e., canopy openings of <200 m2 based on McCarthy's definition (2001), while moderate-severity disturbances created patches, i.e., canopy openings of >200 m2

(McCarthy 2001). This combination of gap and patch dynamics are likely a common secondary disturbance regime in Fennoscandian boreal forests (McCarthy 2001; Kuuluvainen and Aakala 2011).

In our study, the size of the canopy opening resulting from each identified disturbance cannot be estimated precisely because of our methodology; it is therefore impossible to assess whether the moderate-severity disturbances effectively correspond to the creation of patches and low-severity disturbances correspond to the creation of gaps in our study stands. However, Kneeshaw and Bergeron (1998) observed a large diversity in the size of canopy openings in Quebec's boreal forests, corresponding both to gaps and patches. SBW can also create large (>200 m2), yet continuous, mortality areas; this creates a patchy distribution of dead and live trees in a landscape disturbed by this insect (Kneeshaw et al. 2009). Therefore, a combination of gap and patch dynamics may be a common disturbance regime in eastern Canadian boreal old-growth forests.

Our results also fall within the paradigm of a complex forest succession and disturbance regime within boreal forests. Forest succession should not be viewed as a linear pathway from structurally simple, post– stand-replacing disturbance, even-aged stands to structurally complex old stands driven by low-severity disturbances, but rather as several imbricated pathways (Kuuluvainen 2009; Reilly et al. 2015; Halpin and Lorimer 2016). Admittedly, the model describing old-growth dynamics driven solely by small-scale and low-severity disturbance remains partially valid, as some of our stands showed evidence of only low-severity disturbances over the centuries. Yet, the recurrence of moderate-severity disturbances and, more particularly, the fact that they were mainly found in true old-growth stands suggest the existence of other dynamics and succession patterns. First, the occurrence of disturbances of moderate severity in transition old-growth forests may accelerate the shift to the true old-growth stage, as a large part of the post– stand-replacing disturbance cohort is quickly killed and replaced. This may explain why moderate-severity disturbances are almost absent in the studied transition old-growth forests. Thus, the duration of the replacement of the post– stand-replacing disturbance cohort in a boreal old-growth stand may vary significantly from one stand to another. Second, once the true old-growth stage is reached, each stand may be driven by a particular secondary disturbance regime, mixing low- and moderate-severity disturbances at different proportions, and producing the structural diversity observed by Martin et al. (2018). Third, disturbances of moderate severity can create young forest structures that are neither even-aged nor old-growth (Donato et al. 2012; Meigs et al. 2017; Hart and Kleinman 2018). Donato et al. (2012) qualified these stands as "born-complex" forests, i.e., young stands exhibiting a structural complexity usually attributed to old-growth forests. Considering the importance of moderate-severity disturbances in the secondary disturbance regime, it is thus possible that the creation of born-complex forests is relatively common. In this context, structural differences between born-complex and old-growth forests are probably minimal, making it difficult to distinguish between these two ecosystems and thus question the "young forest/old forest" dichotomy. Therefore in Eastern Canada, recent findings regarding the complexity of the secondary disturbance regime should encourage forest ecologists and managers to re-evaluate the dynamics and the succession of boreal forests (Figure 3-5).

Discriminating low- from moderate-severity secondary disturbances by comparing tree and stand growth releases is an uncommon methodological approach. Observing the spatial patterns of tree mortality or canopy opening are preferred methods (e.g., Aakala et al. 2007; Janda et al. 2014; Khakimulina et al. 2016). In particular, it is easier to identify multiple and clustered growth releases that result, for example, from the death of a single large tree using spatialized data. This type of disturbance may challenge our definition of moderate-severity disturbances, as it could significantly change the mean stand growth. However, tree size is relatively limited in eastern Canadian boreal forests and broad-leaved species, i.e., species having the largest canopy disappear quickly during the old-growth transition (Bergeron and Harper 2009). Moderate-severity disturbances were infrequent in transition old-growth stands, i.e., stands that were the most likely to record the death of an old and large broad-leaved tree. This implies that the misclassification of disturbance severity caused by highly clustered growth releases was very unlikely. In contrast, the observed moderate-severity disturbance patterns resulted from multiple and coordinated minor understorey-tree growth releases in a number of stands. Our results therefore support the hypothesis of a mixed low- and moderate-severity secondary disturbance regime in eastern Canadian boreal old-growth forests over the last centuries. Finally, a 400-m2 plot surface is considered to be representative of the sampled boreal stand (MFFP 2016). Hence, we assume that disturbance dynamics observed within our plots are representative of the overall stand dynamics. Admittedly, complementary research analysing the spatial patterns of canopy gaps and their influence on tree growth releases in the studied stands would improve our understanding of secondary disturbance dynamics in boreal old-growth forests. The use of large-scale aerial or satellite images, e.g., Kuuluvainen et al. (2014) or light detection and ranging (LiDAR) data, e.g., Vepakomma et al. (2010), offer methods to overcome the intrinsic limits of plot-scale dendrochronological analysis.

3.7 Conclusion and management implication

Boreal old-growth stand dynamics generated by secondary disturbances are characterized by spatial and temporal complexity. Our study demonstrates that a given secondary disturbance regime will produce disparate severities across the landscape. This disparate pattern occurs because of a regime’s inherent spatial heterogeneity and the diversity of structural characteristics of the stand subjected to the disturbance. Furthermore, two disturbances are rarely comparable, even if they share a similar nature; for example in Eastern Canada, SBW outbreaks are cyclical but differ from each other in terms of spatial distribution and severity (Morin et al. 2009; Navarro et

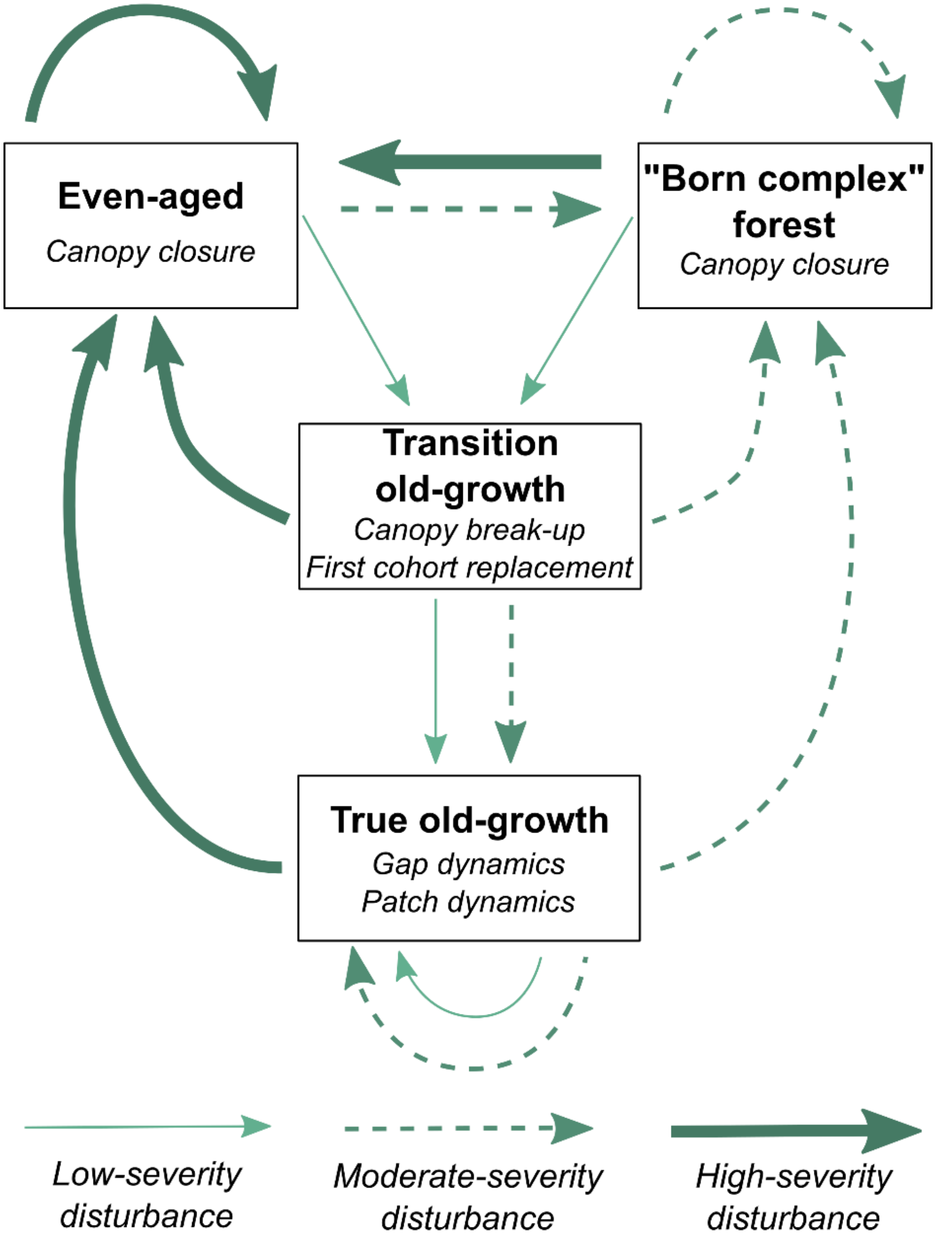


Figure 3-5 Conceptual model of the theoretical dynamics of boreal old-growth forests under a disturbance regime that combines low-, moderate-, and high-severity disturbances. Boxes represent the different successional stages. The "born-complex" forest stage refers to the theoretical and alternative stage described by Donato et al. (2012). Sentences in italics inside the boxes indicate the main processes driving that successional stage.

al. 2018). Our results underline this important “complexity challenge” faced by natural disturbance–based management (Kuuluvainen 2009), as the secondary disturbance regime is a very heterogeneous process.

Martin et al. (2018) hypothesized that boreal old-growth forest structural diversity results from a combination of low- and moderate-severity disturbances. Our results support this hypothesis, highlighting the importance of disturbance heterogeneity in the creation of old-growth structural richness. In addition, such complex disturbance histories are evidence of both the strong resistance and resilience of boreal old-growth forests. Yet, recent studies have emphasized how moderate-severity disturbances can, in some cases, rejuvenate mature and old-growth stands (Donato et al. 2012; Meigs et al. 2017). Similarly, our results illustrate that moderate severity disturbances, due to their abundance and regularity in the boreal forests of Eastern Canada, can probably lead to similar rejuvenation patterns. Therefore, managing old-growth boreal forests requires caution and a thorough knowledge of stand characteristics to ensure their sustainable management.

To emulate low- and moderate-severity secondary disturbance requires the use of partial-cut and stem-selection harvesting. Favouring harvest practices that have varying retention levels could imitate the heterogeneity in the severity of disturbances (Hart and Kleinman 2018). By identifying temporal and severity disturbance patterns, our results can therefore serve as a basis for old-growth forest management. These proposed treatments may, however, cause post-harvest mortality and should be reserved for the most resilient old-growth structures (Girard et al. 2014; Bose et al. 2015). However, in the context of this study, it is impossible to clearly discriminate between stand structures in terms of resilience. Further research should be undertaken to better understand how the structural attributes of old-growth stands identify those stands more suitable for partial-cut or stem-selection harvests. Salvage logging in recently disturbed stands, especially after moderate-severity disturbances, can offer another solution. Exploiting naturally disturbed trees ensures that changes in the canopy structure result from natural processes. However, this type of forest intervention may have negative effects on the biodiversity, especially on saproxylic species, and thus should be used with caution (Nappi et al. 2004, 2015, Lindenmayer et al. 2004; Nappi and Drapeau 2009, St-Germain et al. 2008; Thorn et al. 2018). Furthermore, natural secondary disturbances still occur in managed territories, and their occurrence and severity vary over time. Consequently, during periods of high natural mortality, such as during SBW outbreaks, living-tree harvesting levels should be reduced to limit pressure on the landscape.

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3.10 Supplementary materials

Potential vegetation	Slope	Deposit	Drainage	Number of sites per age class			Total
				Inf.100	100-200	Sup.200	
Balsam fir - white birch	Medium	Till	Mesic	2	1	1	4
Black spruce - balsam fir	Medium	Till	Mesic	1	1	3	5
Black spruce-feather moss	Low	Organic	Hydric	1	1	1	3
Black spruce-feather moss	Low	Sand	Mesic	1	1	1	3
Black spruce-feather moss	Low	Till	Mesic	1	1	1	3
Black spruce-feather moss	Low	Till	Subhydric	1	0	2	3
			Total	7	5	9	21

Appendix A Distribution of the sample sites per environmental type and age class

A

Site	**Site 1**	**Site 2**	**Site 3**	**Site 4**	**Site 5**	**Site 6**	**Site 7**	**Site 8**	**Site 9**	**Site 10**
Cohort basal area proportion	0	0.54	0.98	0	0.12	0.12	0	0	0.15	0.83
Weibull's shape parameter	1.26	1.44	2.75	1.38	0.74	1.19	0.69	1.29	1.05	2.67
Min. time since the last fire (years)	86	219	206	195	184	193	89	89	218	286
Tree density (n.ha^{-1})	1100	1250	1275	1875	950	1025	1575	50	450	1325
Sapling density (n.ha^{-1})	1100	1050	275	2400	1125	1200	3200	4050	1225	650
Basal area (m^{2}.ha^{-1})	30.63	25.19	35.45	21.75	20.13	14.52	29.73	0.36	5.52	20.57
Maximum height (m)	13.4	20.3	19.4	14.4	19.1	16.2	16.7	7.9	13.9	17.5
Slope (%)	35	8	3	0	10	7	5	0	0	27
Depth of the organ. Horizon (cm)	12	39	40	16	40	45	13	65	38	25

B

Site	**Site 11**	**Site 12**	**Site 13**	**Site 14**	**Site 15**	**Site 16**	**Site 17**	**Site 18**	**Site 19**	**Site 20**
Cohort basal area proportion	0.92	1	0.86	0.75	0.83	0.85	0.92	0.93	0.63	0.65
Weibull's shape parameter	0.97	0.72	1.14	0.89	0.69	0.76	0.97	0.89	0.9	0.73
Min. time since the last fire (years)	189	263	281	256	277	279	283	266	193	238
Tree density (n.ha^{-1})	975	675	675	500	1125	950	850	700	850	600
Sapling density (n.ha^{-1})	8550	1750	2150	1800	2525	3650	2800	1175	2250	2750
Basal area (m^{2}.ha^{-1})	15.18	18.48	6.84	7.1	28.29	12.67	17.68	14.27	16.09	20.7
Maximum height (m)	17.7	22.6	16.9	15.8	21.2	17.8	23.4	19.4	21.5	21.6
Slope (%)	18	19	0	0	18	2	26	5	7	22
Depth of the organ. Horizon (cm)	45	17	34	20	31	50	43	15	20	14

Appendix B: Structural and environmental characteristics of the studied (A) transition old-growth and (B) true old-growth stands

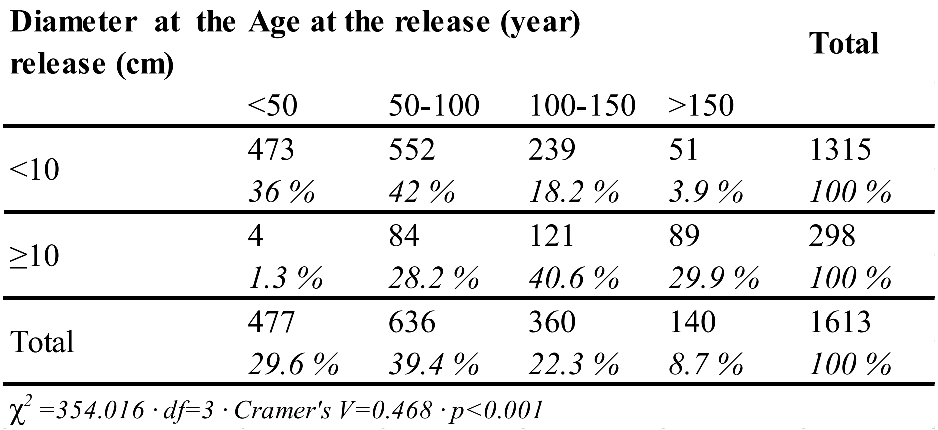
A

Succession stage		Transition old-growth									
Parameter	**Species**	**Site 1**	**Site 2**	**Site 3**	**Site 4**	**Site 5**	**Site 6**	**Site 7**	**Site 8**	**Site 9**	**Site 10**
Number of trees	Black spruce	15	33	50	40	37	37	44	43	18	20
sampled	Balsam fir	3	0	12	0	0	0	0	0	0	3
Year on which n.	Black spruce	1939	1820	1938	1899	1854	1910	1840	1875	1811	1832
trees≥10	Balsam fir	-	-	1907	-	-	-	-	-	-	-

B

Succession stage		Transition old-growth									
Parameter	**Species**	**Site 11**	**Site 12**	**Site 13**	**Site 14**	**Site 15**	**Site 16**	**Site 17**	**Site 18**	**Site 19**	**Site 20**
Number of trees	Black spruce	24	26	30	15	23	34	37	37	36	10
sampled	Balsam fir	16	15	0	0	29	0	8	2	13	13
Year on which n.	Black spruce	1929	1872	1935	1808	1824	1876	1806	1894	1825	1837
trees≥10	Balsam fir	1939	1920	-	-	1869	-	-	-	1925	1892

Appendix C: Number of trees sampled and year (CE) by which at least ten trees were sampled by species in the studied (A) transition old-growth and (B) true old-growth stands



Diameter at the release (cm)	**Age at the release (year)**				**Total**
	<50	50-100	100-150	>150	
<10	473	552	239	51	1315
	36 %	*42 %*	*18.2 %*	*3.9 %*	*100 %*
≥10	4	84	121	89	298
	1.3 %	*28.2 %*	*40.6 %*	*29.9 %*	*100 %*
Total	477	636	360	140	1613
	29.6 %	*39.4 %*	*22.3 %*	*8.7 %*	*100 %*

$\chi^2 = 354.016 \cdot df=3 \cdot \text{Cramer's } V=0.468 \cdot p<0.001$

Appendix D: Contingency table of the age and diameter of trees at the release times within the studied chronologies

CHAPITRE IV

FOREST MANAGEMENT HAS REDUCED THE STRUCTURAL DIVERSITY OF RESIDUAL BOREAL OLD-GROWTH FORESTS LANDSCAPES IN EASTERN CANADA

Accepted research paper

Title: Forest management practices have reduced the structural diversity of remaining boreal old-growth forests in Eastern Canada

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4.1 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 old forest 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.

4.2 Résumé

L'impact de la gestion forestière équienne traditionnelle sur la structure d'âge du paysage, la composition en espèce d'arbres et la connectivité des peuplements a été bien documenté dans les territoires boréaux. Cependant, on en sait très peu de son impact sur la diversité structurelle des peuplements forestiers. Cette étude vise à comparer les caractéristiques structurelles et abiotiques des peuplements forestiers perturbés par les coupes totales et par les feux de forte sévérité dans les paysages boréaux du Québec. Nous avons émis l'hypothèse que, contrairement au feu, l'exploitation forestière visait spécifiquement des peuplements ayant une valeur économique plus élevée, c.-à-d. un fort volume marchand, altérant ainsi les caractéristiques forestières dans les paysages récoltés. Nous avons comparé deux inventaires forestiers aériens réalisés sur une zone d'étude de 2200 km^2, l'un des inventaires ayant été réalisé avant le début de toute activité forestière (relevé préindustriel ; années 1980) et le deuxième inventaire ayant été réalisé plus de 10 ans après le début des activités forestières (relevé moderne ; années 2000). Les peuplements forestiers au moment de l'inventaire préindustriel peuvent être considérés comme des forêts primaires. Nous avons identifié les peuplements brûlés, exploités ou laissés de côté après l'aménagement forestier de la région (peuplements résiduels) entre les deux inventaires et comparé leurs caractéristiques structurelles et abiotiques à l'aide de régressions logistiques. Les caractéristiques structurelles et abiotiques des peuplements brûlés et des peuplements exploités différaient considérablement. Par rapport aux peuplements brûlés, les peuplements exploités étaient plus anciens, plus denses, définis par un drainage moins bon et par une proportion plus élevée d'épinettes noires ; par conséquent, les paysages après récolte et après feu différaient quant à leur diversité structurelle. L'aménagement forestier équien traditionnel a considérablement modifié le paysage de la forêt boréale en ciblant des vieilles forêts spécifiques, définies par une valeur économique plus élevée, et en laissant derrière eux des peuplements de moindre valeur économique. Les peuplements restants à forte valeur économique doivent être protégés et une approche plus équilibrée de la récolte doit être utilisée dans le contexte d'une gestion écosystémique.

4.3 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 for biodiversity that are often absent in younger stands (Imbeau et al. 2001; Tikkanen et al. 2006; Bergeron and Fenton 2012; Drapeau et al. 2016; 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 recently, 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 with a significant portion of old growth stands, particularly in Eastern Canada (Bergeron et al. 2002; Bergeron et al. 2006; Bouchard et al. 2008; Bergeron and Harper 2009; Bergeron and Fenton 2012).

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 (%.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 (Drapeau et al. 2000; Siitonen 2001; Tikkanen et al. 2006; Drapeau et al. 2016; Patry et al. 2017).

To address these concerns, current ecosystem-based management strategies in boreal landscapes aim to use natural disturbance regimes as templates for reducing the gaps between managed and natural forests (Kuuluvainen 2002; Gauthier et al. 2009) or mimic stand-scale natural processes (Vanha-Majamaa et al. 2007; Kuuluvainen 2009). In this context, forest management should aim to produce a wider range of stand structures, that is similar to those observed in a natural boreal landscape instead of mainly relying on conventional even-aged management systems with clearcuts. However, clearcutting-based systems remain the most efficient harvesting systems from an economic standpoint (Perry 1998; Puettmann et al. 2009). They prioritize short-term benefits by maximizing the wood volume logged of the most valuable stand structures (Halme et al. 2013; Ruel et al. 2013), leaving less desirable forest structural attributes in post-harvested landscapes and may therefore cause habitat depletion. Implementing ecosystem-based strategies that rely on the diversification of silvicultural practices to maintain in managed landscapes a wider range of stand structures may thus pose an economic challenge with regards to clearcutting.

Assessing the structural discrepancies between logged and naturally disturbed landscapes 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 commercial timber harvesting. In addition, stand-replacing fires, which are the main natural disturbance in eastern Canadian boreal forests, still occur in managed landscapes (Boucher al. 2017a). It is therefore possible to compare the characteristics of a stands that were disturbed either by logging or fire. Thus, the objective of this study is to determine whether logged stands share similar structural and abiotic characteristics with 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 stand successional stage, density, drainage, and potential vegetation as stand volume proxies. Our study aimed to improve our understanding of the influence of both forestry practices and wildfires on boreal landscapes to help develop more effective ecosystem-based forest management strategies.

4.4 Material and methods

4.4.1 Study area

The study area (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 (Figure 4-1A; 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 (Figure 4-1B). 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).

4.4.2 Cartographic data preparation

The first industrial logging operations in the study area started in 1991. Two aerial surveys completed by the government of Québec are used in this study: one in the years 1983-1984 (preindustrial period) and a second completed in 2007 (modern period). The preindustrial survey divided the territory into 14 ha rectangular polygons (tessels) distributed over a 297x463m grid (15 seconds x 15 seconds in geographic coordinates; Pelletier et al. 2007). The values attributed to each tessel are the result of the photointerpretation of the tessel centroid. In contrast, the modern survey aimed to define polygons representing the natural boundaries of forest stands that are defined as having homogeneous abiotic and structural characteristics. However, the two surveys can be compared along the preindustrial 297x463m grid, taking the modern stand characteristics at the preindustrial centroid (Figure 4-1C**)**. 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 4-1). 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

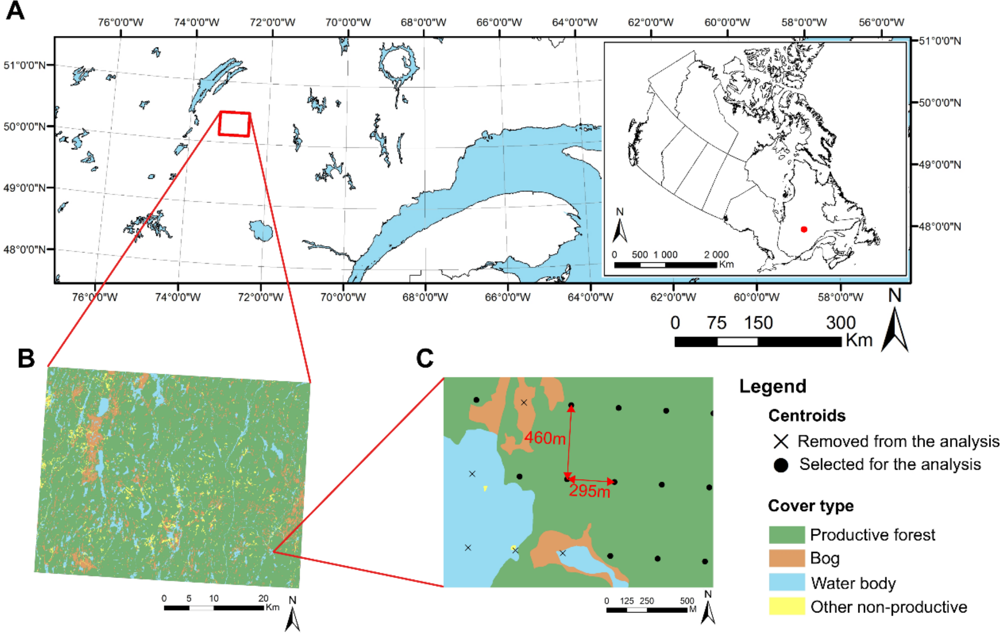

Figure 4-1 (A) Situation of the study territory in the province of Québec. The insert map represents its location in Canada. (B) Spatial distribution of the main cover types on the study territory. (C) Example of the centroid distribution on the study territory and of their selection for the analysis according to the cover type

Table 4-1 Presentation and description of the abiotic and structural covariates and classes of the centroids

Covariate type	**Covariate name**	**Class**	**Description**
Abiotic characteristics	Altitude	400-449m	-
		450-499m	-
		500-549m	-
		550-599m	-
	Surfical deposit	Fluvioglacial	*Fluvioglacial surface deposit (esker, kames...)*
		Glacial	*Glacial surface deposit (tills, moraines...)*
		Organic	*Organic surface deposit*
		Other	*Other type of surface 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 - feather moss (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	Succession 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<7m)*
		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	<12m	*Height of the highest trees <12m*
		12-17m	*Height of the highest trees between 12 and 17m*
		>17m	*Height of the highest trees >17m*

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, Figure 4-2).

4.4.3 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:

$$stand\ replacing\ disturbance\ rate = \frac{n_{disturbed\ plots}}{n_{total\ plots} \times t}$$

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 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:

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

$P(Y)$ 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

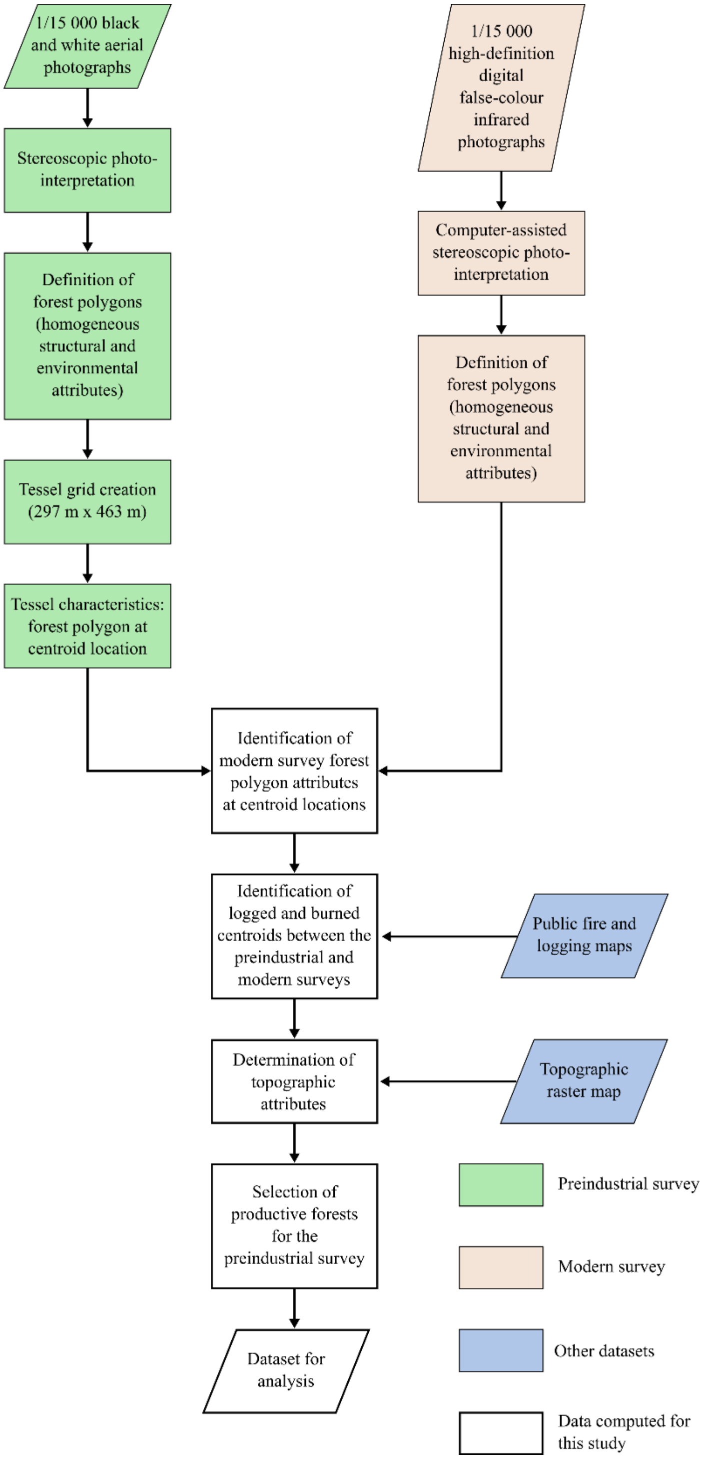

Figure 4-2 Flowchart of the methodology used to obtain the datasets. Trapezoids represent inputs or outputs, rectangles represent processes.

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 (Venables 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 Team 2016) with the *ROCR* (Sing et al. 2005), *MASS* (Venables and Ripley 2002), and *DescTools* (Signorell et al. 2017) packages. We applied a significance threshold of 0.05.

4.5 Results

4.5.1 Evolution of the landscape between the preindustrial and the modern survey

Overall, between the preindustrial and the modern surveys, the old-growth forest abundance decreased by 20% (Figure 4-3). 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 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 4-2). 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.

Table 4-2 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

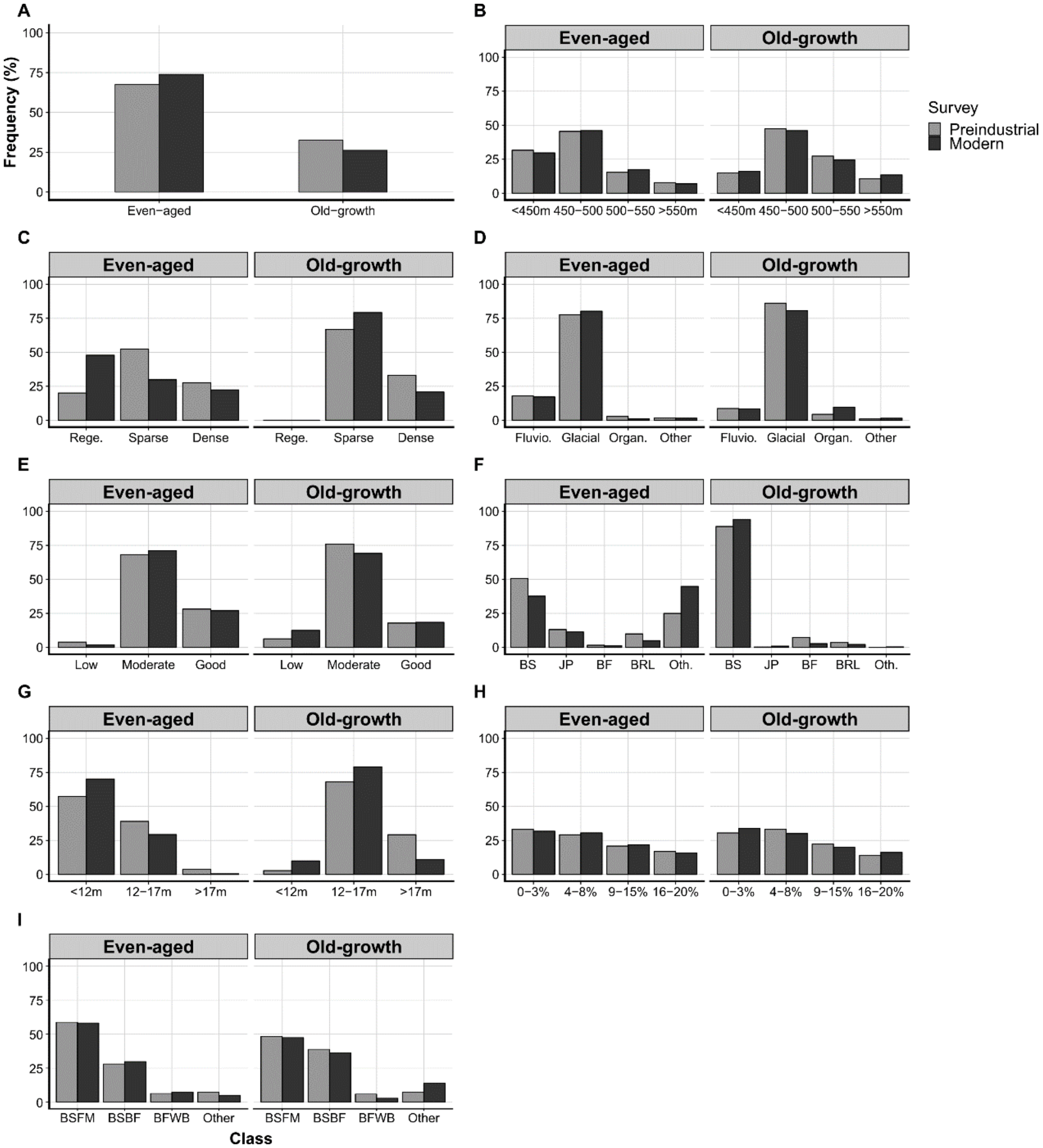

Figure 4-3 Distribution of the even-aged and old-growth centroids in the preindustrial and the modern surveys based on their (A) successional stage, (B) altitude, (C) density, (D) surficial deposit, (E) drainage, (F) dominant species, (G) height, (H) slope and (I) potential vegetation. Rege.: Regeneration, 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.

4.5.2 Differences in the centroids characteristics 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 4-3). In Model 1, all retained covariates had a significant effect. The successional stage was the covariate having the highest influence on the model (Figure 4-4), 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 (Figure 4-5A), 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 (Figure 4-5B). 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.

Table 4-3 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	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	11410	-6	-212.79	<0.001	11211	0.59	0.02	Stage	1	10.92	9447	11259	<0.001
										Density	1	139.91	9448	11270	<0.001
										Pot.Veg.	2	39.34	9443	11197	<0.001
										Drainage	2	22.61	9445	11237	<0.001
Model 3	Remaining/logging	7955	6962.9	-6	-354.2	<0.001	6622.7	0.66	0.05	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

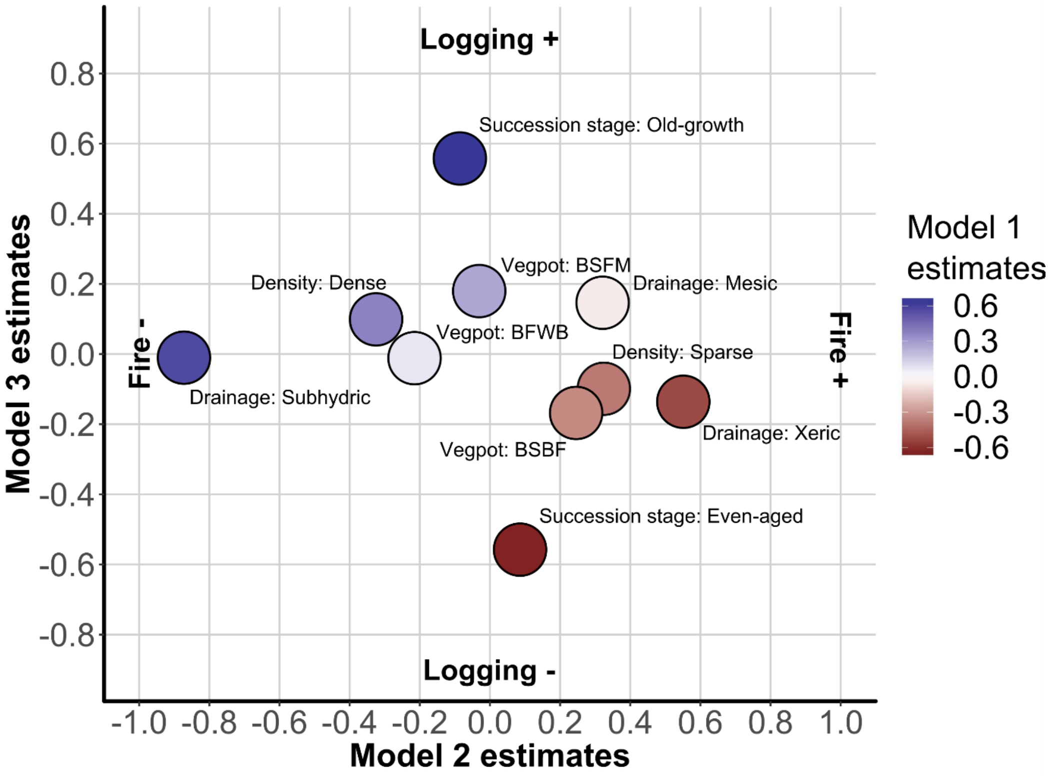

Figure 4-4 Distribution of the estimates of the studied classes according to the logistic regression models that compare the characteristics of burned, logged, and remaining centroids. Positive estimate values for Model 1 indicate those characteristics that are more abundant in logged stands than in 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.

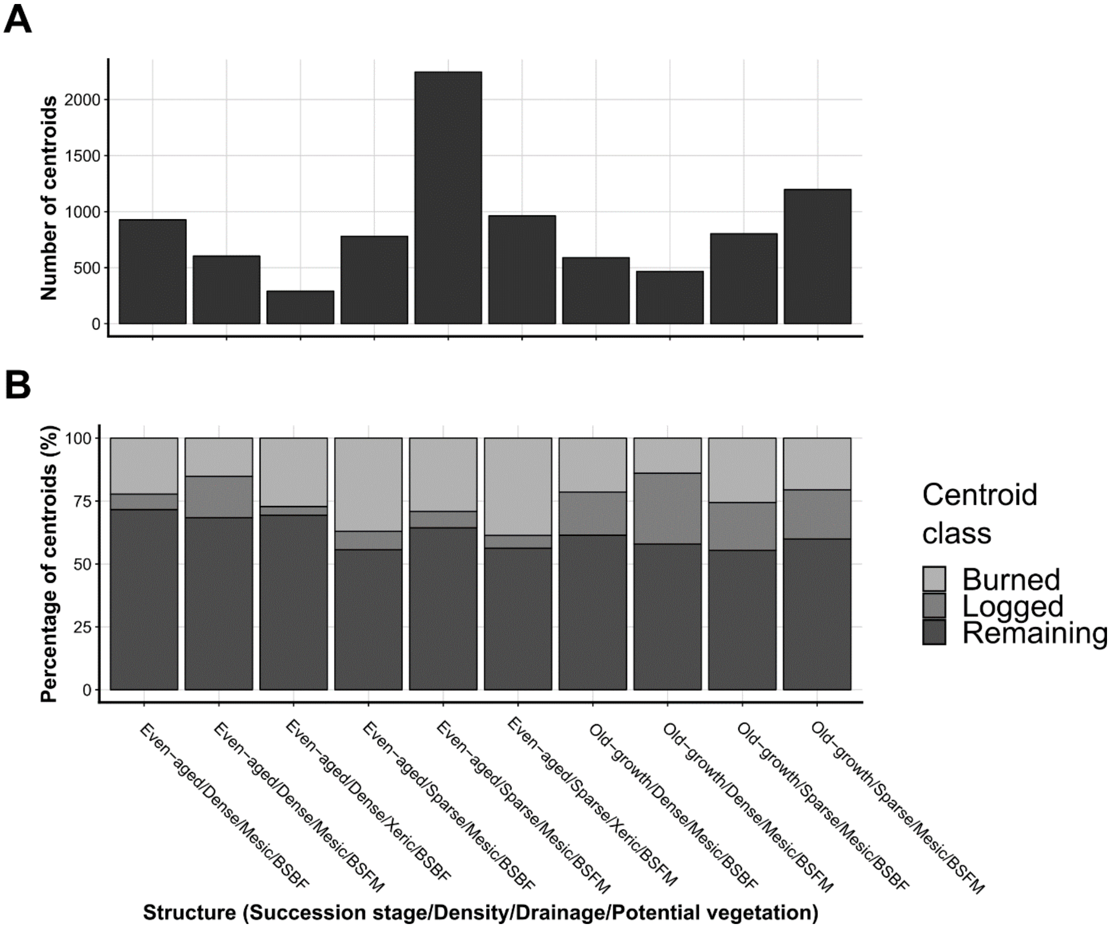

Figure 4-5 (A) Number of centroids and (B) proportion of the centroids according to the disturbance nature of the ten most abundant stand types on the study territory

4.6 Discussion

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 around 12% of the productive forests. 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.

4.6.1 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 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 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; Bernier et al. 2016). 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 whereas old and dense pure black spruce stands with the highest economic value will be significantly less abundant in managed landscapes.

Fire and clearcuts are both contagious disturbances (Peterson 2002; Boucher et al. 2017), which may have affected the accuracy of our models (Valcu and Kempenaers

2010). However, our dataset consists in a complete survey of the study area following a 297x463 m grid. Thus, our methodology constrains the influence of spatial autocorrelation in our models because we are not attempting to generalize from a subsample of points to a larger territory. Our results can be therefore be considered as a relevant description of the evolution of our entire study area according to the nature of the disturbances on the time span studied. Nevertheless, further research should aim to determine at which extent structural and abiotic attributes influence the spatial patterns of fires and clearcuts.

4.6.2 Influence on landscape dynamics and boreal old-growth forests diversity

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 2002; 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 (Drapeau et al. 2003; Baker et al. 2013; Cadieux and Drapeau 2017; 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 lead to stand rejuvenation, 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. Accepted). 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 young forests 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; Splawinski et al. 2019).

4.7 Conclusion and management implications

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.

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CHAPITRE V

BOREAL OLD-GROWTH FOREST STRUCTURAL DIVERSITY CHALLENGES AERIAL PHOTOGRAPHIC SURVEY ACCURACY

Accepted research paper

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

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5.1 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.

5.2 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.

5.3 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.

5.4 Methods

5.4.1 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”). 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

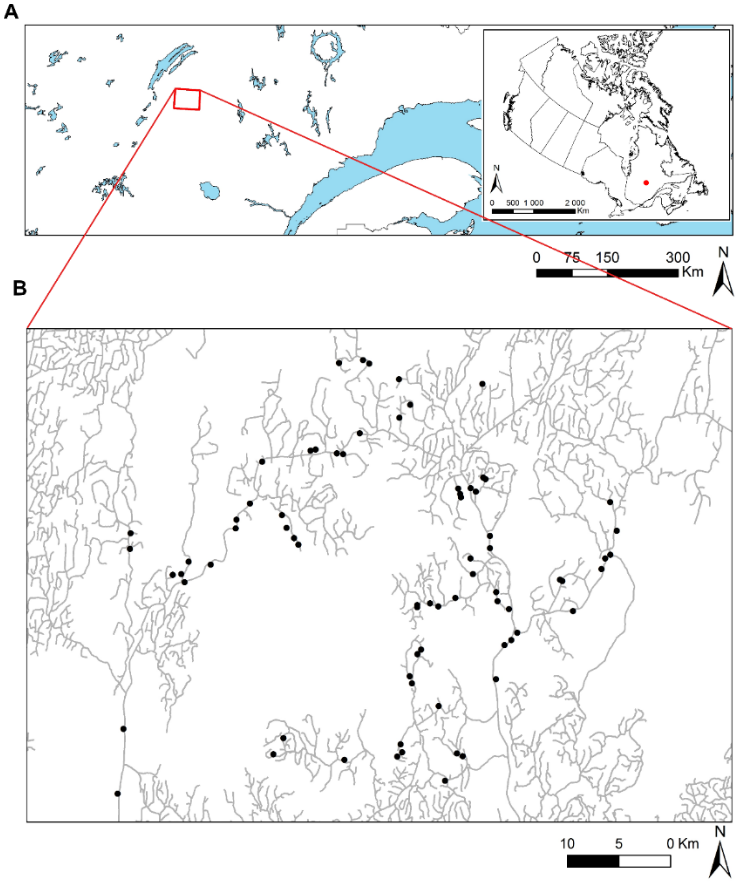

Figure 5-1 (A) Location of the study territory (red rectangle) in the province of Québec. The red dot in the insert map indicates its location in Canada. (B) Field plots (black dots) sampled in the study territory. Grey lines represent the forest road network.

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 5-1). 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 5-1 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 5-1 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): - Dominant: highest trees in the stand - Codominant: height ≥ 2/3 of dominant tree heig - Intermediary: height < 2/3 and ≥1/2 of dominan height - Suppressed: height < 1/2 of dominant tree heig
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

5.4.2 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.

5.4.3 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) $\geqslant 1.5$ 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$\geqslant$ 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 5-2). 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 5-2 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

5.4.4 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 φ 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.

5.5 Results

5.5.1 Comparison of the aerial surveys

Nearly fourty percents of the centroids (40.9%) presented an even-aged structure in both aerial surveys (Table 5-3). 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 5-3 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 5-2). 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.

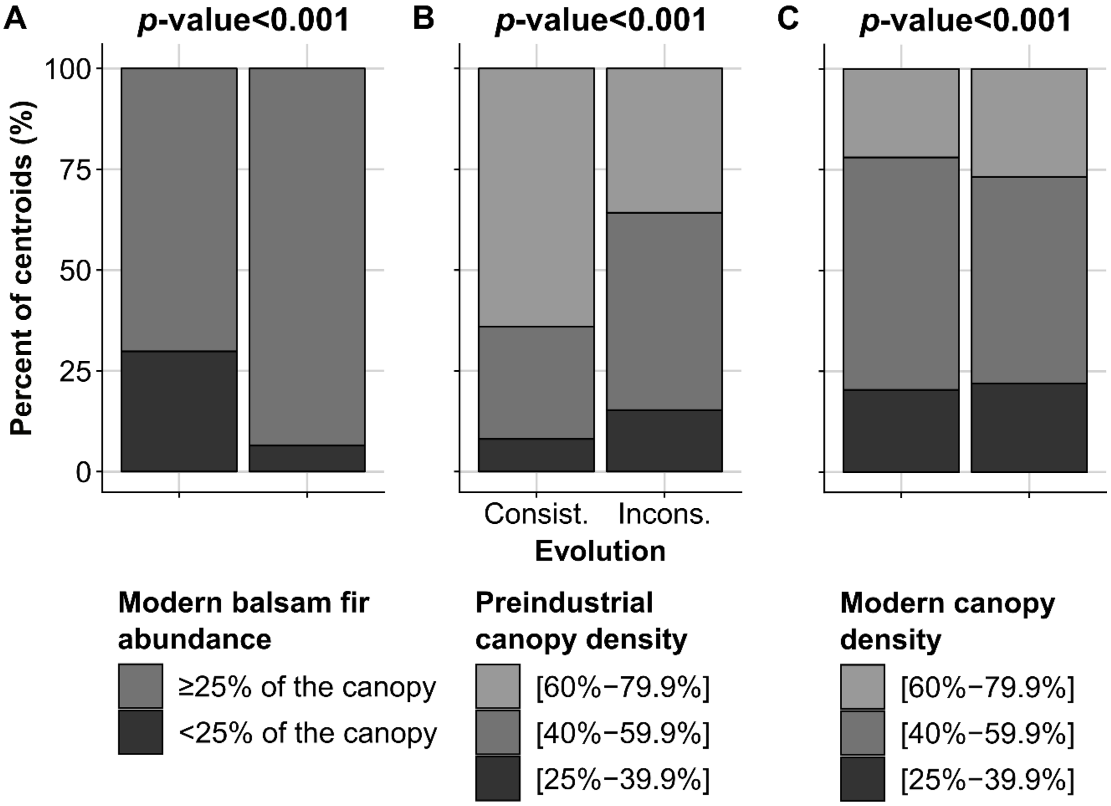

Figure 5-2 Histogram of the class distribution and *p*-value of the significant parameters according to the logistic regression model comparing centroids defined by a consistent or an inconsistent structural evolution, separated depending on the binary dependant variable: (A) Modern balsam fir abundance, (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.

5.5.2 Comparison of cartographic survey with field survey

The modern aerial survey was more accurate in discriminating monocohort and multicohort stands (Overall accuracy = 56%, Table 5-4A) than regular and irregular stands (Overall accuracy = 21.4%, Table 5-4B), 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 5-4C). This error was specifically related to old-growth stands, as 40% of the old-growth field plots were

Table 5-4 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*	

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 5-5). 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

Table 5-5 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

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.

5.5.3 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 5-3), 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 5-6). 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%).

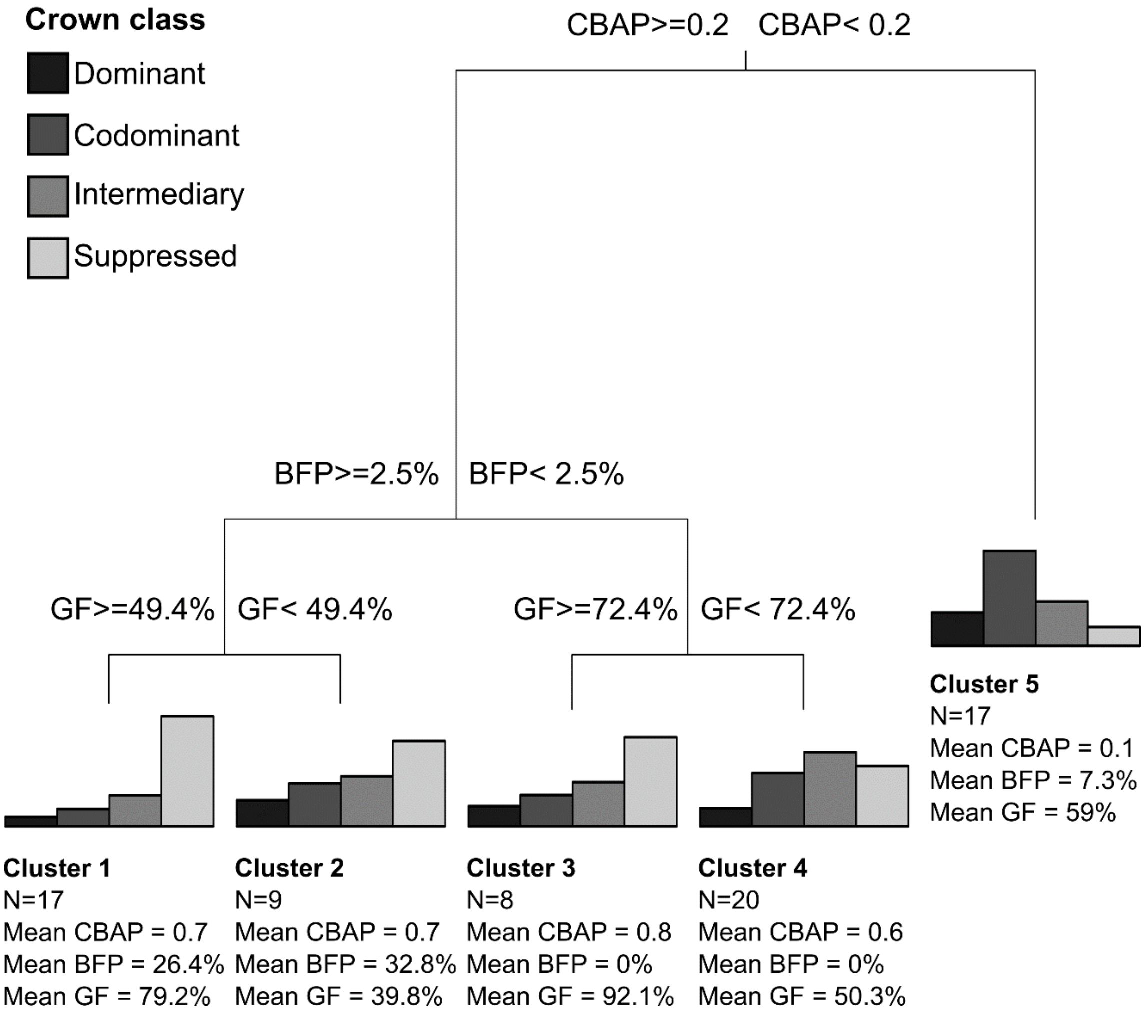

Figure 5-3 Dendrogram of the multivariate analysis performed on the distribution of the canopy layers in the field plots. Histogram represent the mean frequency of the canopy layers category in each class. CBAP: Cohort Basal Area Ratio, BFP: Balsam fir proportion (%), GF: Gap fraction (%).

Table 5-6 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*	

5.6 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.

5.6.1 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.

5.6.2 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.

5.7 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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5.9 References

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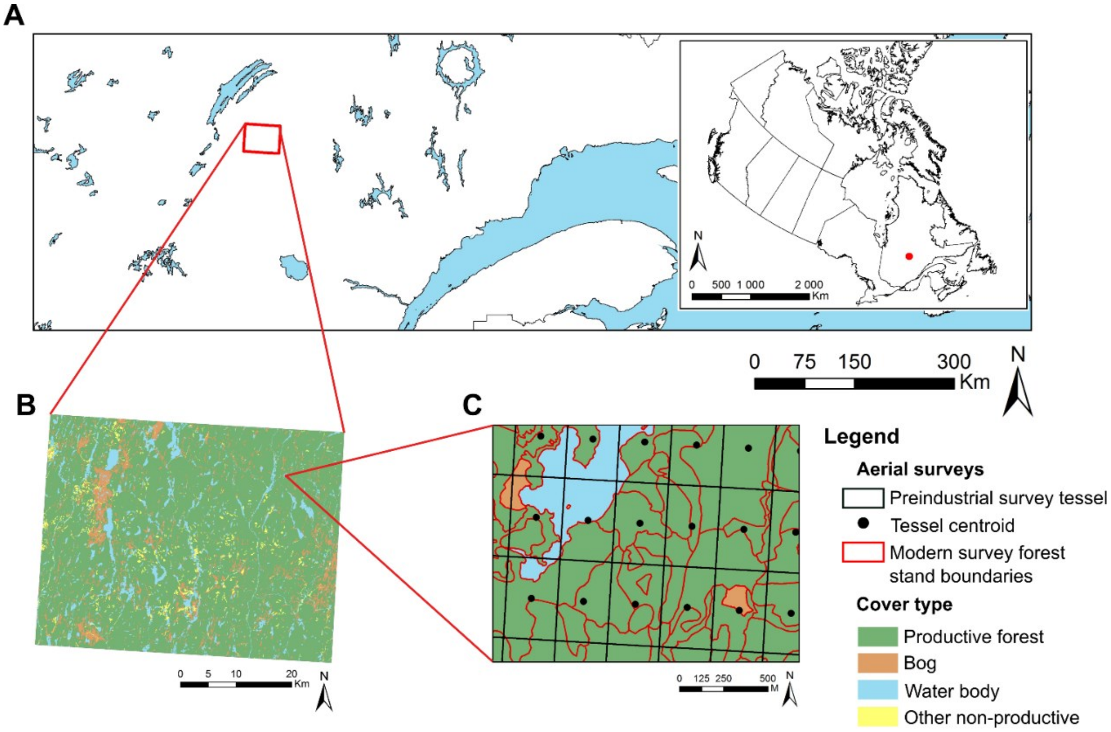
5.10 Supplementary materials



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.

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: $f(x) = \left(\frac{a}{b}\right) \times \left(\frac{x}{b}\right) \times exp\{-(x/b)^a\}; x \geq 0; a>0; b>0$ 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. 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: $CBAP = \frac{(BA_{N \quad 1\,trees\, +\, 0.1})}{(BA_{N+1\,trees\, +\, 0.1} + BA_{First\ cohort\ trees})}$ 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		

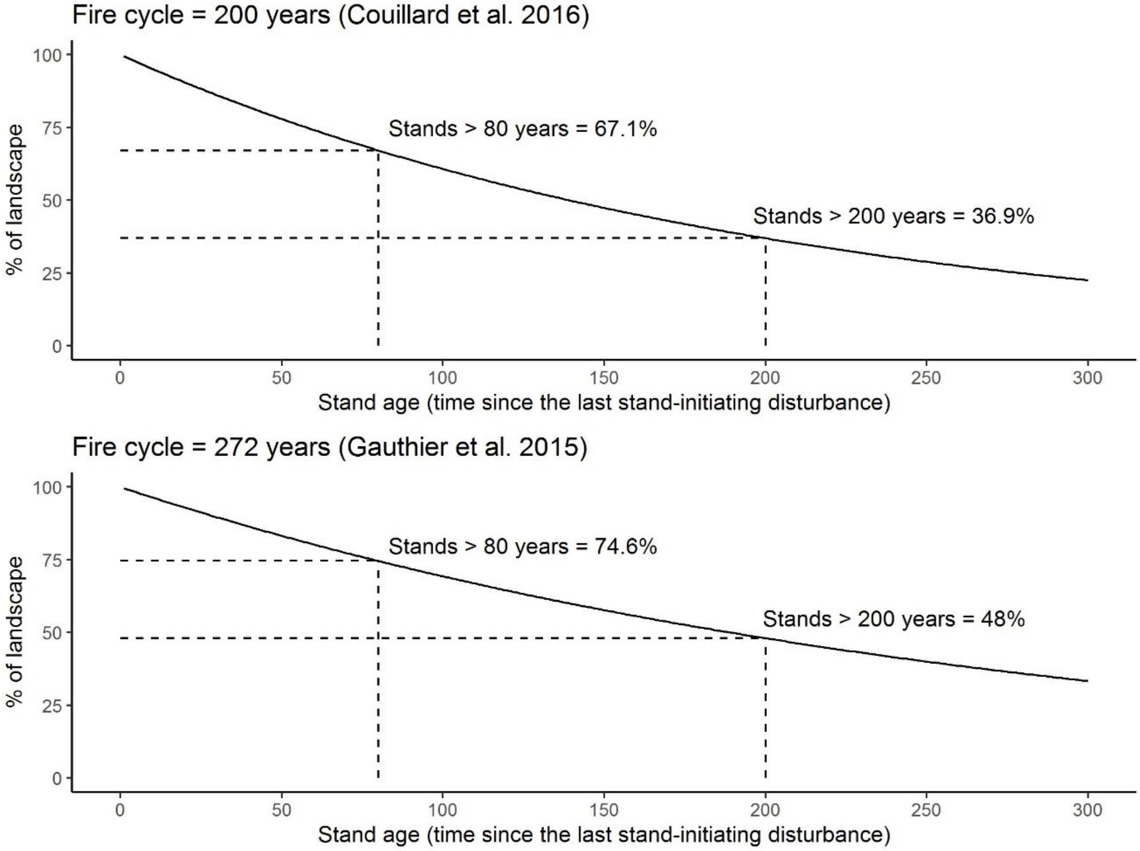
Appendix C Description of the cartographic structure attributes computed for the centroids (1/2).

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.

CONCLUSION

6.1 Contributions, limites et perspectives de l’étude

Les principaux résultats obtenus dans les quatre chapitres de cette thèse sont les suivant : 1) les vieilles forêts boréales présentent une forte diversité structurelle qui augmente avec le temps depuis feu et varie selon la topographie, 2) la dynamique des perturbations secondaires dans les vieilles forêts boréales combine des perturbations naturelles de sévérité variable sur des patrons temporels parfois différents, 3) les vieilles forêts définies par un important volume de bois marchand sont visées en priorité par l’exploitation forestière, 4) les inventaires orthophotographiques sous-estiment l’abondance des vieilles forêts boréales de l’Est du Canada. Notre thèse permet donc de répondre à l’objectif général de notre doctorat, qui visait à améliorer nos connaissances quant à la diversité, à la dynamique et à la conservation des vieilles forêts boréales en territoire aménagé.

L’un des aspects les plus innovants de cette thèse repose sur l’analyse de la diversité interne et de la dynamique des vieilles forêts de l’Est du Canada, y compris une fois le stade de vieille forêt vraie atteint. En effet, la majorité des études réalisées jusqu’à maintenant sur les vieilles forêts boréales dans ce territoire se sont intéressées au processus de transition vers l’état de vieille forêt, c’est-à-dire du passage au stade de forêt équienne à celui de vieille forêt (Bergeron 2000; Desponts et al. 2004; Harper et al. 2005; Lecomte et al. 2006; Bergeron and Harper 2009; Garet et al. 2009; Gauthier et al. 2010). La distinction entre les différents types de vieilles forêts s’interrompait donc une fois la transition terminée. Cette approche a ainsi pu entretenir une certaine confusion vis-à-vis des vieilles forêts vraies en les faisant passer pour des peuplements statiques et structurellement homogènes. Nos résultats soulignent au contraire que la transition vers l’état de vieille forêt n’est qu’une étape et que la diversité structurelle de ces écosystèmes continue d’augmenter une fois le stade de vieille forêt vraie atteint. Il est probable que cette diversité structurelle, en plus de temps depuis la dernière perturbation initiale, influe fortement sur la biodiversité dans ces différents types de vieilles forêts (Drapeau et al. 2003; Tikkanen et al. 2006; Fenton et Bergeron 2011; Boudreault et al. 2018). Les travaux de Portier et al. (2018) et Moussaoui et al. (2019), publiés durant la réalisation de notre doctorat, mettent aussi en avant la diversité structurelle des vieilles forêts boréales de l’Est du Canada et soulignent l’intérêt actuel pour ce sujet. Nous considérons néanmoins que nos résultats sont actuellement les plus exhaustifs, car détaillant la structure des peuplements sous de nombreuses perspectives (structure horizontale, structure verticale, composition en espèces arborescentes, débris ligneux, dynamique de perturbation) et les mettant en relation avec leurs caractéristiques stationnelles. Notre étude est néanmoins limitée par l’utilisation de l’âge des arbres échantillonnés comme indicateurs du temps depuis feu et du remplacement de la première cohorte. Non-seulement cet âge peut être sous-estimé mais il devient aussi impossible de placer les peuplements sur une chronoséquence une fois le stade de vieille forêt vraie atteint (Garet et al. 2012); il est alors difficile de déterminer si la structure des vieilles forêts vraies évolue en suivant des trajectoires spécifiques. De précédentes études suggèrent que certaines vieilles forêts boréales de l'Est du Canada pourraient rester dynamiques durant des siècles, voire des millénaires (Pollock and Payette 2010; Ward et al. 2014). Les analyses au carbone 14 réalisées par Couillard et al. (2016) sur le territoire d'étude montrent ainsi que certaines vieilles forêts n'ont pas été brûlées depuis au moins 800 ans, impliquant que de nombreux changement structuraux ont pu avoir lieu au sein d'un même peuplement sur une telle période. La réalisation d'une chronoséquence de vieilles forêts vraies basée sur les résultats d'analyses au carbone 14 des charbons du sol serait donc un moyen de compenser les limites actuelles de notre étude et de mieux comprendre les changements structuraux sur le long terme.

La structure et la dynamique des peuplements forestiers dépendent de multiples facteurs, souvent inter-reliés. Par conséquent, une séparation discrète de la structure des peuplements ou de la sévérité des perturbations est une simplification de la réalité faite pour faciliter l'interprétation écologique des résultats obtenus (Bunnell and Huggard 1999; Bragg 2002; Pesklevits et al. 2011). Cette approche permet néanmoins d'identifier les principaux paramètres qui vont influencer les caractéristiques des vieilles forêts boréales. Si nous prenons le cas d'une vieille forêt vraie située dont les conditions stationnelles sont favorables à l'épinette noire et au sapin baumier (par exemple un site situé sur des tills et où la température lors de la saison de croissance est suffisamment élevée; Messaoud et al. 2019), non-sujette à la paludification, les changements structuraux prédominants s'observeront ainsi au niveau du degré d'ouverture de la canopée et de l'abondance du sapin baumier, en fonction de la dynamique des perturbations secondaires et de régénération (Figure 6-1).

Si notre étude n'a sans doute pas identifié tous les types de structure que l'on peut observer dans les vieilles forêts boréales de l'Est Canadien, il est par contre probable que nos résultats illustrent les principales trajectoires structurelles pouvant être suivi par ces écosystèmes. Nous avons par ailleurs cherché à produire les résultats les plus représentatifs à l'échelle de ce territoire. Néanmoins, en raison de contraintes d'accessibilité ou de disponibilité, certains types de peuplements ou de stations n'ont été que faiblement échantillonnés, par exemple les sapinières ou les peuplements sur forte pente. Par ailleurs, nous nous sommes concentrés dans cette thèse sur la forêt boréale résineuse du Québec. Il est ainsi possible que dans le domaine de la forêt mixte, certains patrons diffèrent, par exemple en raison de la plus forte productivité des espèces feuillues et de la sévérité plus forte des épidémies de tordeuse des bourgeons de l'épinette (Kneeshaw et Bergeron 1998; Bergeron 2000; Bouchard et al. 2007). Il serait par conséquent sans doute pertinent de réaliser des études similaires à celles de cette thèse dans la forêt boréale mixte. De récentes études ont aussi mis en avant que la dynamique et la succession forestière pouvait se montrer souvent plus complexe que ce qui est théoriquement attendu (Donato et al. 2012; Meigs et al. 2017). Certains des résultats obtenus au cours de notre thèse vont dans le même sens, suggérant que la

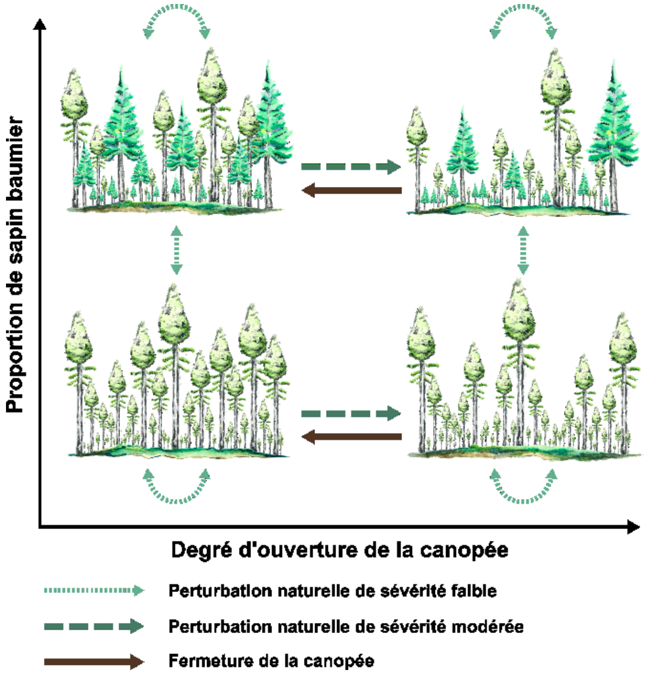


Figure 6-1 Illustration des principaux changements structuraux théoriques pour une vieille forêt vraie située dans une station favorable à l'épinette noire et au sapin baumier, non-sujette à la paludification. Aquarelles par Valentina Buttò.

dynamique de perturbation et de régénération des vieilles forêts boréales peut parfois suivre des chemins complexes (Figure 6-2). Il apparaît donc important d'approfondir cette caractérisation de la structure et de la dynamique des vieilles forêts boréales, afin de s'assurer de la représentativité de nos connaissances vis-à-vis de ces écosystèmes. Le développement de nouvelles technologies pourrait aider à atteindre ces objectifs. Les relevés aériens LIDAR (Light Detection And Ranging) se sont notamment montrés très efficaces pour discriminer des structures forestières complexes (Falkowski et al. 2009; Kane et al. 2010; Jayathunga et al. 2018). Cette technologie permet par ailleurs de couvrir avec précision d'importantes superficies en un temps réduit. Le degré de diversité structurelle des peuplements forestiers dépend en effet fortement de l'échelle à laquelle est faite l'observation (Smith and Urban 1988). Il serait ainsi possible de dépasser l'échelle spatiale de $400m^2$ majoritairement utilisée dans cette thèse afin de mieux comprendre la manière dont se distribue cette diversité structurelle dans les peuplements boréaux.

Les résultats de notre troisième chapitre soulignent qu'en comparaison du feu, l'exploitation forestière vise principalement les vieilles forêts se définissant par un important volume de bois marchand. C'est à notre connaissance la première fois que les vieilles forêts récoltées et brûlées sont comparées au niveau structurel. L'influence de l'exploitation forestière à échelle industrielle dans l'érosion des vieilles forêts boréales du l'Est du Canada a déjà été largement établie, mais ces écosystèmes ont jusqu'à maintenant été en fonction de leur classe d'âge et non selon leur structure (Boucher et al. 2009; Cyr et al. 2009; Bergeron et al. 2017). Étant donné que l'exploitation forestière est avant tout motivée par des objectifs de rentabilité économique, il est logique que les peuplements récoltés en priorité soient ceux définis par la plus forte valeur marchande (Perry 1998; Puettmann et al. 2009). Néanmoins, nos deux premiers chapitres soulignent que les vieilles forêts boréales sont des écosystèmes structurellement diversifiés et dynamiques. Un aménagement durable des forêts, par exemple dans le contexte de l'aménagement écosystémique du Québec, doit donc viser à conserver cette diversité (Gauthier et al. 2009). En se concentrant sur la portion des vieilles forêts dont la valeur marchande est la plus élevée, l'aménagement forestier risque au contraire de non seulement affecter la structure d'âge de la forêt mais également d'éroder la diversité structurale des plus vieux peuplements. La mise en place de stratégies d'aménagement efficaces pour maintenir la diversité structurale de tous les types de couvert forestier, y compris celle des vieilles forêts, nécessite toutefois des données fiables à grande échelle. Or, les résultats du quatrième chapitre montrent que les inventaires photographiques aériens réalisés sur l'ensemble de la forêt productive du Québec sous-estiment fortement l'abondance des vieilles forêts boréales. La majorité des forêts présentant une structure diamétrale et une structure d'âge complexes dans les placettes de terrain sont identifiées comme étant des forêts équiennes de plus de 100 ans. Dans ce contexte, il semble donc difficile d'intégrer efficacement la diversité structurale des vieilles forêts dans l'aménagement du territoire car les données disponibles ne permettent pas de rendre compte de cette diversité. Le nouvel inventaire forestier décennal actuellement en cours de réalisation au Québec intègrera toutefois des relevés LIDAR sur l'ensemble de la forêt productive du Québec. Le développement d'outils capable d'identifier efficacement et de discriminer les vieilles forêts boréales sur la base de données LIDAR pourrait ainsi être une solution permettant de pallier aux limites des inventaires photographiques aériens.

Les données utilisées dans le cadre de cette thèse proviennent d'inventaires réalisés entre 1968 et 2016. Nos résultats dressent donc un portrait de la forêt boréale du l'Est du Canada telles que façonnées par la dynamique des feux et des épidémies de tordeuse des bourgeons de l'épinette du XX^{e} siècle. Or, les impacts attendus du changement climatique dans les 100 prochaines années seront particulièrement importants en forêt boréale (IPCC 2018). Il convient par conséquent de mettre nos résultats en perspective par rapport aux changements à venir. Il est ainsi prévu que les cycles de feux se raccourcissent, causant une diminution des superficies des vieilles forêts (Bergeron et al. 2010; Bedia et al. 2015; Bergeron et al. 2017). Le maintien d'un taux de récolte similaire à celui observé actuellement jouera néanmoins un rôle plus important dans l'érosion des vieilles forêts que l'augmentation de la récurrence des feux (Bergeron et al. 2017). Les changements de température et de précipitation favoriseront aussi les

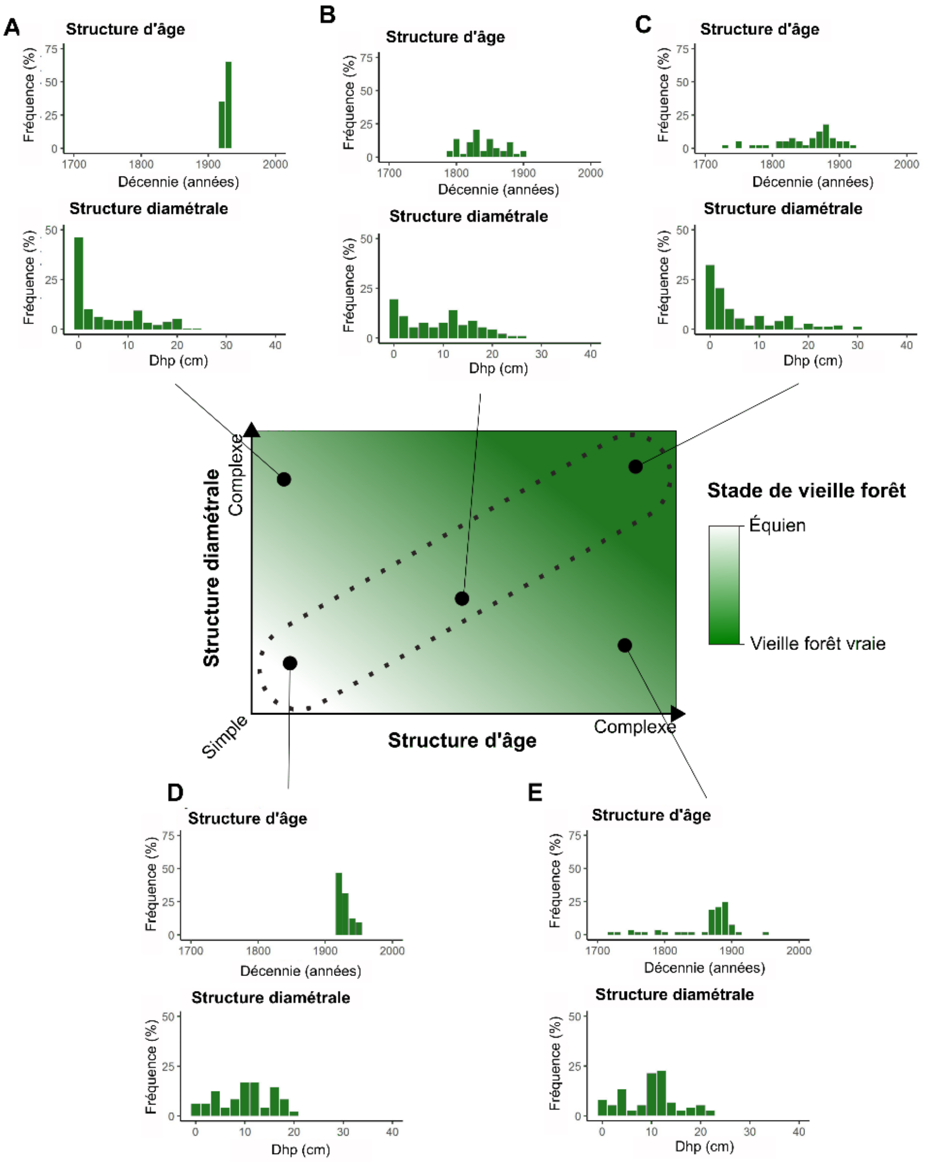


Figure 6-2 Figure conceptuelle représentant la transition du stade de forêt équienne jusqu'au stade de vieille forêt vraie en fonction de l'évolution de la structure diamétrale et de la structure d'âge du peuplement. Les lignes pointillés représentent le chemin de transition vers l'état de vieille forêt couramment attendu (e.g. Oliver and Larson 1996; Wirth et al. 2009). Les points correspondent à certains sites échantillonnés au cours de la thèse et pour lesquels la structure d'âge et la structure diamétrale ont été représentées dans les sous-figures. A : forêt équienne à structure diamétrale complexe, B : vieille forêt en transition, C : vieille forêt vraie, D : forêt équienne, E : forêt inéquienne à structure diamétrale régulière.

espèces forestières tempérées sur la partie sud de la forêt boréale (Périé et al. 2014; Gauthier et al. 2015). Les espèces forestières boréales seront quant à elles moins compétitives dans cette région mais gagneront en productivité au nord, bien que ce gain risque d'être temporaire (D'Orangeville et al. 2016; D'Orangeville et al. 2018a). Ces nouvelles conditions climatiques faciliteront aussi la germination de leurs graines, ce qui pourra mener au développement de peuplements plus denses (Gamache and Payette 2005; Meunier et al. 2007). Il sera par ailleurs possible d'observer des changements phénologiques chez les espèces forestières boréales, notamment un débourrement plus précoce de l'épinette noire, qui pourrait la rendre plus vulnérable à la tordeuse des bourgeons de l'épinette, et par conséquent changer profondément le régime de perturbations secondaire dans la forêt boréale de l'Est du Canada (Pureswaran et al. 2018). La mortalité due aux chablis et aux stress hydriques pourra elle aussi augmenter (Saad et al. 2017; D'Orangevilleet al. 2018a; D'Orangeville et al. 2018b). Les arbres défoliés devenant plus vulnérables en condition de stress hydrique, il est par conséquent possible que les perturbations secondaires gagnent en sévérité (De Grandpré et al. 2018; Bouzidi et al. 2019). La dynamique, la composition et la structure des forêts boréales risquent donc de fortement évoluer dans le futur mais il est encore difficile d'estimer l'impact de ces changements sur les vieilles forêts. Dans ce contexte, les résultats de cette thèse dressent un bilan de la diversité et des dynamiques actuelles des vieilles forêts boréales de l'Est de Canada. Ils pourront cependant être utilisés comme base de travail pour déterminer la manière dont le changement climatique modifiera les caractéristiques de ces écosystèmes.

En raison de l'incertitude quant à la manière dont les vieilles forêts de l'Est Canadien évolueront dans un contexte de changements climatiques, maintenir une proportion suffisante de vieilles forêts dans les territoires aménagés, qui plus est représentative de leur diversité structurelle préindustrielle, paraît être l'option la plus prudente. Les changements de paradigme de gestion forestière observés au cours des dernières décennies, par exemple l'intégration des objectifs d'aménagement écosystèmiques dans la gestion forestière par le Québec en 2013 (Gouvernement du Québec 2013), pourraient contribuer à atteindre ces objectifs. Ainsi, un zonage du territoire forestier, entre forêts à haut rendement basées sur des plantations et des coupes totales, forêts basées sur des coupes partielles ou sélectives et forêts non-aménagées, pourrait ainsi aider à résoudre certaines problématiques mises en avant dans le quatrième chapitre de la thèse, notamment en diminuant la pression de coupe sur les vieilles forêts (Messier et al. 2009; Côté et al. 2010; Tittler et al. 2015). Néanmoins, ce type de stratégie d'aménagement doit aussi s'accompagner d'une démarche active de conservation des vieilles forêts ou des éléments de vieilles forêts au sein des unités d'aménagement. Si le maintien de vieilles forêts résiduelles dans les territoires de coupe est par exemple un objectif à part entière de l'aménagement forestier au Québec, une régression de 70% de leur surface en comparaison de la référence préindustrielle est considéré comme étant le seuil d'altération à ne pas dépasser (MFFP 2016). La valeur de ce seuil a déjà été critiquée par le passé (Vaillancourt et al. 2009) mais des travaux récents sont venus renforcer ces réserves. La proportion de vieilles forêts dans les territoires boréaux de l'Ouest du Québec était ainsi particulièrement stable au cours de l'Holocène (Hennebelle et al. 2018). Réduire la surface des vieilles forêts à 30% de la surface préindustrielle représente donc un changement non-négligeable, potentiellement préjudiciable à de nombreuses espèces (par ex. Drapeau et al. 2009). De plus, ces cibles ne prennent pas à compte l'impact des feux, cumulatif à celui des coupes et pouvant donc contribuer à réduire encore la surface des vieilles forêts résiduelles (Bergeron et al. 2017). Par conséquent, la conservation de vastes surfaces de vieilles forêts dans les territoires exploités est aussi une condition nécessaire pour assurer la soutenabilité de l'aménagement forestier.

De nombreuses expérimentations ont aussi récemment mis en avant la viabilité des coupes partielles ou des coupes sélectives dans les forêts boréales de l'Est Canadien (Ruel et al. 2013; Fenton et al. 2014; Montoro Girona et al. 2016). Ces traitements forestiers pourraient s'approcher de la dynamique de perturbation de sévérité modérée présenté dans le troisième chapitre de la thèse. Il pourrait de cette manière être possible de maintenir une plus large proportion de peuplements présentant des éléments de vieilles forêts dans les territoires aménagés et ainsi de rester plus proche des niveaux préindustriels. Ces traitements doivent néanmoins être utilisés avec précaution afin d'éviter de provoquer une mortalité significative dans les peuplements résiduels (Bose et al. 2014; Montoro Girona et al. 2019) ou de causer l'érosion de certains éléments spécifiques aux vieilles forêts, comme le bois mort (Thorn et al. 2018). De plus, il reste encore des interrogations quant à la viabilité économique de ces systèmes sylvicoles dans des paysages définis par une productivité relativement faible et par un fort éloignement des usines de transformation de la ressource ligneuse (Kneeshaw et al. 2018; Rijal et al. 2018). Les résultats de cette thèse peuvent donc contribuer à modifier la manière dont sont actuellement gérées les vieilles forêts, mais des recherches complémentaires, tant fondamentales qu'appliquées, devraient être réalisées afin de développer des stratégies de gestion forestière et des traitements forestiers permettant de conserver la diversité structurelle préindustrielle des vieilles forêts boréales.

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