UNIVERSITÉ DU QUÉBEC À MONTRÉAL

ACTIVITÉ, FACTEURS DÉTERMINANTS ET CONSÉQUENCES DES FEUX DANS LA FORÊT BORÉALE DU QUÉBEC À L'INTERFACE FORÊTS FERMÉES – FORÊTS OUVERTES

THÈSE

PRÉSENTÉE

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AVANT PROPOS

Ce mémoire de thèse et les articles qu'il contient constituent les contributions originales du doctorat que j'ai effectué au sein de l'Université du Québec à Montréal au Canada (UQAM, programme de sciences de l'environnement).

Cette thèse est constituée d'une introduction générale, de trois chapitres, d'une conclusion générale et d'une annexe. Il s'agit d'une thèse sur articles, ainsi, chacun desdits chapitres constitue un article scientifique qui peut être lu indépendamment du mémoire dans son ensemble. Les chapitres 1 à 3 correspondent aux trois articles scientifiques suivants :

1. Portier, Jeanne, Sylvie Gauthier, Alain Leduc, Dominique Arseneault and Yves Bergeron. « Fire regime along latitudinal gradients of continuous to discontinuous coniferous boreal forests in eastern Canada ». *Forests*, 2016, 7(211), 1-23.
2. Portier, Jeanne, Sylvie Gauthier, André Robitaille and Yves Bergeron. « Accounting for spatial autocorrelation improves the estimation of climate, physical environment and vegetation's effects on boreal forest's burn rates ». *Landscape Ecology*, 2018; 33(1), 19-34.
3. Portier, Jeanne, Sylvie Gauthier, Guillaume Cyr, Yves Bergeron. « Does time since fire drive live aboveground biomass and stand structure in low fire activity boreal forests? Impacts on their management ». Manuscrit soumis à *Journal of Environmental Management* au moment du dépôt de la thèse.

Le paragraphe qui suit vise à préciser mon rôle ainsi que celui des coauteurs dans la réalisation de ces articles. Premièrement, deux campagnes de terrain visant à l'acquisition des données de deux de mes chapitres ont été conduites durant les étés 2013 pour les secteurs de la Baie James, Chibougamau et la Côte Nord, et 2014 pour le secteur de la Rivière Romaine. Avec mes directeurs Sylvie Gauthier et Yves Bergeron, nous avons mis au point le protocole de terrain, qui a également été validé par les deux autres membres de mon comité, Martin P. Girardin (Service Canadien des Forêts, Ressources Naturelles Canada) et André Robitaille (Ministère des Forêts, de la Faune et des Parcs, Direction de la recherche forestière). J'ai préparé et conduit les deux campagnes de terrain afin de récolter les données et échantillons nécessaires. Le matériel et les équipements utilisés ont été fourni par l'UQAM, la station de recherche de Duparquet (UQAT) et par le Centre de Foresterie des Laurentides. Le travail de dendrochronologie en laboratoire a été effectué à l'UQAM, avec les équipements de l'UQAM et du Centre d'étude de la forêt (CEF). Le travail de terrain a été réalisé avec l'aide d'Alix Daguzan et Sylvain Larouche durant la campagne de 2013, et avec l'aide de Dave Gervais, Aurélie Terrier et Joannie Hébert durant la campagne de 2014. Evick Mestre a participé au sablage et aux mesures dendrochronologiques.

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AFD	Aménagement Forestier Durable
AIC	Akaike Information Criterion
BA	Basal Area
BUI	Buildup Index
BR	Burn Rate
CCR	Correct Classification Rate
CI	Confidence Interval
DBH	Diameter at Breast Height
DC	Drought Code
DMC	Duff Moisture Code
FC	Fire Cycle
FFMC	Fine Fuel Moisture Code
FWI	Fire Weather Index
GEMI	Global Environment Monitoring Index
ISI	Initial Spread Index
LD	Land District
MFFP	Ministère des Forêts, de la Faune et des Parcs (Québec)
Moran's I	Moran's Index
NDMI	Normalized Difference Moisture Index
NDVI	Normalized Difference Vegetation Index
NFIP	Northern Forest Inventory Program
PCA	Principal Component Analysis
RAC	Residual AutoCovariate

RSR	Reduced Simple Ratio
SAVI	Soil Adjusted Vegetation Index
SD	Surficial Deposit
TPI	Topographic Position Index
TRI	Terrain Ruggedness Index
TSF	Time Since Fire
WDVI	Wide Dynamic Range Vegetation Index

RÉSUMÉ

En forêt boréale nord-américaine, les feux constituent la perturbation principale. Ils contrôlent de nombreux attributs et processus de la forêt comme la dynamique forestière, la structure des paysages et la composition des peuplements. La variabilité spatiale et temporelle des régimes de feux à travers la zone boréale nord-américaine est très importante, et résulte de divers facteurs environnementaux. Dans la forêt boréale québécoise, les pessières à lichens, des milieux forestiers ouverts et peu productifs, dominent au nord. Plus au sud, les pessières à mousses fermées sont les plus représentées. Les pessières à lichens sont souvent le résultat d'un climat difficile et de perturbations en rafales, principalement les feux, qui mènent à des accidents de régénération. Cependant, la variabilité spatiale et les facteurs déterminants des régimes de feux passés et contemporains sont encore mal connus au nord et à l'interface de ces forêts fermées et ouvertes. De plus, si l'on sait que les feux contrôlent majoritairement le fonctionnement de la forêt boréale, les liens entre le temps depuis feux et la dynamique forestière sont très peu documentés dans les zones soumises à une activité faible des feux.

L'objectif général de cette thèse est d'améliorer les connaissances des régimes de feux passés et contemporains de la forêt boréale résineuse québécoise, à l'interface entre les forêts fermées et les forêts ouvertes, en termes de variabilité spatiale, de facteurs déterminants et de conséquences des feux. La thèse se décline en trois chapitres visant chacun à répondre à une partie de cet objectif général. Le premier chapitre caractérise la variabilité latitudinale des risques de feux des 150-300 dernières années le long de quatre transects orientés nord-sud dans la zone boréale résineuse du Québec. Il fait également le lien entre la variabilité latitudinale du risque de feux et le climat. Le deuxième chapitre cherche à démontrer la performance d'une méthode statistique spatialement explicite dans l'analyse de taux de brûlage. Cette méthode est utilisée pour déterminer la contribution relative du climat, de l'environnement physique et de la végétation à la variabilité spatiale des taux de brûlage contemporains. Le troisième chapitre se concentre sur une zone soumise à un régime de feux caractérisé par des feux rares mais souvent de grande taille, dans le secteur de la rivière Romaine. Ce chapitre vise à caractériser ce territoire en termes de biomasse aérienne, de volume marchand, de structure et de composition des peuplements, ainsi qu'à faire le lien entre ces attributs et le temps depuis feux.

Les résultats de nos travaux indiquent que les régimes de feux dans la forêt boréale résineuse québécoise sont spatialement et temporellement variables. L'activité des feux était la plus importante dans le nord-ouest, pour graduellement diminuer en direction du sud-est. Si la zonation des régimes de feux est restée constante dans le temps, l'activité des feux a diminué entre la période passée et la période contemporaine, à l'exception du nord-ouest de notre zone d'étude. En termes climatiques, nous avons montré que la variabilité latitudinale des risques de feux passés était contrôlée par l'indice de sécheresse (dérivé de températures et précipitations), alors que la variabilité spatiale des taux de brûlage contemporains était climatiquement contrôlée par les précipitations. Les précipitations ont augmenté de façon importante au Canada au cours du XX^{ème} siècle, ce qui expliquerait la différence de contrôles climatiques des feux entre la période passée et contemporaine, ainsi que la diminution de l'activité des feux entre ces deux périodes. Nous avons également montré que sur la période contemporaine, le climat, l'environnement physique et la végétation contribuaient de façon égale à la variabilité spatiale des taux de brûlage. Ceci démontre l'importance de la prise en compte de tous ces facteurs dans les exercices de modélisation des régimes de feux. Nous avons aussi mis en évidence qu'en l'absence de données sur la végétation présente avant un feu, l'utilisation de la végétation potentielle était nécessaire. Contrairement à la végétation actuelle (post-feu), elle permet de prendre en compte la végétation comme une cause et non une conséquence des feux. Par ailleurs, nous avons montré que dans une zone soumise à une rare activité des feux, l'accumulation de biomasse aérienne et de volume marchand était dépendante du temps depuis feux. Ces deux attributs atteignaient leurs pics environ 150 ans après un feu puis commençaient à décliner. Cependant, contrairement à des zones fortement touchées par les feux, la structure des peuplements semblait principalement contrôlée par la productivité des sites et par les perturbations secondaires.

Les implications de nos résultats dans un contexte de changements climatiques sont importantes. En effet, dans le futur l'augmentation des précipitations ne devrait pas permettre de compenser l'augmentation prévue des températures. Ainsi, on pourrait s'attendre à ce que le système climat-feux redevienne contrôlé par les températures, engendrant une augmentation importante des taux de brûlage et de l'occurrence des feux. Ce phénomène est déjà observé dans l'ouest du Canada, et serait peut-être déjà en cours dans le nord-ouest du Québec. En effet, l'activité des feux y a récemment augmenté, ce qui pourrait se propager au reste du territoire dans le futur. Cependant, nous avons montré que malgré les changements temporels de régimes de feux, leur zonation restait stable. Cette zonation correspondait relativement bien à la limite nordique des forêts attribuables qui sépare les forêts ouvertes et naturelles au nord des forêts fermées et aménagées au sud. Si la variabilité future des régimes de feux se maintient à l'intérieur de la variabilité passée, cette zonation devrait ainsi maintenir son inertie. Il serait toutefois important de surveiller l'ouverture des peuplements dans le nord, puisque la transformation de pessières à mousses en pessières à lichens est considérée irréversible naturellement.

Par ailleurs, nos résultats apportent des connaissances utiles pour l'aménagement forestier. En particulier, nous confirmons de précédentes études démontrant que la végétation jouait un rôle important dans le contrôle des taux de brûlage. Ainsi, l'aménagement pourrait se servir de la végétation moins inflammable, principalement les espèces feuillues, pour diminuer les risques de feux et ainsi réduire les impacts des changements climatiques sur les possibilités forestières. Dans le secteur de la rivière Romaine, la biomasse aérienne et le volume marchand sont assimilables à ceux de forêts boréales commerciales. Cependant, puisque l'activité des feux y est faible, les stocks de carbone y sont importants et la proportion de forêts présentant des attributs de vieilles forêts y est considérable. Ces écosystèmes sont extrêmement importants pour le maintien de la biodiversité et des fonctions écologiques. Ainsi, il est indispensable d'implanter des stratégies d'aménagement – possiblement davantage basées sur la structure que sur l'âge des peuplements – adaptées aux vieilles forêts ou aux forêts présentant des attributs de vieilles forêts. D'autre part, le développement économique de cette région, tant d'un point de vue forestier qu'énergétique, doit tenir compte des importants stocks de carbone contenus dans ces forêts.

Mots-clés : Forêt boréale, Québec, limite nordique des forêts attribuables, régime de feux, risque de feux, taux de brûlage, cycle de feux, variabilité spatiale, climat, environnement physique, végétation, biomasse aérienne, volume marchand, structure des peuplements, pessières à lichens, pessières à mousses, forêts ouvertes, vieilles forêts.

ABSTRACT

In the North American boreal forests, wildfires constitute the main disturbance. They control many forest attributes and processes such as forest dynamic, landscape structure and stand composition. The spatiotemporal variability of fire regimes in the North American boreal zone is important, and results from various environmental factors. In the boreal forests of Quebec, spruce-lichen forests, that are mainly composed of unproductive open forests, dominate in the North. Further south, closed spruce-moss forests are the most represented. Spruce-lichen forests often result from harsh climatic conditions and recurring disturbances, especially wildfires, that lead to regeneration accidents. However, the spatial variability of past and current fire regimes as well as their controlling factors are still poorly known in the North and at the limit between closed and open forests. Moreover, if we know that fires are the main drivers of boreal forests, the relation between time since fire and forest dynamics is poorly documented in areas subject to low fire activity.

The main objective of this thesis is to improve knowledge on past and current fire regimes in the coniferous boreal forests of Quebec at the limit between open and closed forests in terms of spatial variability, controlling factors and consequences of fires. This thesis is composed of three chapters, each aiming at answering part of this general objective. The first chapter characterizes the fire risk latitudinal variability of the past 150-300 years along four north-south oriented transects in the coniferous boreal zone of Quebec. It also establishes the relation between the latitudinal variability of fire risks and climate. The second chapter aims at demonstrating the performance of a spatially explicit statistical method for burn rates analyses. This method is used to determine the relative contribution of climate, physical environment and vegetation to the spatial variability of current burn rates. The third chapter focuses on an area subject to a fire regime characterized by rare, but large fires in the Romaine River area. It aims at characterizing this territory in terms of live aboveground biomass, merchantable volume, stand structure and composition, as well as at establishing the relation between these attributes and time since fire.

Our results showed that fire regimes in the coniferous boreal forests of Quebec are both spatially and temporally variable. Fire activity was highest in the Northwest, and gradually decreased towards the Southeast. If the fire regime zonation remained constant through time, fire activity decreased between the past and current period, except for the north-westernmost part of our study area. In terms of climate, we showed

that the latitudinal variability of past fire risks was controlled by the drought code (index derived from temperatures and precipitation), while the spatial variability of current burn rates was climatically controlled by precipitation. Precipitation has increased importantly in Canada during the 20^{th} century, which could explain the differences in climatic controls of fires between the two periods. We also showed that over the current period, climate, physical environment and vegetation contributed equally to the spatial variability of burn rates. This demonstrates the importance of taking all these factors into account when modelling fire regimes. Besides, we pointed out that when data about the vegetation prevailing prior to a fire is unavailable, it is crucial to use potential vegetation. Contrary to current vegetation (post-fire), it takes into account vegetation as a cause instead of a consequence of fires. Furthermore, we showed that in an area subject to low fire activity, the accumulation of live aboveground biomass and merchantable volume depended on the time since the last fire. These two attributes reached their peaks around 150 years after a fire and then started to decline. However, contrary to areas subject to high fire activity, stand structure seemed mainly controlled by sites productivity and non-fire disturbances.

Our results have great implications in a context of climate change. Indeed, the expected increase in precipitation in the future should not be able to compensate for the increase in temperatures. Therefore, the climate-fire system could go back to being controlled by temperatures, leading to an important increase in burn rates and fire occurrence. This phenomenon is already observed in western Canada and could also be happening in northwestern Quebec. Indeed, fire activity has recently increased in this area, which could eventually propagate to the rest of Quebec in the future. However, we showed that despite temporal changes in fire regimes, their zonation remained stable. This zonation corresponded relatively well to the northern limit of commercial forests that separates open, natural forests in the North from closed, managed forests to the South. If the future fire regime variability remains within the past variability, this zonation should also maintain its inertia. Nevertheless, it would be important to monitor the opening of forests in the North, as the transformation of spruce moss forests to spruce lichen forests is considered naturally irreversible.

Furthermore, our results bring useful knowledge for forest management. Particularly, we confirmed previous studies demonstrating that vegetation plays an important role in controlling burn rates. Therefore, forest management could use less flammable vegetation, mainly deciduous species, to decrease fire risks and therefore reduce climate change impacts on allowable cut. In the Romaine River area, the live aboveground biomass and merchantable volume are similar to that of boreal commercial forests. However, as fire activity is low, carbon stocks are high and the proportion of forests presenting attributes of old forests is large. These ecosystems are extremely important for biodiversity and ecological functions. Therefore, it is essential to implement management strategies – possibly based on stand structure rather than on stand age – adapted to old forests or to forests presenting attributes of old forests.

Moreover, economic development for forest products and energy should take into account the large carbon stocks contained in these forests.

Keywords: Boreal forest, Quebec, northern limit of commercial forests, fire regime, fire risk, burn rate, fire cycle, spatial variability, climate, physical environment, vegetation, live aboveground biomass, merchantable volume, stand structure, spruce-lichen forests, spruce-moss forests, open forests, old forests.

INTRODUCTION

0.1 Le biome circumboréal

Le biome boréal est l'une des plus importantes zones biogéographiques de la planète, couvrant environ 30% des forêts mondiales, répartis sur une large proportion de l'Amérique du Nord et de l'Eurasie (Brandt 2009; de Groot et al. 2013a; Gauthier et al. 2015a). Il est défini comme une zone de végétation circumpolaire de hautes latitudes nordiques, contenant des forêts et autres terrains boisés présentant des espèces d'arbres tolérantes aux climats froids (Brandt 2009). On y retrouve majoritairement, en proportions variables d'une zone à une autre, des espèces résineuses issues des genres *Abies*, *Larix*, *Picea* et *Pinus* ainsi que des espèces feuillues des genres *Betula*, *Populus* et *Alnus* (Johnson 1992; Brandt 2009; Shorohova et al. 2011). La zone boréale présente un gradient climatique nord-sud marqué par des températures moyennes plus froides au nord qu'au sud. Ce gradient, en créant des conditions d'établissement et de croissance graduellement plus difficiles vers le nord pour les espèces arborées, est en partie responsable de l'ouverture des peuplements. On retrouve donc généralement des forêts fermées au sud, s'ouvrant progressivement pour finalement former des paysages de toundra au nord (Soja et al. 2007; Brandt et al. 2013).

Outre le climat, la dynamique des forêts boréales est principalement contrôlée par l'occurrence de perturbations telles que les feux, les épidémies d'insectes et le vent (Volney and Fleming 2000; Ryan 2002; Kuuluvainen and Ankala 2011; Gauthier et al. 2015a). Ces perturbations peuvent jouer un rôle à différentes échelles, affectant des zones allant de quelques ares à des millions d'hectares (Shorohova et al. 2011; de Groot et al. 2013a; Gauthier et al. 2015a). Cependant, les feux sont reconnus comme étant la perturbation principale dans les forêts boréales du globe, et sont indispensables au maintien de ces écosystèmes et de leur biodiversité (Wein and MacLean 1983; Johnson 1992; Weber and Flannigan 1997; Ryan 2002). Les feux contrôlent la composition mais aussi la structure des forêts boréales et la mosaïque de leurs paysages (Wein and MacLean 1983; Johnson 1992; Weber and Flannigan 1997; Ryan 2002). En effet, un paysage soumis à une forte activité de feux sera composé d'une proportion importante de peuplements jeunes (Van Wagner 1978), contenant majoritairement des espèces de début de succession qui se régénèrent rapidement après un feu (Johnson 1992). Les espèces d'arbres que l'on retrouve en forêt boréale ont évolué avec les feux, et ont ainsi développé des stratégies leur permettant d'y faire face, bien que celles-ci puissent différer d'un continent à l'autre. En Russie, certains arbres (ex : *Pinus sylvestris* L.) présentent par exemple une écorce épaisse leur permettant de survivre aux feux de surface qui y sont majoritaires (Wein and MacLean 1983; de Groot et al. 2013a; Rogers et al. 2015). En Amérique du Nord, certaines espèces ont développé des cônes sérotineux (ex : *Pinus blanksiana* Lamb., *Pinus contorta* Dougl.) ou semi-séritoneux (ex : *Picea mariana* (Mill.) BSP) qui protègent les graines des feux et assurent ainsi la régénération de ces espèces dans une région boréale où l'on retrouve majoritairement des feux de couronne (Lotan 1976; Gauthier et al. 1993; de Groot et al. 2013b).

Les feux peuvent être causés par la foudre ou encore être d'origine humaine. Par exemple en Russie, 86% des feux sont causés par l'homme (Shvidenko and Nilsson 2000), ce qui explique pourquoi la majorité des feux surviennent au printemps dans ce pays (de Groot et al. 2013a). Au Canada, bien que les feux de foudre ne représentent que 35% des feux, ils causent plus de 80% de l'aire brûlée annuellement (Weber and Stocks 1998; Stocks et al. 2003). En effet, les feux d'origine humaine se produisent le plus souvent dans des régions plus peuplées où leur détection est rapide et où les agences de suppression peuvent intervenir dans de cours délais. Au contraire, les feux de foudre peuvent prendre plus de temps à être détectés et ainsi devenir incontrôlables avant même que les agences de suppression ne puissent intervenir. Cependant, lorsque les conditions météorologiques sont propices aux feux et que le combustible est majoritairement résineux, les risques que les feux s'échappent et induisent de grandes aires brûlées sont très élevés, indépendamment de l'origine de ces feux (Stocks et al. 2003; Chabot et al. 2009; de Groot et al. 2013a).

0.2 Variabilité spatiale des régimes de feux en forêt boréale

Un régime de feux peut être caractérisé par différents attributs dérivés des distributions de taille, de forme, d'occurrence, de la saisonnalité, de l'intensité ou encore de la sévérité des feux dans un territoire donné et sur une certaine période de temps (Johnson and Gutsell 1994; Krebs et al. 2010). Parmi les plus utilisés, on retrouve par exemple le taux de brûlage annuel, c'est-à-dire la proportion d'une zone qui est brûlée annuellement ; ou encore son inverse, le cycle de feu qui est défini comme le temps requis pour brûler une superficie égale à celle de la zone d'étude (Van Wagner 1978). Les régimes de feux sont grandement variables à travers toute la zone boréale (Wein and MacLean 1983; de Groot et al. 2013a; Rogers et al. 2015). En dépit de la nature semi-aléatoire des feux, cette variabilité spatiale est malgré tout le résultat de divers processus et facteurs environnementaux. Ceux-ci peuvent être classés en deux groupes : ceux agissant du haut vers le bas (« top-down ») à des échelles régionales à globales, et ceux agissant du bas vers le haut (« bottom-up ») à des échelles locales à régionales.

Dans le premier groupe, on retrouve principalement le climat (Stocks et al. 1998; Flannigan et al. 2005; Soja et al. 2007; Girardin et al. 2009), alors que le deuxième est constitué par exemple de l'environnement physique et de la végétation (Johnson 1992; Parisien et al. 2014; Rogers et al. 2015; Rogeau and Armstrong 2017). Les variations spatiales des régimes de feux dans la zone boréale peuvent être liées à l'un ou à plusieurs de ces facteurs, dépendamment de l'échelle à laquelle on se positionne (Bélisle et al. 2016). Par exemple, il a été montré que les taux de brûlage actuels en Sibérie sont plus importants que ceux du Canada (de Groot et al. 2013a), et que ces différences seraient dues majoritairement aux espèces d'arbres dominantes (Rogers et al. 2015). En effet, les forêts boréales russes contiennent principalement des espèces moins propices aux feux de couronnes et résistant aux feux de surface. Au contraire, les forêts boréales nord-américaines sont dominées par des espèces qui ont besoin des feux pour se disperser et qui sont plus propices aux feux de couronne (de Groot et al. 2013a; Rogers et al. 2015). Si l'on se place à l'échelle de la forêt boréale nord-américaine, on observe que les taux de brûlage sont plus importants à l'ouest qu'à l'est (Zhang and Chen 2007). Dans ce cas, les différences climatiques expliquent ce phénomène puisque l'Ouest connait un climat plus sec que l'Est (Flannigan and Harrington 1988; Girardin and Wotton 2009; Brandt et al. 2013). A une échelle plus locale, il a été démontré que l'environnement physique comme les combinaisons de dépôt de surface-drainage au centre du Québec (Mansuy et al. 2010) ou encore l'altitude et la topographie dans les montagnes Rocheuses de l'Alberta (Rogeau and Armstrong 2017) jouaient un rôle dans la variabilité spatiale des régimes de feux.

0.3 Variabilité temporelle des régimes de feux en forêt boréale et changements climatiques

Outre la variabilité spatiale des régimes de feux, leur variabilité temporelle a elle aussi été démontrée dans l'ensemble de la zone boréale à diverses échelles allant d'annuelle à milléniale. Cette variabilité temporelle résulte principalement des variabilités climatiques et météorologiques (Flannigan and Harrington 1988; Brandt et al. 2013). En effet, le climat et la météorologie influencent non seulement l'ignition naturelle des feux, mais aussi les conditions d'humidité du sol et du combustible qui régulent la capacité de propagation, l'intensité et la sévérité des feux (Stocks et al. 1998; Girardin and Wotton 2009; Flannigan et al. 2016). De nombreuses études ont démontré qu'au cours de l'Holocène, les grandes périodes de feux en termes d'aire brûlée et de nombre de feux étaient liées à des conditions climatiques plus chaudes et plus sèches (Carcaillet et al. 2001; Girardin et al. 2009; Kelly et al. 2013). Sur une échelle centennale, les conditions humides qui ont prévalu en Amérique du Nord après la fin du Petit Age Glaciaire (~1850) ont mené à une diminution de l'activité des feux (Bergeron and Archambault 1993; Macias Fauria and Johnson 2008). Enfin, à l'échelle annuelle, l'activité des feux peut être extrêmement variable (Stocks et al. 2003). Il a été montré que les années de grands feux étaient liées aux années de sécheresse extrême tant en Sibérie, en Alaska qu'au Canada (Soja et al. 2007; Girardin 2010; Beck et al. 2011; Kelly et al. 2013).

Dans un contexte de changements climatiques, le contrôle du climat sur les régimes de feux est l'une des préoccupations les plus importantes en forêt boréale. En effet, la zone boréale est l'un des biomes risquant d'être le plus durement touché par les changements climatiques (IPCC 2014). Les régions boréales pourraient faire face à des augmentations de températures de 4 à 11°C d'ici la fin du 21ème siècle ainsi qu'à une faible augmentation des précipitations (IPCC 2014). Cependant, l'augmentation des précipitations ne devrait pas être en mesure de compenser les températures plus élevées, entrainant potentiellement une fréquence accrue des épisodes de sécheresse responsables des années de grands feux (Girardin and Mudelsee 2008; Bergeron et al. 2010; Kelly et al. 2013; Flannigan et al. 2016). Dans un futur relativement proche, la littérature scientifique s'accorde ainsi sur une augmentation de la longueur et l'intensité des saisons de feux (Wotton and Flannigan 1993; Westerling et al. 2006; Liu et al. 2012; Flannigan et al. 2013), pouvant possiblement mener à l'occurrence de feux auxquels les agences de protection contre les feux ne pourraient pas faire face (Flannigan et al. 2009; Podur and Wotton 2010). Les conséquences sur la société peuvent être dramatiques, à l'image de celles du feu de Fort McMurray qui a sévi en Alberta au printemps 2016.

De plus, la forêt boréale détient une large proportion des stocks terrestres de carbone (de Groot et al. 2013a; IPCC 2014; Bradshaw and Warkentin 2015). Dans le contexte actuel de changements climatiques, on cherche à limiter les émissions et à maximiser les puits de carbone (IPCC 2014). Or, les feux relarguent une quantité importante de carbone dans l'atmosphère (de Groot et al. 2007; Bond-Lamberty et al. 2007). Ainsi, une augmentation de l'activité des feux aura des répercussions importantes sur le bilan de carbone de la forêt boréale. Cependant, les vieilles forêts, majoritaires dans les zones soumises à une faible activité des feux, sont connues pour stocker des quantités très importantes de carbone (Luyssaert et al. 2008). Ainsi, ces régions peu affectées par les feux nécessitent une attention particulière face aux changements climatiques due à leur rôle de grands séquestrateurs de carbone (Luyssaert et al. 2008).

0.4 Forêt boréale et aménagement forestier

En plus des pressions climatiques et liées aux perturbations, la forêt boréale est également soumise aux pressions associées aux activités humaines. En Scandinavie, l'exploitation intensive de la matière ligneuse a mené à une quasi-disparition des forêts naturelles, à des pertes importantes de biodiversité et à une dégradation importante des paysages (Kuuluvainen 2002). Au Canada, dont presque un tiers de la surface est couvert par la zone boréale (Brandt 2009), l'exploitation forestière intensive n'a débuté qu'au début du XIX^{ème} siècle (CCMF 2008). Durant la première partie du XX^{ème} siècle, une mauvaise perception du fonctionnement des régimes de feux et une volonté de maximiser le rendement ont cependant entraîné la généralisation de grandes coupes à blanc supposées recréer les patrons spatiaux des feux (Seymour and Hunter Jr 1999; Gunderson 2000; Burton et al. 2003). Cependant, bien que responsables d'une large proportion de l'aire brûlée annuellement, les grands feux ne représentent en réalité qu'une faible part de la variabilité naturelle des régimes de feux (Stocks et al. 2003). Ainsi, les impacts négatifs de ce type de coupes ainsi que du fort taux de récolte appliqué se sont rapidement manifestés (Bergeron et al. 2017).

L'exemple de la Scandinavie a finalement permis une prise de conscience qui a mené le Canada à s'engager à intégrer le concept d'aménagement forestier durable (AFD) dans les lois régissant le secteur forestier en 1992. L'AFD au Canada implique une meilleure compréhension du fonctionnement de l'écosystème forestier boréal permettant une récolte soutenable dans le temps et dans l'espace de la matière ligneuse, tant d'un point de vue écologique que socio-économique. En effet, la forêt boréale représente aujourd'hui une source considérable de ressources naturelles et de biodiversité (Brandt et al. 2013; Gauthier et al. 2015a), et constitue ainsi une part importante de l'économie du Canada (Bogdanski 2008). Cependant, le secteur forestier va devoir rapidement faire face aux défis et enjeux qu'apportent les changements climatiques (Gauthier et al. 2014; Gauthier et al. 2015a). Les altérations attendues de la composition et de la structure des écosystèmes forestiers boréaux s'ajoutent aux enjeux de l'aménagement et questionnent la pérennité de l'AFD tel qu'il est pratiqué aujourd'hui si aucune mesure n'est prise rapidement. Il y a une volonté tant de la part de la communauté scientifique que des gouvernements fédéral et provinciaux de faire progresser nos connaissances sur les impacts des changements climatiques sur les écosystèmes forestiers boréaux et leurs perturbations, afin de mettre en place de nouvelles stratégies d'AFD capables de faire face à ces défis (Hirsch et al. 2004; Johnston et al. 2006; Gauthier et al. 2015a).

0.5 La forêt boréale québécoise et ses enjeux

Au Québec, la zone boréale est constituée, du nord vers le sud, des domaines bioclimatiques de la toundra forestière, la pessière à lichens, la pessière à mousses et enfin la sapinière à bouleau blanc. La limite nordique des forêts attribuables traverse le domaine de la pessière à mousses du Québec d'est en ouest. Elle sépare les forêts commerciales au sud des forêts naturelles au nord où l'aménagement forestier n'est pas permis. Cette limite a été établie principalement dans le but d'éviter l'exploitation de territoires où l'aménagement forestier ne pourrait pas être durable (MFFPQ 2013). En effet, ces forêts font face à des conditions climatiques et de régimes de perturbations rendant difficiles les conditions d'établissement et de croissance des arbres. Au nord de la limite nordique, on retrouve la quasi-totalité des pessières à lichens. Ces milieux forestiers ouverts et peu productifs sont le résultat du climat mais surtout de l'occurrence de perturbations en rafales menant à des accidents de régénération (Payette et al. 2000; Jasinki and Payette 2005; Mansuy et al. 2013). En effet, l'occurrence de feux à courts intervalles peut limiter la disponibilité de semences (élimination des semenciers ou graines brûlées si elles ont déjà été dispersées - Sirois 2000), l'établissement des semis (Moss and Hermanutz 2009) et la disponibilité des lits de germination (Greene et al. 2007).

Dans un contexte de changements climatiques où l'on s'attend à une augmentation de l'activité des feux (Zhang and Chen 2007; Bergeron et al. 2010; Boulanger et al. 2013; Flannigan et al. 2016), ce phénomène constitue un enjeu majeur. En effet, le passage d'une pessière à mousses dense et fermée à une pessière à lichens ouverte est considéré irréversible (Jasinki and Payette 2005). Les 50 dernières années ont déjà connu une expansion importante des landes à lichens due principalement à l'augmentation récente de l'activité des feux (Girard et al. 2008). La zone de transition entre la pessière à mousses et la pessière à lichens nécessite donc une attention particulière tant de la part des scientifiques que des preneurs de décisions et des aménagistes. Dans l'hypothèse où cette zone de transition se déplacerait vers le sud en réponse aux changements du climat et des régimes de perturbations, la limite nordique des forêts attribuables devrait nécessairement être réajustée. Pourtant, la variabilité des régimes de feux de part et d'autre de la limite nordique, ainsi que les mécanismes la contrôlant sont aujourd'hui encore mal connus.

Le long du gradient longitudinal, la forêt boréale québécoise présente une intensification des régimes de feux de l'est vers l'ouest (Gauthier et al. 2015b). En particulier, l'activité des feux contemporaine la plus importante se situe au nord-ouest du Québec dans la région de la Baie James (Héon et al. 2014; Gauthier et al. 2015b; Erni et al. 2016), avec des cycles de feux très courts de l'ordre de 45 à 60 ans (Gauthier et al. 2015b). A l'inverse, la région de la Côte Nord, localisée au sud-est, est soumise à des cycles de feux beaucoup plus longs atteignant jusqu'à plus de 8000 ans (Gauthier et al. 2015b). Le gradient de précipitations au Québec suit ce gradient de régime de feux, avec des précipitations moyennes annuelles augmentant graduellement du nord-ouest vers le sud-est. Cependant, la contribution relative du climat par rapport à des facteurs environnementaux agissant du bas vers le haut (« bottom-up ») comme l'environnement physique ou encore la végétation est mal connue à l'échelle du Québec, bien qu'elle ait en partie été documentée à des échelles plus locales dans certains secteurs (e.g. Mansuy et al. 2014; Cavard et al. 2015).

Si les régimes de feux et les dynamiques forestières en résultant sont très bien documentés dans les forêts commerciales de l'ouest du Québec (Bergeron et al. 2002; Harper et al. 2002; Simard et al. 2009), ces processus sont moins bien compris dans les forêts de l'est de la Côte Nord, et surtout dans les territoires encore fermés à l'aménagement. Pourtant, le secteur de la rivière Romaine a récemment été ouvert au développement économique pour les secteurs forestier et énergétique (MFFPQ 2013). L'aménagement forestier écosystémique, prôné dans les forêts aménagées du Québec, vise « à maintenir des écosystèmes sains et résilients en misant sur une diminution des écarts entre les paysages naturels et ceux qui sont aménagés afin d'assurer, à long terme, le maintien des multiples fonctions de l'écosystème et, par conséquent, de conserver les bénéfices sociaux et économiques que l'on en retire » (Landres et al. 1999; Franklin et al. 2002; Gauthier et al. 2008b). Cette approche aspire ainsi à reproduire la variabilité historique à laquelle la forêt s'est adaptée. Celle-ci étant largement façonnée par les régimes de perturbations (Johnson 1992; Brandt et al. 2013), c'est en amenant l'aménagement forestier à reproduire la variabilité naturelle de ceux-ci que les attributs principaux de la forêt naturelle devraient pouvoir être conservés (Landres et al. 1999; Drever et al. 2006; Bergeron et al. 2007; Gauthier et al.

2009). Pour appliquer ces concepts, il est évident qu'une connaissance détaillée des régimes de perturbations ainsi que de la dynamique forestière de chacune des unités d'aménagement est indispensable.

La Côte Nord, puisque soumise à des cycles de feux très longs (Bouchard et al. 2008; Gauthier et al. 2015b), comprend des proportions importantes de vieilles forêts (Van Wagner 1978) qui stockent de grandes quantités de carbone (Luyssaert et al. 2008). Ces vieilles forêts sont souvent soumises à des perturbations secondaires comme les épidémies d'insectes et les chablis engendrant des dynamiques de trouées (Blais 1983; De Grandpré et al. 2000; McCarthy 2001; Pham et al. 2004; Girard et al. 2014). La protection et la conservation de ces vieilles forêts constituent l'une des priorités dans la mise en place de stratégies d'aménagement écosystémique dans un contexte de changements climatiques (Comité d'experts sur l'aménagement écosystémique des forêts et les changements climatiques 2017). Un certain nombre de recherches propose déjà des stratégies permettant de conserver une certaine proportion de ces vieux peuplements ou encore d'utiliser des techniques de sylviculture permettant de reproduire leurs attributs (Burton et al. 1999; Bauhus et al. 2009; Shorohova et al. 2011). En effet, les vieilles forêts possèdent des attributs qui leurs sont propres, comme la présence de vieux arbres vivants ou morts sur pied de gros diamètre, ainsi que d'importantes quantités de bois mort au sol (Kneeshaw and Gauthier 2003; Bergeron and Fenton 2012). De ce fait, elles renferment une importante biodiversité dépendante de ces attributs, en particulier des espèces d'oiseaux (Schmiegelow and Mönkkönen 2002; Drapeau et al. 2009), d'insectes (Saint-Germain et al. 2007) et de bryophytes (Bergeron and Fenton 2012), qui même si elles ne sont pas toujours restreintes à ce stade de la succession forestière, y atteignent tout de même leur pic d'abondance (Bergeron and Fenton 2012).

Ainsi, des territoires nouvellement ouverts à l'aménagement comme ceux du secteur de la Rivière Romaine qui sont soumis des feux rares mais de grande taille, à des régimes de perturbations secondaires non négligeables, contenant de larges proportions de vieilles forêts et stockant d'importantes quantités de carbone, doivent nécessairement être mieux compris si l'implémentation d'un aménagement écosystémique est souhaitée. En particulier, une estimation de la biomasse forestière disponible constitue une information importante pour les aménagistes, puisqu'elle permet de déterminer si la récolte dans un secteur peut, à première vue, être rentable. Toutefois, il est crucial de comprendre comment cette biomasse est répartie en fonction du temps depuis le dernier feu, mais aussi en fonction de la structure des peuplements afin de définir si elle est majoritairement contenue dans les vieux peuplements ou dans les peuplements présentant des attributs de vieilles forêts, auxquels cas elle ne serait pas nécessairement disponible pour la récolte.

0.6 Présentation des chapitres de la thèse

Cette thèse a pour objectif général la caractérisation de la variabilité spatiale des régimes de feux passés et contemporains à l'interface forêts fermées – forêts ouvertes dans la zone boréale résineuse du Québec. Elle vise également la détermination des facteurs environnementaux responsables de cette variabilité spatiale, ainsi que des conséquences des régimes de feux observés sur les peuplements – en particulier dans une zone soumise à une faible activité des feux où les liens entre le temps depuis feux et la biomasse et dynamique des peuplements sont encore mal compris.

La thèse est constituée de trois chapitres représentant trois publications scientifiques tentant de répondre à des questions relatives au régime des feux de part et d'autre de la limite nordique des forêts attribuables du Québec.

Le premier chapitre a pour objectif de i) reconstituer l'historique des feux des 300 dernières années au Québec le long de gradients latitudinaux répartis de part et d'autre de la limite nordique des forêts attribuables, et ii) tester l'effet du climat sur la variabilité latitudinale des risques de feux. Dans ce chapitre, nous testons également la constance temporelle de la zonation spatiale des régimes de feux en comparant les points de rupture en termes de risque de feux le long des gradients latitudinaux avec la zonation des cycles de feux contemporains effectuée par Gauthier et al. (2015b). L'historique des feux a été reconstitué à partir de données d'archives de feux et d'une campagne de terrain effectuée le long de quatre transects orientés nord-sud et distribués équitablement d'est en ouest dans les pessières à mousses et à lichens du Québec. Des analyses de survie ont ensuite permis de caractériser le risque de feux relatif le long des transects et de délimiter des zones de feux homogènes dans chaque transect, dans lesquelles les cycles de feux ont été calculés.

Le deuxième chapitre se concentre sur la période contemporaine et cherche à mieux comprendre les régimes de feux à travers une plus grande variété de facteurs déterminants que le premier chapitre. Il a pour objectif de tester la validité d'une méthode spatialement explicite impliquant des modèles logistiques ordinaux pour analyser la contribution relative du climat, de l'environnement physique et de la végétation à la variabilité spatiale des taux de brûlage.

Le troisième chapitre se concentre sur le secteur de la Rivière Romaine situé dans la région de la Côte Nord du Québec, où le régime de feux se définit par des feux rares mais de grande taille. Il a pour objectif : i) la caractérisation de la biomasse aérienne vivante, du volume marchand, de la structure et de la composition des peuplements, et ii) d'établir les liens entre le temps depuis feux et la biomasse, le volume marchand, la structure et la composition des peuplements.

La thèse se poursuit avec une conclusion générale où nous revenons sur les principaux résultats et en synthétisons les apports à la compréhension des régimes de feux boréaux, leurs facteurs déterminants ainsi que leurs conséquences. Les implications de nos résultats dans un contexte de changements climatiques ainsi que pour l'aménagement forestier sont également discutées. Finalement, une annexe décrit les caractéristiques principales du régime de feux contemporain de la forêt boréale résineuse du Québec, ainsi que les distributions de taille et de nombre de feux dans les zones de feux homogènes déterminées par Gauthier et al. (2015b). Cela a permis de documenter la variabilité spatiale contemporaine des régimes de feux dans les pessières à mousses et à lichens québécoises.

CHAPITRE I

FIRE REGIME ALONG LATITUDINAL GRADIENTS OF CONTINUOUS TO DISCONTINUOUS CONIFEROUS BOREAL FORESTS IN EASTERN CANADA

(RÉGIME DE FEUX LE LONG DE GRADIENTS LATITUDINAUX DE LA FORÊT BORÉALE CONIFÉRIENNE CONTINUE À DISCONTINUE DE L'EST DU CANADA)

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1.1 Abstract

Fire is the main disturbance in North American coniferous boreal forests. In Northern Quebec, Canada, where forest management is not allowed, the landscape is gradually constituted of more opened lichen woodlands. Those forests are discontinuous and show a low regeneration potential resulting from the cumulative effects of harsh climatic conditions and very short fire intervals. In a climate change context, and because the forest industry is interested in opening new territories to forest management in the north, it is crucial to better understand how and why fire risk varies from the north to the south at the transition between the discontinuous and continuous boreal forest. We used time-since-fire (TSF) data from fire archives as well as a broad field campaign in Quebec's coniferous boreal forests along four north-south transects in order to reconstruct the fire history of the past 150 to 300 years. We performed survival analyses in each transect in order to (1) determine if climate influences the fire risk along the latitudinal gradient; (2) fractionate the transects into different fire risk zones; and (3) quantify the fire cycle—defined as the time required to burn an area equivalent to the size of the study area—of each zone and compare its estimated value with current fire activity. Results suggest that drought conditions are moderately to highly responsible for the increasing fire risk from south to north in the three westernmost transects. No climate influence was observed in the last one, possibly because of its complex physical environment. Fire cycles are shortening from south to north, and from east to west. Limits between high and low fire risk zones are consistent with the limit between discontinuous and continuous forests, established based on recent fire activity. Compared to the last 40 years, fire cycles of the last 150–300 years are shorter. Our results suggest that as drought episodes are expected to become more frequent in the future, fire activity might increase significantly, possibly leading to greater openings within forests. However, if fire activity increases and yet remains within the range of variability of the last 150–300 years, the limit between open and closed forests should stay relatively stable.

Keywords: fire history reconstruction; fire cycle; fire risk; black spruce–moss forests; lichen woodlands; boreal ecosystems; fire weather; survival analyses.

1.2 Résumé

Les feux sont la principale perturbation dans la forêt boréale nord-américaine. Dans le nord du Québec, où l'aménagement forestier n'est pas permis, les paysages sont constitués d'une partie importante de pessières à lichens ouvertes. Ces forêts sont discontinues et ont un faible potentiel de régénération résultant des effets cumulatifs des conditions climatiques difficiles et des intervalles courts entre les feux. Dans un contexte de changements climatiques, et du fait de territoires nouvellement ouverts à l'aménagement forestier au nord, il est crucial de mieux comprendre comment et pourquoi les risques de feux varient du nord au sud à la transition entre les forêts boréales discontinues et continues. Nous avons utilisé des données de temps depuis feux provenant d'archives ainsi que d'une campagne de terrain dans la forêt boréale résineuse québécoise, le long de quatre transects orientés nord-sud, afin de reconstruire l'historique des feux des dernières 150-300 années. Nous avons effectué des analyses de survie dans chaque transect afin de 1) déterminer si le climat influençait le risque de feux le long du gradient latitudinal ; 2) fractionner les transects en différentes zones de risque de feux ; et 3) quantifier les cycles de feux – définis comme le temps requis pour brûler une surface équivalente à celle de la zone d'étude – de chaque zone et les comparer avec les cycles de feux actuels. Les résultats suggèrent que les conditions de sécheresse étaient modérément à hautement responsables de l'augmentation des risques de feux du sud vers le nord dans les trois transects les plus à l'ouest. Dans le dernier transect, l'influence climatique n'a pas pu être démontrée, possiblement à cause de la complexité de son environnement physique. Les cycles de feux se raccourcissaient du sud vers le nord, et d'est en ouest. Les limites entre les zones à haut et faible risque de feux étaient relativement similaires à la limite entre les forêts continues et discontinues qui résulte de l'activité contemporaine des feux. Les cycles de feux que nous avons

calculés sur les derniers 150-300 ans étaient plus courts que les cycles de feux des 40 dernières années. Nos résultats suggèrent que puisque les épisodes de sécheresse devraient être plus fréquents dans le futur, l'activité des feux pourrait augmenter de façon importante, ce qui pourrait aggraver l'ouverture des peuplements au nord. Cependant, si l'activité future des feux augmente tout en se maintenant dans la gamme de variabilité de l'activité passée des feux, la limite entre les forêts ouvertes et fermées devrait rester relativement stable.

Mots-clés : Reconstruction de l'historique des feux; cycle de feux; risque de feux; pessière à mousses; pessières à lichens; forêt boréale; indices forêt-météo; analyses de survie.

1.3 Introduction

By controlling structural and compositional attributes, fire is the main disturbance shaping the North American boreal forest (Johnson 1992; Payette 1992). Fires affect the forest's structure by creating a mosaic of stands of different ages and sizes (Gauthier et al. 1996; Johnson et al. 1998), thus constantly rejuvenating stands and landscapes. Fire cycles, defined as the time required to burn an area equivalent to that of the study area (Johnson and Gutsell 1994; Li 2002), determine the age structure of forest stands (Van Wagner 1978; Cyr et al. 2009) across the landscape. Fires also influence stands' composition by controlling succession patterns, for instance, by favoring fire-adapted species such as jack pine (*Pinus banksiana*) or black spruce (*Picea mariana*) (Gauthier et al. 2000; Bouchard et al. 2008; Girard et al. 2009). Fire regimes are highly variable in space as a result of various environmental factors acting on different scales (Senici et al. 2010; Parisien et al. 2011; Bélisle et al. 2016). Climate acts as a top-down factor from regional to continental scales. In Canada, for instance, the increasing gradient of fire activity observed from east to west is caused by the spatial variability in the frequency of drought events (Flannigan and Harrington 1988; Girardin and Wotton

2009). However, topography (Van Wagner 1988; Bélisle et al. 2016), surficial deposits and drainage (Mansuy et al. 2010), or fuel type and availability (Hély et al. 2010) are bottom-up factors which act from stand to regional scales. Fire regimes also vary in time; for example, the end of the Little Ice Age that occurred around 1850 represents a well-known transition to lower fire cycles in eastern Canada (Ali et al. 2009; Cyr et al. 2009). Temporal variations in fire activity are mainly driven by climatic factors such as shifting air masses responsible for dry conditions (Girardin et al. 2004; Girardin et al. 2006; Ali et al. 2009).

The coniferous boreal forest of Quebec, eastern Canada, experiences a gradient of dense, continuous forests to the south that transition to discontinuous, less productive forests (Gauthier et al. 2015; Jobidon et al. 2015), and finally to the forest tundra in the north (Payette 1992). The northern open forests are mainly constituted of lichen woodlands resulting from numerous factors such as limited post-fire regeneration due to low seed production (Sirois 2000), unfavorable climate, short intervals between successive fires (Payette et al. 2000; Jasinki and Payette 2005; Jayen et al. 2006; Girard et al. 2008), and high severity of large fires (Arseneault 2001).

Transition ecosystems are known to be extremely vulnerable to climate change (IPCC 2014), and particularly so for the boreal forest where fire activity is expected to increase (Flannigan et al. 2005). Because the opening of these forests is closely related to fire activity, studying their fire regime is crucial. In Quebec, there is evidence that current fire activity is higher in northern discontinuous forests than in the commercial boreal forest further south (Gauthier et al. 2015). However, it is not clear whether climate is responsible for this latitudinal gradient, or if the underlying climate factors are constant.

Moreover, from a forest management perspective, it is important to understand how fire regimes vary depending on the latitude. In Quebec, northern discontinuous forests are protected from commercial forest harvesting by the legal limit of the commercial forest. It is thought that forest management could worsen the problem of regeneration failures at high northern latitudes under climatic influence. However, the spatial and temporal variability of fire regimes along the latitudinal gradient is still poorly known. The zonation of fire activity is also of interest, as zones with high annual area burned can jeopardize forests' post-fire recovery (Jayen et al. 2006), although recent studies have shown that the boreal forest could express a certain resistance toward high burn rates (Héon et al. 2014). Learning more about the spatial consistency of high fire risk zones is particularly important in the context of the northern limit of the commercial forest because their expansion to the south could lead to a reduction in the area available for forest management.

The objective of this research is to assess the latitudinal variability of fire regime at the transition between continuous and discontinuous coniferous boreal forests in Quebec over the last 150–300 years, and its relation to climatic conditions. Even if a zonation of fire activity had been developed in previous studies based on current fire regimes (Gauthier et al. 2015), the spatiotemporal consistency of the fire zones over a longer temporal scale has not been explored. The first step of this study was to reconstruct the fire history along four north-south roads almost equally distributed over the black spruce forest of Quebec, using fire archives and dendroecological surveys. We used survival models to assess whether climate was influencing fire risk — defined here as the relative hazard of burning compared with the road average — along each road. The latitudinal distribution of fire risk was then used to delimit homogeneous fire risk zones for each road. Then, the fire cycle of each fire risk zone was calculated allowing for an assessment of fire risk variability along the longitudinal gradient. Finally, fire cycles were compared to previous estimates based on the recent fire history in order to highlight the temporal variability of the fire regime in the study area.

1.4 Materials and methods

1.4.1 Study area

The study area is located in the boreal zone of Quebec and lies between latitudes 49.5° N and 53° N. The region is mainly coniferous and dominated by black spruce. It covers a gradient from closed, dense forests in the spruce-moss domain to the south, to more open and fragmented forests in the spruce-lichen domain to the north (Figure 1.1b). The limit of the commercial forest crosses the study area separating managed forests in the south from unmanaged ones in the north.

In order to cover the latitudinal gradient and because access is difficult in the north of the study area, four north-south roads that are almost evenly distributed from west to east were chosen as a means in which to reach forest stands and served as a basis for our sampling design. Those roads were divided into consecutive 2500 ha-cells (5 km long by 5 km wide) and will hereafter be referred to as transects (Figures 1.1 and 1.2).

The transects are located in the James Bay region (A), the Chibougamau area (B), the North Shore (C), and along the Romaine River (D). They are 81, 94, 83, and 34-cell-long, respectively. Transect D comprises less cells because of a shorter road. However, 28 cells were added to the original dataset using plots previously sampled for the Northern Forest Inventory Program of the Ministère des Forêts, de la Faune et des Parcs (MFFP) (NFIP; 2005 to 2009). These additional cells are located at a maximum distance of 45 km on either side of the transect.

1.4.2 Time Since Fire data

As the study area is remote and not easily accessible, we developed a data collection strategy which attempts to maximize the use of fire archive data available for the area between 1924 and 2014 and to complement it with field sampling.

1.4.2.1 Fire archive data (1924–2014)

First, fire archives for the 1924–2014 period obtained from the MFFP were used to reconstruct the most recent fire history (Appendix Figure 1.6). However, this database may gradually become less complete or lose dating precision with time, particularly towards the northern areas, as it becomes more likely that some fires were either overlapped by most recent fires, or not detected, reported, and archived. The database precision is excellent after 1972 (Gauthier et al. 2015), very good after 1940, but some small fires can be missing or not perfectly delimited between 1924 and 1940. In some cases—mainly in the north and for the oldest fires recorded—the fire date is noted to the nearest five- to ten-year interval. For those fires, the middle year of the range was used in the analyses.

Using ArcGIS 10.0, fires at least partially overlapping a cell were identified for each transect. The corresponding time-since-fire (TSF) was then assigned to the cells regardless of the relative importance of the area burned in the cell. When more than one fire partly overlapped a cell, only the most recent TSF was kept. This last situation concerned mostly areas where fires are recurrent (Figure 1.2).

1.4.2.2 Field sampling design

The field campaign took place in 2013 for transects A, B, and C, and in 2014 for transect D. In the north of transect A, from the top of the transect to Broadback River, the TSF data from Héon et al. and Erni et al. (2014; 2016) collected along a 200 km long transect was used. The data was adapted to our study design and sampling effort by rescaling their original 2 km by 1 km sampling cells.

In each cell where no TSF was assigned from the fire archives, a point corresponding to a sampling plot was randomly generated from 100 m to 750 m on either side of the road. We assumed that those random points are representative of their corresponding cells in terms of TSF because in our study area, the mean fire size—calculated over the 1924–2014 period—is 5200 ha while our cells are 2500 ha. For this reason, a random point is very likely to capture the most representative fire that occurred in a cell.

In our effort to compare our results with those of Gauthier et al. (2015) who studied the fire regime between 1972 and 2009, all cells that burned between 1972 and 2014 needed to be assigned with a pre-1972 TSF. Therefore, an additional point was sampled outside the polygon of the post-1972 fire in those cells if no pre-1972 fire date was recorded in the fire archives.

For each plot, 10-dominant trees were sampled (section or core taken as close to the ground as possible), with priority given first to jack pine (*Pinus blanksiana*), and then to black spruce (*Picea mariana*), paper birch (*Betula papyfera*), trembling aspen (*Populus tremuloides*) and, lastly, to balsam fir (*Abies balsamea*). This order of priority was determined based on the rapidity of these species to regenerate after a fire in order to better approximate the real TSF. The trees' age was determined by counting their annual growth rings. In a given cell, if all trees were the same age plus or minus 20 years, the TSF of the cell was considered equal to the age of the oldest tree. Otherwise, the age of the oldest tree was considered a minimum TSF, and therefore right-censored. Because post-fire trees are eventually replaced by new ones as succession proceeds, assessing the exact TSF becomes more difficult as a stand ages.

1.4.2.3 Relative importance of recent fires

Road layout depends on different physical attributes of the landscape as they are usually built on specific surficial deposits. They are also more used by humans than the rest of the landscape. Both these particularities of our transect roads, which have all been built after 1924, can bias the TSF distribution toward more recent fires, thereby affecting estimations of burn rate. Moreover, in some areas, fires can be rare and yet very large. When roads cross such large fires, it can lead to an overestimation of the number of burned cells compared with the average burn rate of the corresponding region. For all those reasons, we computed for each transect the proportion of recent fires (after 1924) in the cells as well as in a 45 km-wide buffer around the transect. Because recent fires were slightly overestimated in all transects comparatively to the 45 km-wide buffers, the cells that burned after 1924 were down-weighted in the analyses. Weights were calculated in each transect in order to match the relative frequency of recent fires with the relative area recently burned in the surrounding landscape. Weights of cells burned between 1924 and 2014 of transects A, B, C, and D are 0.57, 0.41, 0.36, and 0.46, respectively; while all other cells were assigned a weight of 1.

1.4.3 Climate data

The Fire Weather Index (FWI) System consists of six indices derived from meteorological observations—namely temperature, relative humidity, wind speed, and 24-h rainfall—which provide numeric ratings of relative potential for wildland fire. The Fine Fuel Moisture Code (FFMC), the Duff Moisture Code (DMC), and the Drought Code (DC) constitute the fuel moisture codes, and the Initial Spread Index (ISI), the Buildup Index (BUI), and the Fire Weather Index (FWI) constitute the fire behaviour indices. We extracted the value of these indices for each cell within each transect using the BioSIM 9 software (Régnière and Saint-Amant 2008). BioSIM allows the user to compensate for the scarcity of weather stations in a study area by interpolating climate data from nearby weather stations, with adjustments for elevation, latitude, and longitude (Régnière and Saint-Amant 2008). We extracted the mean value of each index in the FWI system over the period of 1971 to 2000 at the cell's centroids. Means of each index in each cell were calculated for spring months (April to June), summer months (July to September), and fire season months (May to August).

1.4.4 Statistical analyses

Survival analyses are often used in fire studies because of their ability to examine the time required for an event to occur, which in our case refers to the TSF, and its relationship with one or more covariates. They produce a survival distribution function corresponding to the probability of having gone without fire at each time t, from which a fire cycle can be calculated. Not only are survival analyses adapted to time to event data, but they also allow for censored observations in the modelling process. This is a major advantage compared to regular fire cycle analyses, which strictly assume that TSF is given by the stand age, with no distinction in stands that have been attributed a minimum age. This often leads to an underestimation of the fire cycle that can be attenuated with survival analyses (Cyr et al. 2016).

Among the different types of survival analyses available, we selected a semi-parametric model known as the Cox proportional hazard regression (Cox 1972). Although this model is one of the most commonly used for survival analyses in other fields—mainly in medicine—still very few fire studies have explored its potential (e.g. Cyr et al. 2007; Bélisle et al. 2011).

The Cox proportional hazard model is made of two distinct parts. The first part corresponds to the baseline hazard function (cumulative hazard function when all covariates values are set to zero), i.e., the non-parametric portion of the model, which is initially left unspecified. This has great advantage over parametric models (such as the Weibull distribution, which has been widely used in fire cycle studies) because it avoids making arbitrary and possibly incorrect assumptions about the form of the baseline hazard function. Instead, it is derived from the empirical TSF distribution. In terms of fire history, it means that since the model does not assume a constant risk of burning through time, it allows for variations in the fire regime that could have happened in the past, resulting, for example, from human activities or climate change. Those variations are therefore taken into account while calculating the fire cycle, giving a more precise fire history estimate (Cyr et al. 2016). The second part of the Cox model is parametric and is estimated using the method of partial likelihood (Cox 1972). It is used to evaluate the relationship between the tested covariates and survival. Our survival models were built using the coxph function of the survival R package (Therneau 2015).

Cox proportional hazard models were used all along the analysis process. They were built either with covariates in order to test the effect of climate on fire risk and delimitate fire risk zones along the transects, or as null models in order to calculate the fire cycle of each fire risk zone previously determined. Analyses were performed for each transect separately, as four independent entities, each representative of their surrounding region. Indeed, the four transects are under very different climatic regimes, and merging them into the same analysis process would make impossible the estimation of the climate effect at the scale of one particular transect. Moreover, we wanted to identify variables affecting the fire risk independently for each transect. Although analyses are realized per transect and allow for the latitudinal assessment of the fire risk variability, calculating fire cycles provides a means of assessing the longitudinal variability by comparing fire activity among transects.

1.4.4.1 Climate influence on fire risk

For each transect, survival models were built in order to examine the influence of the different FWI indices—hereafter referred to as climate variables—on TSF. A supervised forward model selection was conducted in order to select the climate variables that best explained the fire risk. This multi-step process was conducted using the Akaike Information Criterion (AIC). Figure 1.3 summarizes the different steps of the model selection process. First, univariate models were built in order to test for each climate variable individually. For each model, the AIC and ΔAIC (i.e., the difference from the model having the lowest AIC) were calculated. Models with a ΔAIC higher than 6 from the best univariate model were discarded (Symonds and Moussalli 2011). The second step consisted in adding a second variable to each model selected. Only variables that were not collinear with the first one (threshold: correlation coefficient of Pearson < 0.7) were tested as second variables. A second variable was kept only if the model with two variables showed a lower AIC value by at least 2 than the AIC of the corresponding univariate model, in which case the univariate model was discarded. The same process of adding variables was repeated until the model could not be improved by any additional variable. The AIC of all selected models were compared and those having a ΔAIC value higher than 2 from the best model were discarded. Among all models having a ΔAIC lower than 2, only the most parsimonious ones were retained, and the one with the lowest AIC value was kept as the final model. The AIC of this model was finally compared with the AIC of a null model to ensure the overall improvement. Bootstrap was then applied by randomly sampling with replacement (1000 iterations) the original dataset containing TSF and climate variables to extract a 95% confidence interval on the variables' estimates using the lower and upper percentiles.

1.4.4.2 Relative fire risk and latitudinal risk zonation

For each transect, the predicted fire risk of each cell was extracted from the final best-fitted model containing the selected climate variables (Figure 1.3). A 95% confidence interval on the fire risk was calculated using the same bootstrapping process detailed in the previous section. Because the Cox model is a relative risk model, the predicted risk is relative to the sample used in the model, so it can only be interpreted within a transect. The mean risk of a transect is set to one, and is associated with the mean value of the variables used in the model. The value of the risk can then take any positive value and show how many times the risk equals the mean risk of the transect. We chose to graphically represent the results using the log-transformed values of the predicted risk. This scale indeed implies the same range of risk values on both sides of the mean risk value, which on this scale equals zero. For each transect, the log-transformed predicted fire risk variations along the latitudinal gradient allowed us to identify fire risk zones where the fire risk was diverging significantly from the mean risk of the transect. Each transect was thereby separated into different zones, where each was attributed either a low, moderate, or high fire risk relative to the mean risk of the entire transect.

1.4.4.3 Fire cycle

Calculating the fire cycle of each transect zone allows for the comparison of fire activity between transects, as we are no longer dealing with relative estimates within transects. Fire cycles can therefore be used to assess the fire activity variability along both latitudinal and longitudinal gradients. Moreover, in order to compare our results with those of Gauthier et al. (2015) who regionalized the entire coniferous boreal vegetation domain based on fire cycles over the period 1972–2009, fire cycles were calculated for two different periods (i.e., previous to 2014 and to 1972). Calculating fire cycles with and without the 1973–2014 years also allows for the ability to highlight the impact of recent years (post-1972) on past fire regimes, and therefore to assess the temporal variability of fire activity over these two periods.

In order to calculate the observed fire cycle of each transect zone, a stratified null Cox model was built for each transect. No variables were added to the models in order to capture the observed fire cycle per zone, as opposed to a predicted fire cycle, based on the prevailing climate conditions. A special strata term specifying which cell belongs to which transect zone was added to the models in order to take into account how transects were split into different zones. The estimated cumulative hazard of burning (baseline hazard function) could then be extracted for each transect zone (Therneau 2015), representing the accumulated hazard of burning through time. The time it takes for the cumulative hazard to reach 1 is equivalent to the fire cycle (Bélisle et al. 2011; Cyr et al. 2016). To estimate the fire cycle, the time at which the cumulative hazard reached or exceeded 1 was then divided by its associated cumulative hazard. In case the cumulative hazard never reached 1, the fire cycle was calculated as the time at which the cumulative hazard reached its maximum value, divided by this maximum cumulative hazard value. A 95% bootstrap confidence interval on the fire cycle was calculated using 1000 randomizations with replacement of the original TSF dataset. The confidence interval was computed using the lower and upper percentiles.

1.5 Results

The frequency distributions of TSF (Figure 1.4) show that whereas most recent fires are dated to the year, they are mostly dated with a minimum TSF beyond 90–100 years. Transects A, B, C, and D show 26%, 32%, 43%, and 44% of minimum TSF data, respectively, thus underlining the importance of considering censored data in survival analyses. Transects C and D are located in the North Shore region of Quebec where the proportion of balsam fir, a fire-sensitive species, is much greater than in the other transects, suggesting that these stands did not establish themselves immediately after a fire event. In these old stands, it is usually difficult to date the TSF precisely, which explains the higher percentage of censored data in these two transects. The minimum dates we recorded for transects A, B, C, and D are 1719, 1703, 1731, and 1663, respectively.

Peaks of TSF can sometimes correspond to single fires. For example, the most recent peak in transect A results at 80% from a very large 2013 fire, although immense fires are common in this region (Héon et al. 2014; Erni et al. 2016). In transect D, a large fire occurred in the 1940s in its southernmost part that covered close to 26% of the entire transect. Unlike in transect A, this fire appears as an exceptional event when compared to the surrounding landscape. It is not only the largest, it also covers more than 31% of the area burned since 1924 within a 200 km-wide area centered on the transect and delimited in the north by the breakpoint in the latitudinal zonation section (see below), and in the south, by the bottom of the transect. Moreover, the fire is about 16 times larger than the mean size of all fires that have occurred in this area since 1924. For this reason, the cells associated to this particular fire were either removed or re-associated with a previous TSF (obtained from field data or fire archives). We will refer to this configuration as transect D2. This approach also allows for a clearer demonstration of how this fire is influencing our results, as it could either lead to an overestimation of the fire risk or to a misinterpretation of the climate's influence on the fire risk.

1.5.1 Climate influence on fire risk

In all transects, the selected models have a lower AIC than the null models with ΔAIC values higher than 7 (Table 1.1), meaning that null models can be discounted (Richards 2005). Moreover, in all transects except B, the ΔAIC values with null models are higher than 10, a threshold indicating with high certainty that the selected models are highly plausible (Burnham and Anderson 2002). Pseudo-R^2 are all above 0.35, except for transect B.

All variables in AIC selected models have significant effects on the fire risk (Table 1.2). In transect A, the Drought Code (DC) during the fire season increases the fire risk. In transects B and C, models with two variables were selected. The first variables (lowest p-value) with the most important positive effect on the fire risk, are maximum DC and DC during spring, respectively. The second variables selected show a slight negative effect on the fire risk for both transects, suggesting an adjustment to the positive effects of the first variables. In transects D and D2, the main climatic factor selected is the Fine Fuel Moisture Code (FFMC) during fire season. In contrast to the other transects, FFMC decreases the fire risk even though it is an indicator of sustained flaming ignition and fire spread (Van Wagner 1987; Amiro et al. 2004).

In the Cox proportional hazard model, the relevant estimates are the exponentiated coefficients, which represent the multiplicative effect on the risk of burning. Thus, if we take the example of transect C (Table 1.2), when holding the DC fire season constant, an increase of 1 in the DC spring value increases the risk of burning by an average factor of 2.12. Likewise, an increase of 1 in the DC fire season value decreases the risk of burning by a factor of 0.79 on average.

1.5.2 Relative fire risk and latitudinal risk zonation

For each transect, we defined homogeneous fire risk zones based on whether or not the predicted risk diverged from the mean fire risk of the transect (Figures 1.2 and 1.5). Because the predicted fire risks extracted from the models are relative to each transect, relative risk values cannot be compared from one transect to another.

In transect A, the fire risk gradually increases from south to north, thus allowing two zones (north and south) to emerge. On average, the northern zone shows a fire risk

15.61 times higher than the mean risk of the transect, while the southern zone shows a risk 3.33 times lower. 95% confidence intervals (CI95) for the average relative fire risk of each zone can be found in Appendix Table 1.4.

In transect B, the predicted fire risk increases from moderate (not significantly different from the mean fire risk of the transect) in the south to high in the north, except within the zone between latitudes 51.707° N and 52.105° N (coinciding with the plateau located between the Otish Mountains to the east and the Tichegami Mountains to the west, Figure 1.1a), where the risk abruptly drops (dashed lines in Figure 1.5b). The fire regimes of high elevation areas are often idiosyncratic because hilltops and upperslopes can be subject to lower fire frequency (Cyr et al. 2007) due to shorter fire seasons and lower temperatures. Because those mountains are not representative of the regions they cross, this section has been removed from the rest of the analyses. Transect B was divided into a southern zone with an average fire risk similar to the mean risk of the transect (1.05 times higher), and a northern zone with a fire risk 3.70 times higher than the mean risk of the transect (excluding the plateau near the Otish Mountains).

In transect C, the predicted fire risk increases stepwise from south to north. This transect was therefore split into a high risk zone in the north, with a risk 10.48 times higher than the mean risk of the transect, a moderate risk zone in the center, with a risk 1.92 times higher than the mean risk, and a low risk zone in the south, showing a risk 2.63 times lower than the mean risk.

In transect D, the fire risk increases from south to north, although the southernmost portion was highly influenced by the 1940s fire (Figure 1.5d,e). The transect was thus split into three zones when this fire is included in the analysis, with the southernmost zone—almost exclusively inside the 1940s fire area—showing a moderate to high fire risk 3.75 times higher than the mean risk of the transect. The rest of the transect includes a high fire risk zone in the north and a low fire risk zone in the center, showing fire risks 48.14 times higher and 1.75 times lower than the mean risk of the transect, respectively. When removing the 1940s fire from the analysis, transect D2 could be split into two zones (north and south) with risks 21.30 times higher and 1.45 times lower than the mean risk of the transect, respectively. The breakpoint separating the northern and southern zones in D2 was located 4.4 km south of the northern breakpoint in D. This slight difference results from the increased mean fire risk of the transect due to the 1940s fire in transect D.

1.5.3 Fire cycles

In all transects, fire cycles (Table 1.3) calculated over the whole period are seen to lengthen from north to south. Globally, there is also a lengthening from west to east. Fire cycles were calculated over two different periods, prior to 1972 and prior to 2014, in order to check for recent changes in fire regimes. Except for zones A north and B north, the fire cycles calculated for the period before 1972 are shorter in all zones than those calculated over the whole period (prior to 2014). The temporal variability in fire activity in each transect zone (Appendix Figure 1.8) also shows that over the last 300 years most fire activity recorded in each transect zone occurred before 1972, except for A north and B north.

1.6 Discussion

1.6.1 Climate influence on fire risk

The Drought Code (DC) significantly increased the fire risk in the three westernmost transects (i.e., A, B, and C) while no climate influence was detected in transect D. This result is consistent with other studies that have shown a similar effect of the DC on fire risk (Girardin et al. 2006; Girardin and Wotton 2009; Girardin et al. 2009) and on the number of fires and annual area burned (Boulanger et al. 2013) in the Canadian boreal forest. The DC is a numeric rating of the average moisture content of deep, compact organic layers and is an indicator of seasonal droughts (Van Wagner 1987; Amiro et al. 2004). This suggests that drought conditions are partly responsible for the variability of the fire risk along the latitudinal gradient over most of our study area. However, the better model fit for transects A and C compared with transect B may indicate that climate is not the only factor influencing the fire risk. In particular, the large Mistassini Lake to the west and the Tichégami and Otish Mountains to the southern and northern zones (Figure 1.1a), respectively, may have acted as large firebreaks. Indeed, in Quebec, prevailing winds blow predominantly from west to east. These geographical features may thus be accompanied by large fire shadows that attenuate the effect of climate in this region.

As Cox survival models from both transects D and D2 show good fits (pseudo-$R^2 \geq 0.48$), the negative, counterintuitive effect of the FFMC on the fire risk could reflect the influence of some bottom-up drivers. For instance, this region is known for its complex topography, from plains on the edge of St. Lawrence River to mountains toward the north (Robitaille et al. 2015) (Figure 1.1a). The region is also characterized by an important variability of surficial deposits, from organic deposits and bedrock to till dominance from south to north (Robitaille et al. 2015). Topography and surficial deposits are two significant factors of fire risk because they influence the drying potential of the forest floor as well as fuel composition and structure (Cyr et al. 2007; Mansuy et al. 2010; Bélisle et al. 2016). Well-drained stands are more likely to burn (Mansuy et al. 2010), and the slopes found in the northern portion of the transect could, for example, help with draining and thus drying the forest floor, thereby facilitating fire spread. Moreover, a limited fire ignition due to a very low occurrence of lightning strikes (Morissette and Gauthier 2008) is an additional factor that may explain the low fire activity of this region, as well as the difficulty to detect any climate effect on fire risk. When lightning strikes happen in conjunction with weather favorable to fire spread, the accumulated fuel can, therefore, allow for very large fires to occur. This control over fire activity could therefore prevail over other factors in this transect.

1.6.2 Fire cycle

The computation of the fire cycle of each fire risk zone allowed the assessment of the spatiotemporal variability of fire activity within the study area. Although recent fires (after 1924) were over-represented in our transects, we trust the down-weighting applied to recently burned cells significantly reduced this bias and allowed for the calculation of realistic fire cycles. On a broad scale, other studies have shown the same gradient of increasing fire activity from south to north (Boulanger et al. 2013; Gauthier et al. 2015) and from east to west (Bergeron et al. 2006; Girardin et al. 2006; Boulanger et al. 2013; Gauthier et al. 2015) in eastern Canada.

On a narrower spatial scale, our fire cycle estimates are consistent with values calculated for similar regions over the same time period. In the southern zone of transect A, our fire cycle is consistent with previous estimates made in the commercial forest further south (Bergeron et al. 2001; Bergeron et al. 2004; Bergeron et al. 2006). In the northern zone of the same transect, one of the most fire-prone regions of boreal Canada where very large fires occur at a high frequency (Héon et al. 2014; Erni et al. 2016), we estimated a fire cycle of five years. However, compared to the size of those fires, our transect zone is relatively small, meaning that individual fires can intersect a large fraction of the transect (Figure 1.2a). In this particular region where very large fires occur, thus regularly erasing marks of older fires, a method using TSF data over a relatively short transect in order to estimate fire cycles does not appear to be well suited. In this situation, the use of archive data to compute annual area burned, or a different sampling design covering a larger area better adapted to accounting for immense fires could be used instead. Based on fire interval data for the same transect zone, Héon et al. (2014) estimated a fire cycle of 42 years for the time period 1910–2013. With such a short fire cycle, shifts of vegetation from black spruce- to jack pine-dominated stands can occur in this area (Lavoie and Sirois 1998; Le Goff and Sirois 2004). Short fire intervals are also likely to limit stand regeneration and consequently lead to an opening of the forest (Lavoie and Sirois 1998; Brown and Johnstone 2012), possibly into lichen-woodlands (Lavoie and Sirois 1998). However, recent studies have shown that a negative feedback between fuel availability and fire activity has strongly limited the occurrence of these short intervals during the last two centuries (Héon et al. 2014; Parisien et al. 2014). The whole landscape could nonetheless burn regardless of the fuel continuity if either the number of ignition points or the frequency of extremely severe weather events are high enough. The northern zone of transect A thus constitutes a very interesting area to monitor in the future in order to better understand how strong the forest's resilience to high fire activity is in this boreal ecosystem (Erni et al. 2016).

Our fire cycle estimates along transect B are similar to values obtained in previous studies of the same region. Indeed, in the southern zone and in the plateau near the Otish Mountains, Mansuy et al. (2010) calculated fire cycles of 205 (CI95: 128; 502) and 237 (CI95: 136; 929), respectively. Southeast of the transect, Bélisle et al. (2011) also found a similar fire cycle (247 (CI95: 187; 309)) to our southern zone. Mansuy et al. (2010) did estimate a longer fire cycle (129 (CI95: 86; 257)) in the region corresponding to the northern zone of our transect. However, our estimate may have been highly influenced by the most recent decades as 60% of the cells in this zone have a TSF of <14 years.

Transects C and D are both located in the North Shore region where fire cycles have been shown to lengthen on an eastward course. Previous studies have estimated fire cycles varying from 250 years around the southern and center zones of transect C (Bouchard et al. 2008) to between 295 (Bergeron et al. 2006; Cyr et al. 2007; Gauthier et al. 2009) and 600 years (Bouchard et al. 2008) further east, toward transect D. Those values are in agreement with our results as they are included within the confidence intervals of our fire cycle estimates of these regions. Furthermore, our study is one of the first that analyzes the fire regime from empirical data in the area covered by the northern zones of transects C and D, thus making it difficult to compare our results with others. However, we assume our fire cycle estimates are realistic based on the overall consistency between our results and those of other studies as well as the reliability of the estimates produced by the Cox analyses (Cyr et al. 2016).

1.6.3 Fire risk zonation and temporal variability

Our study indicates that the fire risk increases from south to north, either gradually as in transects A, B, and D2, or stepwise as in transect C. In all transects, high and low fire risk zones could be delimited in the north and south, respectively. The localization of the breakpoints between fire risk zones is generally consistent with the regional boundaries set by Gauthier et al. (2015) based on the recent fire regime (1972–2009), except for transect B which they consider to be more homogeneous.

The fire cycles estimated by Gauthier et al. (2015) are longer than ours for all transect zones (Table 1.3). Temporal variations in the fire regime can explain these differences. Indeed, our fire cycle estimates for the time period prior to 1972 are generally shorter than estimates for the entire study period, suggesting a decrease in fire activity during the last four decades. Similar shifts were previously observed in Quebec around the middle of the 20th century, thus pursuing the decrease in fire activity experienced since the end of the Little Ice Age that occurred around 1850 (Bergeron et al. 2006; Le Goff et al. 2007; Gauthier et al. 2009). Moreover, previous studies targeting the fire activity of the last 150–300 years (e.g. Bergeron et al. 2004; Cyr et al. 2007; Bouchard et al. 2008; Mansuy et al. 2010; Bélisle et al. 2011) have estimated fire cycles similar to ours. In the northern zone of transect A however, the difference between our estimates and the ones calculated by Gauthier et al. (2015) seems to results from the most recent years (i.e., after 2009) when most of this zone was burned (Appendix Figure 1.8). This is consistent with previous studies showing that fire activity has been increasing since 1980 in this area (Erni et al. 2016).

All indices of the FWI, particularly the DC, are expected to increase in the future in response to climate change (Wang et al. 2015; Flannigan et al. 2016). During the last few decades, the northern zone of transect A, which is the driest sector of the study area, has experienced very high fire activity (Figure 1.2a and Appendix Figure 1.8). With climate change, this phenomenon could propagate over the whole study area, leading to a large-scale increase of fire activity in the near future (Boulanger et al. 2013), possibly returning to the fire regime levels of the last 150–300 years.

The relative stability of fire zone boundaries in the past may have resulted either from top-down or bottom-up processes. The climatic zonation may have remained somewhat constant with proportional changes among regions. Alternatively, bottom-up factors, such as fuel availability or surficial deposits, may have determined the observed spatial variability. As these factors are spatially stationary, they could account for the inertia of the limit between fire risk zones regardless of any changes in climate, provided that future fire risks remain in the range of past ones. In both cases, this could suggest that if climate and fire regimes are predicted to change in the future, the limits between fire risk zones might remain stable. This has great implications for forest management planners, as if they have to adjust for future changes in fire activity they will nonetheless be able to rely on the stability of their management unit layout in regards to fires. However, this should be accepted with caution as Boulanger et al. (2013) have shown that in the future slight changes in fire regions could occur based on the projected area burned and the number of fires.

1.7 Conclusion

Considered as a whole, the latitudinal breakpoints separating our fire risk zones are largely consistent with the recent evaluation of the northern limit of the commercial forest. This limit has been drawn across the coniferous boreal forest of Quebec to delineate the more opened forests to the north from the tall and dense forests that are suitable for forest management to the south (Ministère des Ressources Naturelles du Québec 2013; Jobidon et al. 2015). As there is a direct link between high fire activity and the opening of forests (Payette et al. 2000; Jasinki and Payette 2005; Jayen et al. 2006; Girard et al. 2008), as we have shown that fire risk appears to be higher in the northern zones over the last 150–300 years, and as these zones have been relatively stable through time, it seems reasonable to conclude that the limit between open and closed forests has also been somewhat stable. If the expected climate change leads to a fire activity level that remains in the same range of variability as the last 150–300 years, which Girardin et al. (2013) consider a plausible scenario, this limit may also remain stable in the future. Indeed, boreal forests south of the northern limit of the commercial forest seem to be well-adapted to large changes in fire activity (Bergeron et al. 2010; Girardin et al. 2013). However, if fire activity increases beyond its range of variability in the south, dense forests could start opening (Payette 1992; Brown and Johnstone 2012) and thus eventually change the location of the limit.

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1.9 Tables

Table 1.1 Best models according to the supervised forward model selection procedure for each transect. AIC of the best and null models are given as well as their difference (Δ_{AIC}). Cox and Snell's pseudo-R^2 of best models, their associated maximum value, and the corresponding pseudo-R^2 value for max pseudo-R^2 = 1 are also shown.

Transect	Best Model	AIC	AIC Null Model	Δ_{AIC}	Pseudo-R^2 (Max Pseudo-R^2)	Pseudo-R^2 for Max Pseudo-R^2 = 1
A	~ DC fire season	206.11	262.03	55.92	0.51 (0.96)	0.53
B	~ DC max spring + DMC fire season	213.11	220.49	7.38	0.16 (0.91)	0.18
C	~ DC spring + DC fire season	110.34	133.34	23.00	0.28 (0.80)	0.35
D	~ FWI fire season + FFMC fire season	90.78	111.73	20.95	0.39 (0.82)	0.48
D2	~ FFMC fire season	55.46	96.12	40.66	0.43 (0.81)	0.53

DC, Drought Code; DMC, Duff Moisture Code; FWI, Fire Weather Index; FFMC, Fine Fuel Moisture Code.

Table 1.2 Coefficients of models presented in Table 1.1.

The 95% confidence interval (CI95) for each coefficient was obtained after 1000 randomizations with replacement of the original dataset. p-values and exponentiated coefficients with their CI are also shown.

Transect	**Variables**	**Coefficient (CI95)**	**exp (Coefficient) exp (CI95))**	***p*-value**
A	DC fire season	0.16 (0.13; 0.19)	1.17 (1.14; 1.21)	$3.61e^{-11}$
B	DC max spring	0.30 (0.21; 0.40)	1.35 (1.23; 1.49)	$9.32e^{-5}$
	DMC fire season	−0.61 (−0.89; −0.35)	0.54 (0.41; 0.70)	$5.67e^{-4}$
C	DC spring	0.75 (0.55; 1.00)	2.12 (1.73; 2.72)	$8.59e^{-6}$
	DC fire season	−0.23 (−0.38; −0.08)	0.79 (0.68; 0.92)	$3.08e^{-2}$
D	FFMC fire season	−3.97 (−5.42; −2.88)	0.02 (0.00;0.06)	$1.14e^{-5}$
	FWI fire season	4.11 (1.66; 6.80)	60.95 (5.26; 897.85)	$1.25e^{-2}$
D2	FFMC fire season	−2.73 (−3.62; −2.14)	0.07 (0.03; 0.12)	$2.10e^{-6}$

Table 1.3 Fire cycle (FC) of each transect zone calculated from the cumulative baseline survival function of stratified null models.

For each transect zone, we assume that the FC calculated is representative of a period starting with the 10th percentile of the TSF data (i.e., from that date on, 90% of the cells in that particular transect zone were burned). The 95% bootstrap confidence interval (CI95) was obtained after 1000 randomizations with replacement of the original dataset and computation of the FC for each transect using the upper and lower percentiles. FC are calculated for the entire period (prior to 2014) and for the period prior to 1972. FC calculated over the 1972–2009 period by Gauthier et al. (2015) in the corresponding regions are also given.

Transect	Zone	Starting Date of Period Covered	FC (CI95) (<2014)	FC (CI95) (<1972)	FC (CI95) (1972–2009) (Gauthier et al. 2015)
A	North	1994	5 * (2; 9)	44 (23; 57)	94 (85; 105)
	South	1756	168 (104; 263)	125 (71; 219)	712 (636; 816)
B	North	1836	33 (11; 71)	38 (9; 102)	
	Plateau	1739	408 (101; 1544)	145 (37; 264)	183 (155; 221)
	South	1822	233 (144; 354)	154 (109; 218)	
C	North	1957	37 (22; 50)	8 (4; 10)	183 (155; 221)
	Center	1800	183 (29; 396)	143 (26; 361)	712 (636; 816)
	South **	1763	720 (326; 1515)	361 (71; 1014)	712 (636; 816) / 1668 (1286; 2380)
D	North	1924	60 (35; 112)	20 (11; 32)	272 (239; 312)
	Center	1725	785 (290; 1970)	170 (72; 404)	712 (636; 816)
	1940s fire	1929	57 (26; 98)	18 (10; 29)	1668 (1286; 2380)
D2	North	1927	53 (32; 83)	19 (10; 29)	272 (239; 312)
	South **	1737	732 (201; 1747)	177 (65; 543)	712 (636; 816) / 1668 (1286; 2380)

* 89% of the cells in this zone have a TSF of <13 years; the remaining 11% have a TSF of <40. Moreover, an important fire that occurred in 2013 burned 51% of the cells, also highly influencing the FC estimate. As large fires are common in this region, the size of the transect zone is small when taking the full variability of the fire regime of that region into account when using TSF data. We thus consider the five-years FC observed here to be highly underestimated.

** As both C South and D2 South cross two fire regions delimited by Gauthier et al. (2015), two corresponding FC values are shown for each of these zones, respectively.

1.10 Figures

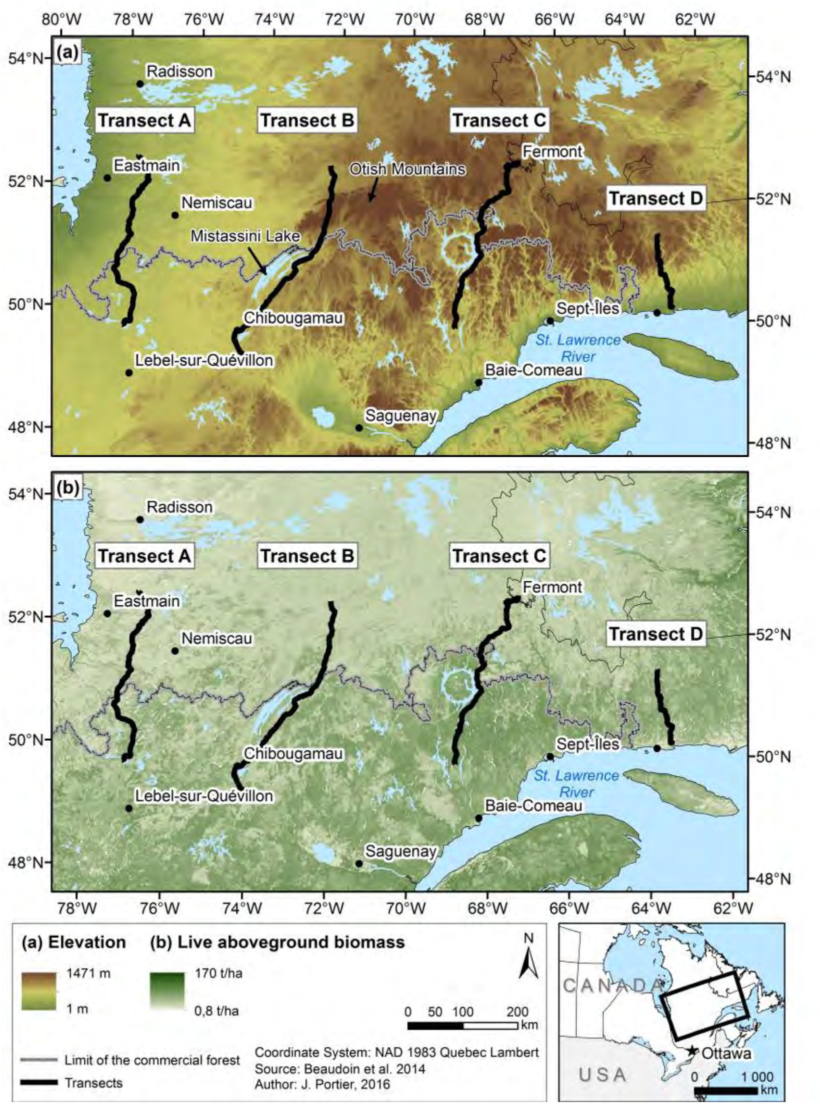

Figure 1.1 Maps of the study area showing the four transects being analyzed.

(a) elevation profile and (b) live aboveground biomass in tons per hectare from Beaudoin et al. (2014). The northern limit of the commercial forest in Quebec (2002) is also shown.

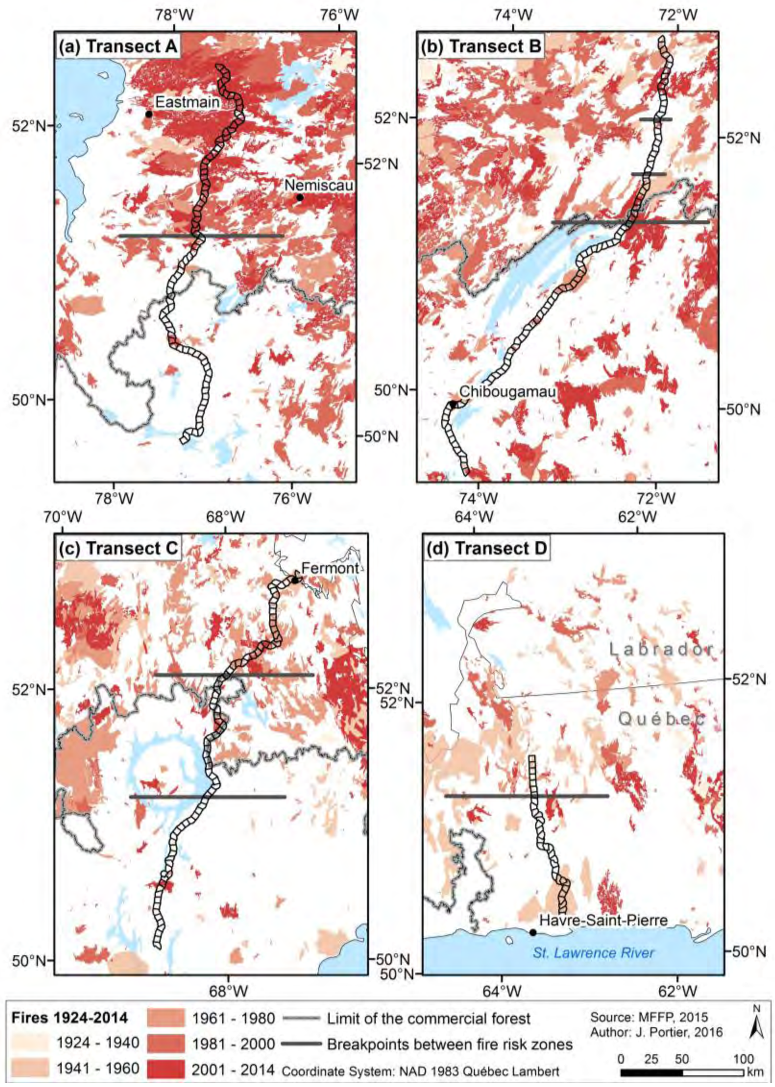

Figure 1.2 Detailed maps of the four transects showing the corresponding 2500 ha-cells.

Fire archives (from 1924 to 2014) and the northern limit od the commercial forest in Quebec are also shown. Each cell that is not overlapped by a recent fire has been subject to a dendroecological survey at a randomly located point in order to determine its time-since-fire (TSF). Latitudinal breakpoints between the fire risk zones are also presented; the two smaller lines in panel (b) delimit the mountainous area excluded for the calculation of fire cycles.

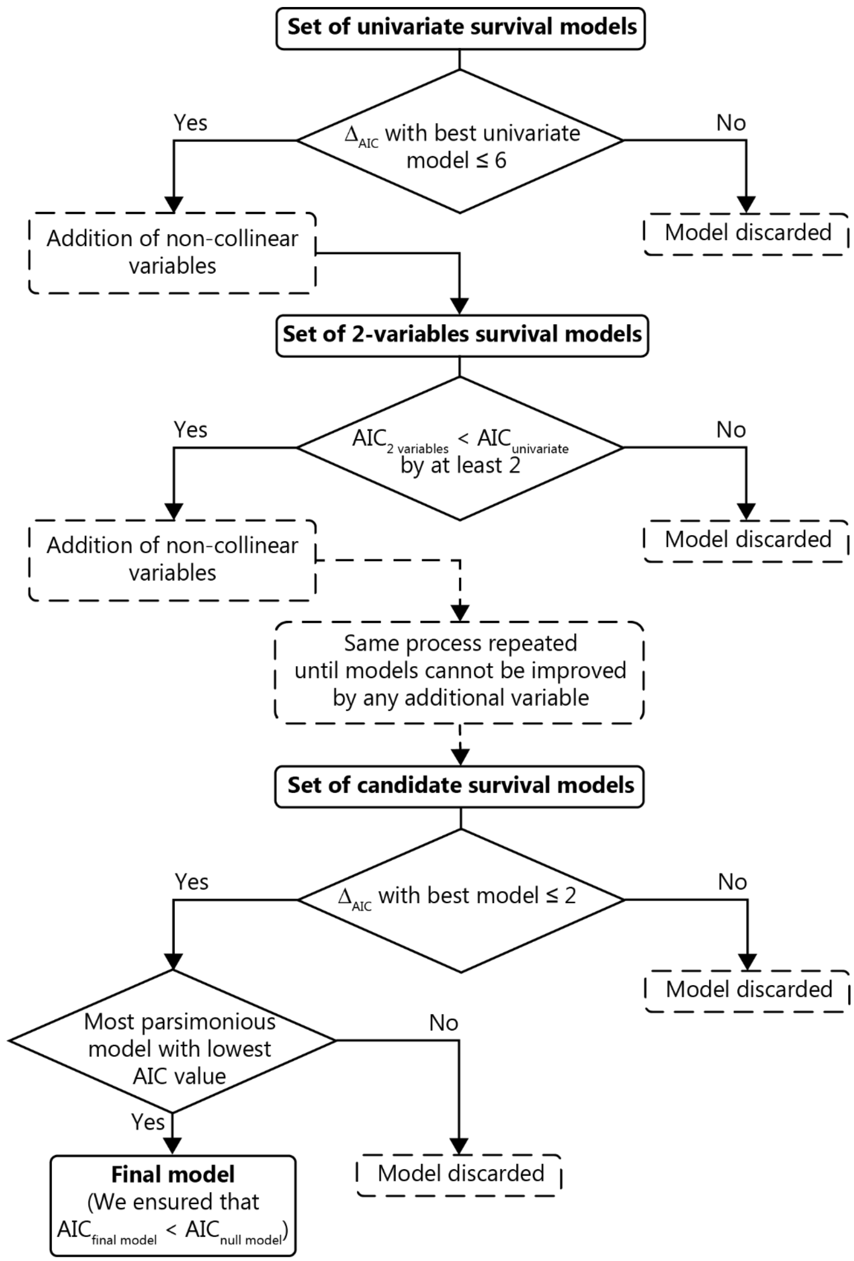

Figure 1.3 Diagram summarizing the different steps of the model selection process using Akaike Information Criterion (AIC).

This procedure is applied to each transect individually. The set of univariate survival models is built using each climate variable separately.

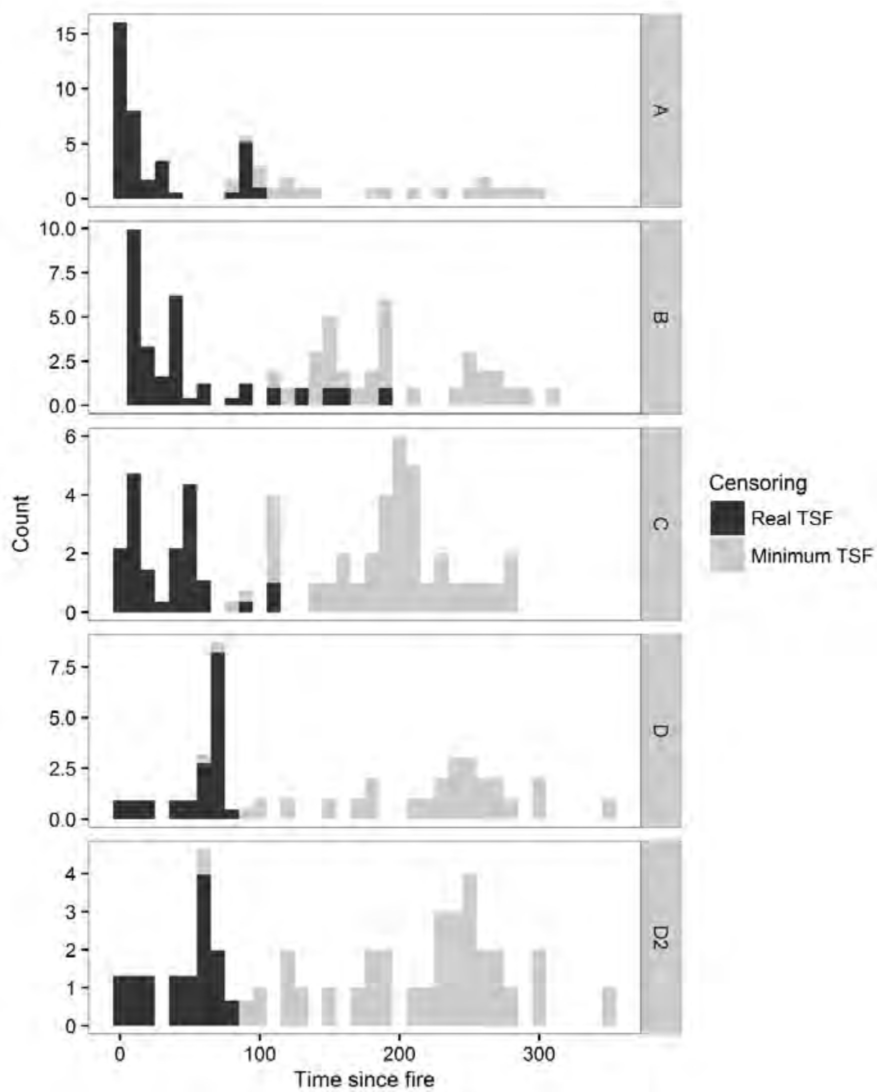

Figure 1.4 Decadal weighted frequency distribution of TSF for each transect.

Weights are calculated in the same way that they were in the survival analyses in order to compensate for the over-representation of recent fires (after 1924) in transects. The non-weighted frequency distribution of TSF is presented in Appendix Figure 1.7. The proportion of right-censored data (minimum TSF) and real TSF are shown in grey and black, respectively.

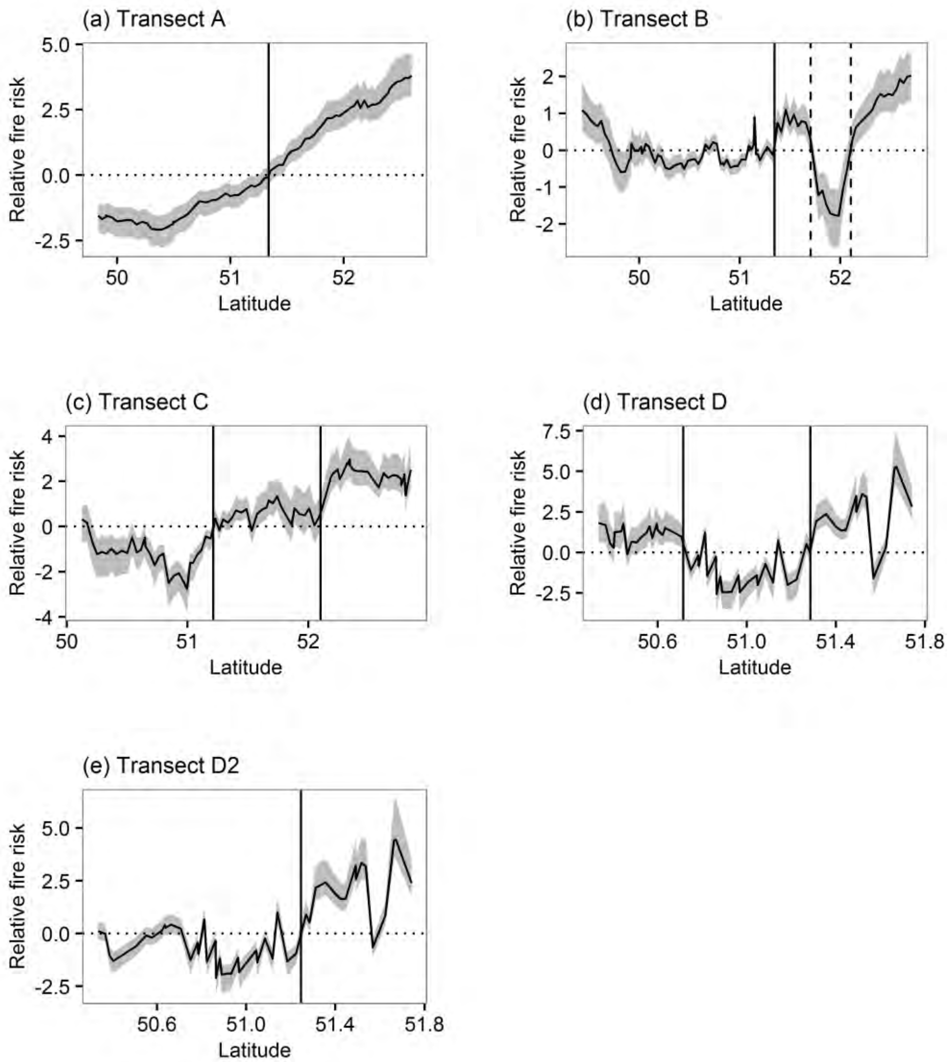

Figure 1.5 Log-Transformed predicted fire risk according to latitude for each transect.

Zero represents the mean fire risk of each transect. Vertical lines separate fire risk zones where for each transect the relative fire risk differs from the mean fire risk of the transect. 95% bootstrap confidence intervals (CI95) are represented by shaded areas. CI95 were obtained after 1000 randomizations with replacement of the original dataset. The two vertical dashed lines in panel (b) delimit the non-representative mountainous area excluded for the calculation of fire cycles.

1.11 References

Ali AA, Carcaillet C, Bergeron Y (2009) Long-term fire frequency variability in the eastern Canadian boreal forest: the influences of climate vs. local factors. Glob Chang Biol 15:1230–1241. doi: 10.1111/j.1365-2486.2009.01842.x

Amiro BD, Logan KA, Wotton BM, et al (2004) Fire weather index system components for large fires in the Canadian boreal forest. Int J Wildl Fire 13:391–400. doi: 10.1071/WF03066

Arseneault D (2001) Impact of fire behavior on postfire forest development in a homogeneous boreal landscape. Can J For Res 31:1367–1374. doi: 10.1139/x01-065

Beaudoin A, Bernier PY, Guindon L, et al (2014) Mapping attributes of Canada's forests at moderate resolution through kNN and MODIS imagery. Can J For Res 44:521–532. doi: 10.1139/cjfr-2013-0401

Bélisle A, Leduc A, Gauthier S, et al (2016) Detecting local drivers of fire cycle heterogeneity in boreal forests: A scale issue. Forests 7:1–21. doi: 10.3390/f7070139

Bélisle AC, Gauthier S, Cyr D, et al (2011) Fire regime and old-growth boreal forests in central Quebec, Canada: An ecosystem management perspective. Silva Fenn 45:889–908.

Bergeron Y, Cyr D, Drever CR, et al (2006) Past, current, and future fire frequencies in Quebec's commercial forests: implications for the cumulative effects of harvesting and fire on age-class structure and natural disturbance-based management. Can J For Res 36:2737–2744. doi: 10.1139/X06-177

Bergeron Y, Cyr D, Girardin MP, Carcaillet C (2010) Will climate change drive 21st century burn rates in Canadian boreal forest outside of its natural variability: collating global climate model experiments with sedimentary charcoal data. Int J Wildl Fire 19:1127–1139. doi: 10.1071/WF09092

Bergeron Y, Gauthier S, Flannigan M, Kafka V (2004) Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec. Ecology 85:1916–1932.

Bergeron Y, Gauthier S, Kafka V, et al (2001) Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. Can J For Res 31:384–391. doi: 10.1139/cjfr-31-3-384

Bouchard M, Pothier D, Gauthier S (2008) Fire return intervals and tree species succession in the North Shore region of eastern Quebec. Can J For Res 38:1621–1633. doi: 10.1139/X07-201

Boulanger Y, Gauthier S, Gray DR, et al (2013) Fire regime zonation under current and future climate over eastern Canada. Ecol Appl 23:904–923.

Brown CD, Johnstone JF (2012) Once burned, twice shy: Repeat fires reduce seed availability and alter substrate constraints on Picea mariana regeneration. For Ecol Manage 266:34–41. doi: 10.1016/j.foreco.2011.11.006

Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach (2nd ed), Springer. New York, USA

Cox DR (1972) Regression models and life-tables. J R Stat Soc Ser B 34:187–220.

Cyr D, Gauthier S, Bergeron Y (2007) Scale-dependent determinants of heterogeneity in fire frequency in a coniferous boreal forest of eastern Canada. Landsc Ecol 22:1325–1339. doi: 10.1007/s10980-007-9109-3

Cyr D, Gauthier S, Bergeron Y, Carcaillet C (2009) Forest management is driving the eastern North American boreal forest outside its natural range of variability. Front Ecol Environ 7:519–524. doi: 10.1890/080088

Cyr D, Gauthier S, Boulanger Y, Bergeron Y (2016) Quantifying fire cycle from dendroecological records using survival analyses. Forests 7:1–21. doi: 10.3390/f7070131

Erni S, Arseneault D, Parisien M-A, Bégin Y (2016) Spatial and temporal dimensions of fire activity in the fire-prone eastern Canadian taiga. Glob Chang Biol. doi: 10.1111/gcb.13461

Flannigan MD, Harrington JB (1988) A study of the relation of meteorological variables to monthly provincial area burned by wildfire in Canada (1953–80). J Appl Meteorol 27:441–452.

Flannigan MD, Logan KA, Amiro BD, et al (2005) Future area burned in Canada. Clim Change 72:1–16. doi: 10.1007/s10584-005-5935-y

Flannigan MD, Wotton BM, Marshall GA, et al (2016) Fuel moisture sensitivity to temperature and precipitation: climate change implications. Clim Change 134:59–71. doi: 10.1007/s10584-015-1521-0

Gauthier S, De Grandpré L, Bergeron Y (2000) Differences in forest composition in two boreal forest ecoregions of Quebec. J Veg Sci 11:781–790.

Gauthier S, Leduc A, Bergeron Y (1996) Forest dynamics modelling under natural fire cycles: a tool to define natural mosaic diversity for forest management. Environ Monit Assess 39:417–434.

Gauthier S, Leduc A, Bergeron Y, Le Goff H (2009) La fréquence des feux et l’aménagement forestier inspiré des perturbations naturelles. In: Gauthier S, Vaillancourt M-A, Leduc A, et al. (eds) Aménagement écosystémique en forêt boréale, Presses de. Québec, QC, Canada, pp 61–78

Gauthier S, Raulier F, Ouzennou H, Saucier J-P (2015) Strategic analysis of forest vulnerability to risk related to fire: an example from the coniferous boreal forest of Quebec. Can J For Res 45:553–565. doi: 10.1139/cjfr-2014-0125

Girard F, Payette S, Gagnon R (2008) Rapid expansion of lichen woodlands within the closed-crown boreal forest zone over the last 50 years caused by stand disturbances in eastern Canada. J Biogeogr 35:529–537. doi: 10.1111/j.1365-2699.2007.01816.x

Girard F, Payette S, Gagnon R (2009) Origin of the lichen-spruce woodland in the closed-crown forest zone of eastern Canada. Glob Ecol Biogeogr 18:291–303. doi: 10.1111/j.1466-8238.2009.00449.x

Girardin MP, Ali AA, Carcaillet C, et al (2009) Heterogeneous response of circumboreal wildfire risk to climate change since the early 1900s. Glob Chang Biol 15:2751–2769. doi: 10.1111/j.1365-2486.2009.01869.x

Girardin MP, Ali AA, Carcaillet C, et al (2013) Fire in managed forests of eastern Canada: Risks and options. For Ecol Manage 294:238–249. doi: 10.1016/j.foreco.2012.07.005

Girardin MP, Tardif J, Flannigan MD, et al (2004) Trends and periodicities in the Canadian Drought Code and their relationships with atmospheric circulation for the southern Canadian boreal forest. Can J For Res 34:103–119. doi: 10.1139/X03-195

Girardin MP, Tardif JC, Flannigan MD, Bergeron Y (2006) Forest fire-conducive drought variability in the southern Canadian boreal forest and associated climatology inferred from tree rings. Can Water Resour J 31:275–296.

Girardin MP, Wotton BM (2009) Summer moisture and wildfire risks across Canada. J Appl Meteorol Climatol 48:517–533. doi: 10.1175/2008JAMC1996.1

Hély C, Fortin CM-J, Anderson KR, Bergeron Y (2010) Landscape composition influences local pattern of fire size in the eastern Canadian boreal forest: role of weather and landscape mosaic on fire size distribution in mixedwood boreal forest using the Prescribed Fire Analysis System. Int J Wildl Fire 19:1099–1109. doi: 10.1071/WF09112

Héon J, Arseneault D, Parisien M-A (2014) Resistance of the boreal forest to high burn rates. Proc Natl Acad Sci 111:13888–13893. doi: 10.1073/pnas.1409316111

IPCC (2014) Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC: Geneva, Switzerland

Jasinki JPP, Payette S (2005) The creation of alternative stable states in the southern boreal forest, Québec, Canada. Ecol Monogr 75:561–583.

Jayen K, Leduc A, Bergeron Y (2006) Effect of fire severity on regeneration success in the boreal forest of northwest Québec, Canada. Ecoscience 13:143–151.

Jobidon R, Bergeron Y, Robitaille A, et al (2015) A biophysical approach to delineate a northern limit to commercial forestry: the case of Quebec's boreal forest. Can J For Res 45:515–528. doi: 10.1139/cjfr-2014-0260

Johnson EA (1992) Fire and Vegetation Dynamics - Studies from the North American Boreal Forest, Cambridge. Cambridge, UK

Johnson EA, Gutsell SL (1994) Fire frequency models, methods and interpretations. Adv Ecol Res 25:239–287.

Johnson EA, Miyanishi K, Weir JMH (1998) Wildfires in the western Canadian boreal forest: Landscape patterns and ecosystem management. J Veg Sci 9:603–610.

Lavoie L, Sirois L (1998) Vegetation changes caused by recent fires in the northern boreal forest of eastern Canada. J Veg Sci 9:483–492.

Le Goff H, Flannigan MD, Bergeron Y, Girardin MP (2007) Historical fire regime shifts related to climate teleconnections in the Waswanipi area, central Quebec, Canada. Int J Wildl Fire 16:607–618. doi: 10.1071/WF06151

Le Goff H, Sirois L (2004) Black spruce and jack pine dynamics simulated under varying fire cycles in the northern boreal forest of Quebec, Canada. Can J For Res 34:2399–2409. doi: 10.1139/X04-121

Li C (2002) Estimation of fire frequency and fire cycle: a computational perspective. Ecol Modell 154:103–120. doi: 10.1016/S0304-3800(02)00069-8

Mansuy N, Gauthier S, Robitaille A, Bergeron Y (2010) The effects of surficial deposit-drainage combinations on spatial variations of fire cycles in the boreal forest of eastern Canada. Int J Wildl Fire 19:1083–1098. doi: 10.1071/WF09144

Ministère des Ressources Naturelles du Québec (2013) Rapport du Comité scientifique chargé d’examiner la limite nordique des forêts attribuables. Québec, Canada

Morissette J, Gauthier S (2008) Study of cloud-to-ground lightning in Quebec: 1996-2005. Atmosphere-Ocean 46:443–454. doi: 10.3137/AO919.2008

Parisien M-A, Parks SA, Krawchuk MA, et al (2014) An analysis of controls on fire activity in boreal Canada: Comparing models built with different temporal resolutions. Ecol Appl 24:1341–1356. doi: 10.1890/13-1477.1

Parisien M-A, Parks SA, Miller C, et al (2011) Contributions of ignitions, fuels, and weather to the spatial patterns of burn probability of a boreal landscape. Ecosystems 14:1141–1155. doi: 10.1007/s10021-011-9474-2

Payette S (1992) Fire as a controlling process in the North American boreal forest. In: Shugart HH, Leemans R, Bonan GB (eds) A System Analysis of the Global Boreal Forest. Cambridge University Press, Cambridge, pp 144–169

Payette S, Bhiry N, Delwaide A, Simard M (2000) Origin of the lichen woodland at its southern range limit in eastern Canada: the catastrophic impact of insect defoliators and fire on the spruce-moss forest. Can J For Res 30:288–305.

Régnière J, Saint-Amant R (2008) BioSIM 9 - User’s Manual, Information Report LAU-X-134, Natural Re. Sainte-Foy, Quebec, Canada

Richards SA (2005) Testing ecological theory using the information-theoretic approach: Examples and cautionary results. Ecology 86:2805–2814. doi: 10.1890/05-0074

Robitaille A, Saucier J-P, Chabot M, et al (2015) An approach for assessing suitability for forest management based on constraints of the physical environment at a regional scale. Can J For Res 45:529–539. doi: 10.1139/cjfr-2014-0338

Senici D, Chen HYH, Bergeron Y, Cyr D (2010) Spatiotemporal variations of fire frequency in central boreal forest. Ecosystems 13:1227–1238. doi: 10.1007/s10021-010-9383-9

Sirois L (2000) Spatiotemporal variation in black spruce cone and seed crops along a boreal forest - tree line transect. Can J Bot 30:900–909.

Symonds MRE, Moussalli A (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behav Ecol Sociobiol 65:13–21. doi: 10.1007/s00265-010-1037-6

Therneau TM (2015) Package "Survival". Available online: https://cran.r-project.org/web/packages/survival/ survival.pdf (accessed on July 12th 2016).

Van Wagner CE (1978) Age-class distribution and the forest fire cycle. Can J For Res 8:220–227.

Van Wagner CE (1988) Effect of slope on fires spreading downhill. Can J For Res 18:818–820.

Van Wagner CE (1987) Development and structure of the Canadian forest fire weather index system. Ottawa, Canada

Wang X, Thompson DK, Marshall GA, et al (2015) Increasing frequency of extreme fire weather in Canada with climate change. Clim Change 130:573–586. doi: 10.1007/s10584-015-1375-5Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T. & Curtis-McLane, S. (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications*, **1**, 95–111.

1.12 Supporting information

Table 1.4 Mean relative fire risk of transect zones compared to mean risk of the transect with 95% bootstrap confidence intervals (CI95)

(e.g., zone north of transect A has a risk 15.61 times higher than the mean risk of the transect, while zone south of the same transect has a risk 3.33 times lower or equals to 0.30 times the mean risk of the transect). Relative fire risk values take into account the down-weighting of recently burned cells.

Transect	Zone	Mean Relative Risk	CI95
A	North	15.61	(7.96; 34.91)
	South	0.30 (−3.33)	(0.18; 0.47)
B	North	3.70	(2.16; 6.76)
	Plateau	0.33 (−3.03)	(0.18; 0.59)
	South	1.05	(0.75; 1.56)
C	North	10.48	(5.29; 24.09)
	Center	1.92	(1.00; 4.09)
	South	0.38 (−2.63)	(0.19; 0.70)
D	North	48.14	(14.66; 306.15)
	South	0.57 (−1.75)	(0.29; 1.06)
	1940s fire	3.75	(1.59; 11.64)
D2	North	21.30	(8.40; 98.19)
	South	0.69 (−1.45)	(0.43; 1.16)

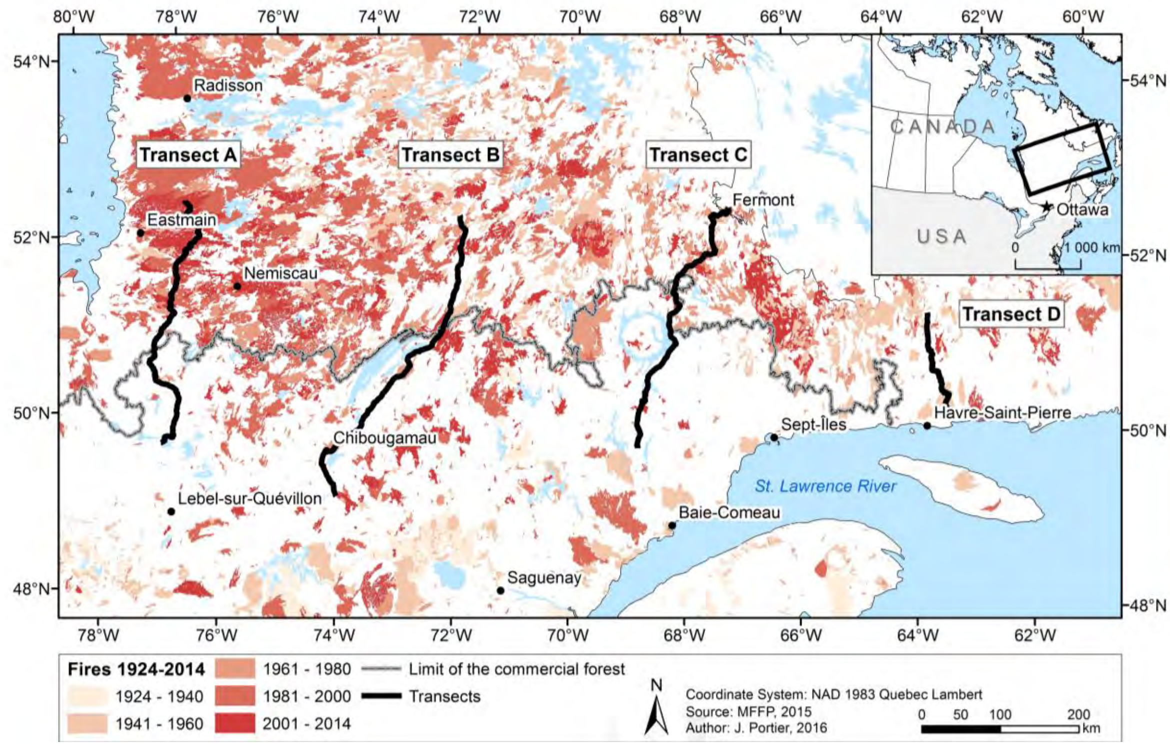

Figure 1.6 Map of the study area showing the four transects being analysed, along with the recent fires from 1924 to 2014. The northern limit of the commercial forest in Quebec is also shown.

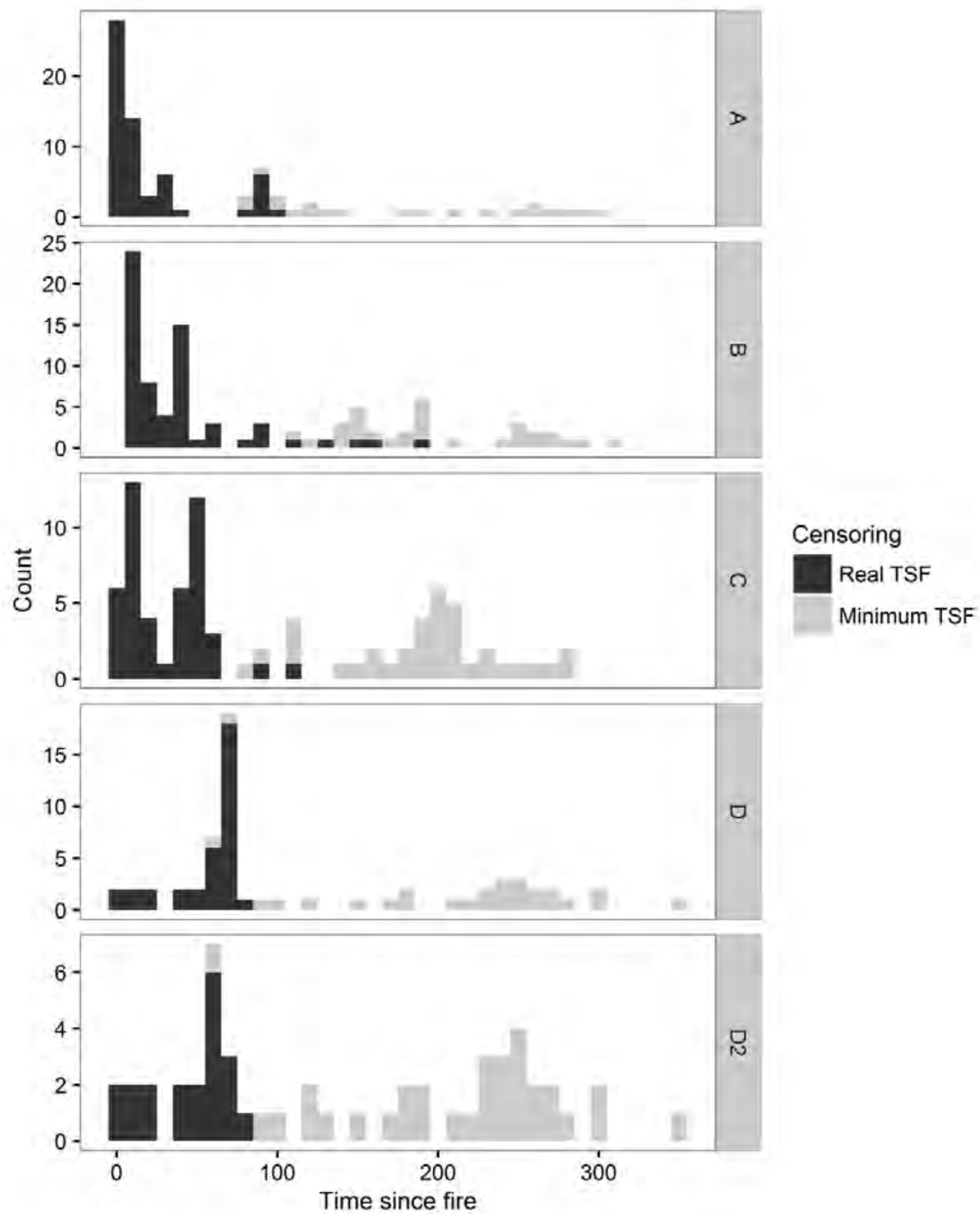

Figure 1.7 Decadal frequency distribution of TSF for each transect.
No weights are applied to cells where a fire occurred between 1924 and 2014. The proportion of right-censored data (minimum TSF) and real TSF are shown in grey and black, respectively.

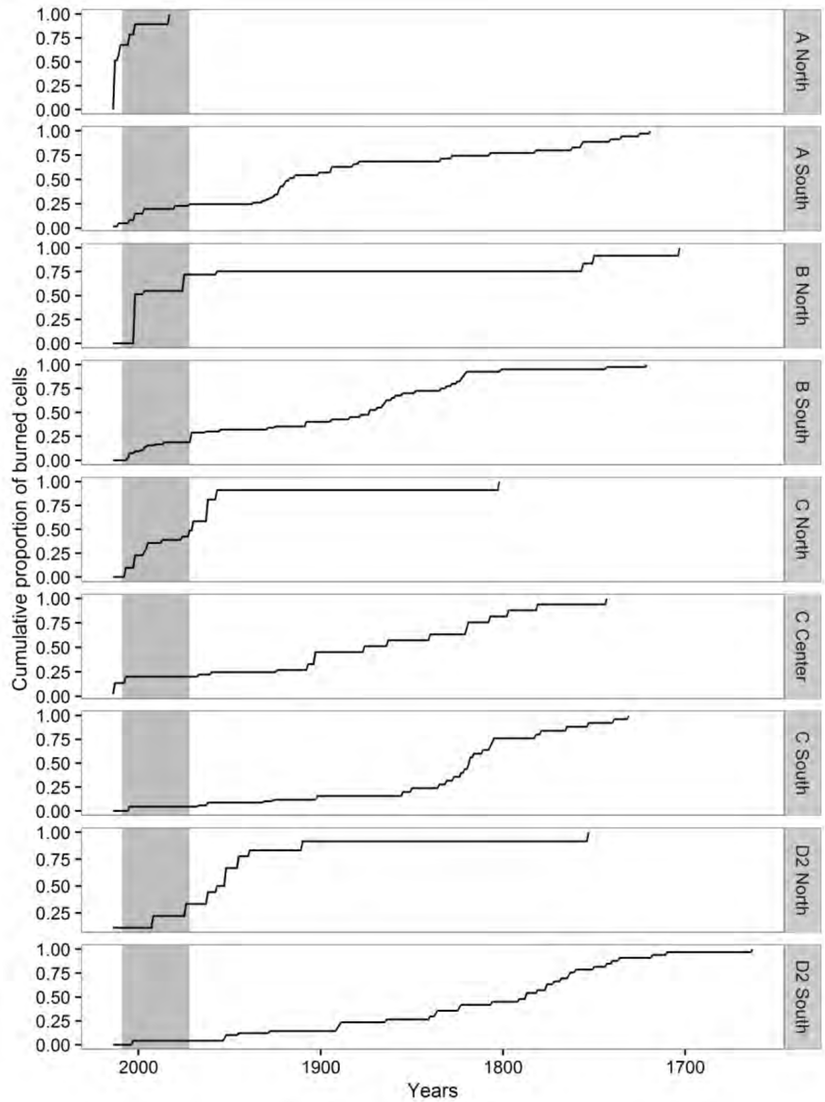

Figure 1.8 Reverse weighted cumulative proportion of cells that burned per decade in each transect zone.

Weights are calculated in the same way that they were in the survival analyses in order to compensate for the over-representation of recent fires (after 1924) in transects. The shaded area shows the 1972–2009 period covered by the fire cycle estimates calculated by Gauthier et al. (2015).

CHAPITRE II

ACCOUNTING FOR SPATIAL AUTOCORRELATION IMPROVES THE ESTIMATION OF CLIMATE, PHYSICAL ENVIRONMENT AND VEGETATION'S EFFECTS ON BOREAL FOREST'S BURN RATES

(PRENDRE EN COMPTE L'AUTOCORRÉLATION SPATIALE AMÉLIORE L'ESTIMATION DE L'EFFET DU CLIMAT, DE L'ENVIRONNEMENT PHYSIQUE ET DE LA VÉGÉTATION SUR LES TAUX DE BRÛLAGE DE LA FORÊT BORÉALE)

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2.1 Abstract

Context

Wildfires play a crucial role in maintaining ecological and societal functions of North American boreal forests. Because of their contagious way of spreading, using statistical methods dealing with spatial autocorrelation has become a major challenge in fire studies analyzing how environmental factors affect their spatial variability.

Objectives

We aimed to demonstrate the performance of a spatially explicit method accounting for spatial autocorrelation in burn rates modelling, and to use this method to determine the relative contribution of climate, physical environment and vegetation to the spatial variability of burn rates between 1972 and 2015.

Methods

Using a 482,000 km² territory located in the coniferous boreal forest of eastern Canada, we built and compared burn rates models with and without accounting for spatial autocorrelation. The relative contribution of climate, physical environment and vegetation to the burn rates variability was identified with variance partitioning.

Results

Accounting for spatial autocorrelation improved the models' performance by a factor of 1.5. Our method allowed the unadulterated extraction of the contribution of climate, physical environment and vegetation to the spatial variability of burn rates. This contribution was similar for the three groups of factors. The spatial autocorrelation extent was linked to the fire size distribution.

Conclusions

Accounting for spatial autocorrelation can highly improve models and avoids biased results and misinterpretation. Considering climate, physical environment and vegetation altogether is essential, especially when attempting to predict future area

burned. In addition to the direct effect of climate, changes in vegetation could have important impacts on future burn rates.

Keywords
Coniferous boreal forest, Quebec, eastern Canada, wildfires, burn rate, spatial autocorrelation, RAC models, autocovariate

2.2 Résumé

Contexte
Les feux de forêt jouent un rôle crucial pour maintenir les fonctions écologiques et sociétales des forêts boréales nord-américaines. Les feux se propageant de façon contagieuse, l'utilisation de méthodes statistiques prenant en compte l'autocorrélation spatiale est devenue un enjeu majeur dans l'analyse de l'effet de facteurs environnementaux sur leur variabilité spatiale.

Objectifs
Nous cherchons à démontrer la performance d'une méthode spatialement explicite prenant en compte l'autocorrélation spatiale dans la modélisation de taux de brûlage. Cette méthode est utilisée pour déterminer la contribution relative du climat, de l'environnement physique et de la végétation à la variabilité spatiale des taux de brûlage entre 1972 et 2015.

Méthodes
Dans un territoire de 482,000 km² situé dans la forêt boréale résineuse de l'Est du Canada, des modèles de taux de brûlage sont comparés en tenant en compte ou non l'autocorrélation spatiale. La contribution relative du climat, de l'environnement physique et de la végétation à la variabilité spatiale des taux de brûlage est identifiée grâce à la partition de variance.

Résultats

La prise en compte de l'autocorrélation spatiale a amélioré la performance des modèles d'un facteur de 1.5. Notre méthode a permis l'extraction inaltérée de la contribution du climat, de l'environnement physique et de la végétation à la variabilité spatiale des taux de brûlage. Cette contribution était similaire pour les trois groupes de facteurs. L'étendue de l'autocorrélation spatiale était liée à la distribution de taille des feux.

Conclusions

Prendre en compte l'autocorrélation spatiale peut améliorer de façon considérable les modèles et éviter les résultats biaisés et les mauvaises interprétations. Considérer le climat, l'environnement physique et la végétation ensemble dans les études sur les feux est essentiel, en particulier lorsqu'on tente de prédire les aires brûlées futures. En plus des effets directs du climat, des changements de végétation pourraient avoir d'importants impacts sur les futurs taux de brûlage.

Mots-clés

Forêt boréale résineuse, Québec, est du Canada, feux de forêt, taux de brûlage, autocorrélation spatiale, modèles RAC, autocovariable.

2.3 Introduction

Wildfires have been shaping boreal forests for millennia by creating mosaics of landscapes of different age structure, size, and composition (Stocks et al. 2003; Gauthier et al. 2015a). In the north American coniferous boreal forest, the spatial variability of fire regimes has been demonstrated at scales of millennia (Hu et al. 2006; Senici et al. 2015), centuries (Girardin and Mudelsee 2008) and decades (Kasischke and Turetsky 2006). This spatiotemporal variability is decisive for many ecological attributes such as biodiversity (Gauthier et al. 2015a), and societal attributes such as forest management (Johnson et al. 1998). For these reasons, better understanding wildfires constitutes a burning challenge in landscape ecology, especially as their semi-random nature makes them a complex process to study.

A notable issue is the spatial autocorrelation related to the contagious nature of fire spreading which requires appropriate spatially explicit methods (Reed et al. 1998). Indeed, two locations close to each other are unlikely to be independent, which breaks the assumptions of most standard statistical analyses (Dormann et al. 2007). Spatial autocorrelation is often disregarded by fire studies, but this omission can lead to type I error and consequently to incorrect estimation of parameters and important misinterpretation (Reed et al. 1998; Dormann et al. 2007; Mishra et al. 2016).

Fire regimes often vary depending on various environmental factors (Larsen 1997; Hu et al. 2006). Many fire studies in boreal ecosystems attempt to better understand the spatial heterogeneity of fire regimes by investigating top-down effects, such as climate at regional to global scales (Drever et al. 2008; Girardin and Wotton 2009), or bottom-up effects, such as vegetation (Cumming 2001; Terrier et al. 2013) and physical environment (Rogeau and Armstrong 2017) at local to regional scales. Some studies have evaluated the relationship between the spatial heterogeneity of fire regimes and several of these attributes (e.g. Drever et al. 2008; Marchal et al. 2017; Rogeau and Armstrong 2017). However, some uncertainties remain about the contribution of all these factors relative to each other.

The goal of our study was i) to implement a spatially explicit method involving residuals autocovariate (RAC) models (Crase et al. 2012) in burn rates analyses, and to test its performance against more standard models not accounting for spatial autocorrelation; and ii) to use this method to determine the relative contribution of climate, vegetation and physical environment to the spatial variability of burn rates in the coniferous boreal forest of eastern Canada. First, we used ordinal logistic models to test for the effects of climate, vegetation and physical environment on the spatial variability of burn rates. Then, in order to account for spatial autocorrelation, RAC models (Crase et al. 2012) were built based on the ordinal logistic models. The extent of the spatial autocorrelation was linked to the fire size distribution of the study area. The relative importance of each group of factors to the variability of burn rates was calculated and their individual effects were identified.

2.4 Material and methods

2.4.1 Study area

The study area is located in the boreal vegetation zone of Quebec, eastern Canada. It covers 482,000 km² and stretches between latitudes 49°N to 53°N and between longitudes 79°30'W to 57°W. Total mean annual precipitation increases from west to east, and to a lesser extent from north to south, ranging from 651 mm to 1,236 mm (Figure 2.1a). The mean annual temperatures vary from -4.9°C in the north to 1.6°C in the south. The topography notably varies across the study area (Robitaille et al. 2015). While the West has a relatively flat topography and low elevation, the north-central portion experiences a higher elevation with a gentle relief. Towards the Southeast, relief is strongly dissected by broad north-south valleys. Further east, highly fractured relief rises gradually from sea level to 1,000 m. Magnitudes of relief and elevation then gradually decrease towards the eastern lower north shore region of the Saint Lawrence River. In terms of surficial deposits, thick and thin tills and organic deposits are the most abundant, although an important amount of rock is found in the Southeast (Figure 2.1b; Robitaille et al. 2015). Forests are largely dominated by black spruce (*Picea mariana* (Mill.) B.S.P.), but also contain other species in smaller proportions, such as jack pine (*Pinus banksian*a Lamb.), balsam fir (*Abies balsamea* (L.) Mill.), trembling aspen (*Populus tremuloides* Michaux) and white birch (*Betula papyrifera* Marsh.).

Analyses were performed at the scale of Land Districts (LDs) that are “areas of land characterized by a distinctive pattern of relief, geology, geomorphology, and regional vegetation" (Jurdant et al. 1977) and are levels of the Ecological Land Classification Hierarchy developed in Quebec (Robitaille and Saucier 1996). A notable advantage of using LDs is that there is a number of environmental variables available at this level. Our study area contains 1,114 LDs, with an average size of 42,700 ha. Three LDs were removed from the dataset because they were almost exclusively composed of large bodies of water (Lake Mistassini, Lake Albanel, and Manicouagan reservoir).

2.4.2 Data

2.4.2.1 Fire

Fire archives obtained from the Ministère de la Forêt, de la Faune et des Parcs du Québec (MFFP) were compiled over the 1972-2015 period (Figure 2.2a). All recorded fires were included in the analyses, regardless of their size. South of the limit of the commercial forest established in 2002 (Figure 2.2a), data has been submitted to quality control and fire dates are considered more precise (Gauthier et al. 2015b) than in the North where remote sensing techniques have been used to delimitate the boundaries of burns and to determine fire dates. Consequently, a few fires in the North could not be precisely dated, which is why the fire dates have been specified in 5-year intervals (Leboeuf et al. 2012). For those, the middle year of the class was used in the analyses. Minimum, maximum, and mean fire size in the study area were respectively 0.4 ha, 494,340 ha and 5,138 ha. In total, 2,079 fires were recorded.

2.4.2.2 Climate

Variables were extracted at each LD's centroid using the BioSIM 9 software (Régnière and Saint-Amant 2008). BioSIM compensates for the scarcity of weather stations in the study area by interpolating climate data from nearby weather stations, adjusting for elevation, latitude, and longitude (Régnière and Saint-Amant 2008). Climate data was extracted over the 1971-2009 period (Lord 2013). Climate variables included mean annual precipitation (Figure 2.1a) and Drought Code (DC) calculated for spring months (May and June) and for the month of July. The DC is part of the Fire Weather Index System and is derived from meteorological observations, namely rainfall and temperature (Amiro et al. 2004).

2.4.2.3 Physical environment

The physical environment was represented by three variables compiled at the LD level: dominant relief, dominant surficial deposit (SD) (Figure 2.1b) and percentage of water. Dominant relief and SD refer to the dominant type of relief and SD (i.e., type covering the largest area) in an LD. The dominant relief was classified as either plains and valley bottoms (flat), low hills and hills (minimally rugged) or high hills and mounts (moderately to highly rugged). SDs are an indicator of the drainage potential of the forest floor. This variable was classified based on the texture of the dominant SD, i.e., coarse, medium or fine, except when the dominant SD was organic or when an LD presented mostly bare bedrock at its surface, in which cases the variable was classified as organic or bedrock, respectively. The percentage of water refers to the percentage of an LD covered by lakes and large rivers.

2.4.2.4 Vegetation

Potential vegetation (Figure 2.1c) was compiled at the LD level and refers to the dominant type of potential vegetation in an LD. This variable was used as an indicator of the type of fuel theoretically dominating an LD while minimizing the influence of the last disturbances that occurred. Potential vegetation represents a specific tree assemblage that was determined based on physical environment's characteristics, established vegetation, presence of indicator species, pre-established regeneration, and successional pathways (Grondin et al. 2007). Potential vegetation was grouped into five forest categories: spruce-moss, fir-dominated, open, wetlands and mixed forests. Analyses have also been performed with current vegetation (see Supplementary material) in order to compare the results with potential vegetation. Contrary to potential vegetation, current vegetation is mainly determined by the recent disturbance history (Grondin et al. 2014). This variable represents the dominant vegetation type that was present in an LD in 2009 (Leboeuf et al. 2012).

2.4.3 Statistical analyses

2.4.3.1 Burn rates

Compiling burn rates at the LD level was realized using ArcGIS software v10.2.2. First, one grid with a resolution of 1 km x 1 km was built for each year of the 44-year study period. In each grid, each cell was assigned with one if a fire burned part or the entirety of the cell during the year into consideration, or with zero if it did not burn during that year. The grids were then smoothed using a 400 km^2-window, the approximate mean size of an LD. To achieve this step, each cell was assigned with the mean value of the surrounding 400 cells, corresponding to the proportion of the surrounding landscape that burned during the year into consideration. All 44 yearly grids were then averaged so that each cell showed the mean smoothed annual burn rate (Figure 2.2b). The mean annual burn rate (BR) was then extracted at each LD's centroid and converted to percentages. This smoothing process reduced the bias resulting from the fact that fires do not stop spreading at LDs' boundaries. Moreover, this method uniformized the area on which BRs were calculated, therefore dealing with potential biases associated with the varying size of LDs.

BRs were then classified into 4 classes representing the recent past natural variability of BRs in eastern Canada (Bergeron et al. 2006): Null (BR = 0; n = 331); Low (BR < 0.5%; n = 486); Medium (0.5% < BR < 1.5%; n = 219); and High (BR > 1.5%; n = 78) (Figure 2.2c).

2.4.3.2 Ordinal logistic regression

Statistical analyses were performed using *R* software v3.3.2 (R Core Team 2016). Ordinal logistic regression was used to test the relationship between BR classes and vegetation, climate and physical environment at the LD level. First, a full model was built containing all variables, on which the proportional odds assumption was verified. Secondly, a backward AIC (Akaike Information Criterion) model selection was realized. In order for a variable to be removed, the AIC value of the model without the variable had to be no greater than two compared with the AIC value of the model with the variable. Once no variable could be further removed, and in case several models were within two delta-AIC of the best model, the most parsimonious model was kept as final model. The AIC of the final model was compared with the AIC of the null model to ensure the overall improvement. Ordinal logistic models were built using the *lrm* function of the "rms" R package (Harrell 2016).

2.4.3.3 Residual Autocovariate (RAC) models

Our data cannot be considered independent because of the spatial autocorrelation between LDs. Indeed, two neighboring LDs are more likely to share common characteristics than those further apart, whether it is in terms of area burned because of the contagious way fires are spreading, or in terms of environmental factors. Autoregressive models are widely used to account for spatial autocorrelation in species distribution studies (Lichstein et al. 2002; Dormann et al. 2007), and have shown interesting results in at least one fire study (Mishra et al., 2016). They are built by adding an autocovariate, calculated from the spatial autocorrelation contained in the response variable, as an additional variable to a regular model. It efficiently reduces the bias resulting from spatial autocorrelation that can often lead to biased parameter estimates and increase type I error rates (Dormann et al. 2007; Crase et al. 2012).

Here, we used an extension of the common autoregressive approach, known as the Residuals Autocovariate (RAC) approach (Crase et al. 2012). The autocovariate of a RAC model, derived from the model residuals instead of the response variable itself, represents the strength of the relationship between model residuals at a given location and residuals at neighboring locations (Crase et al. 2012). The advantage of RAC models over usual autoregressive models is that by fitting the autocovariate on model residuals, explanatory variables that are also spatially correlated have a chance to account for the spatial autocorrelation of the response variable. RAC models better estimate the true influence of explanatory variables because the autocovariate only represents the variance resulting from the spatial autocorrelation that is unexplained by these variables (Crase et al. 2012).

Several steps were required to build the RAC model. First, a distance matrix was calculated based on the geographic coordinates of LDs' centroids and the size of a predefined lag using the *dnearneigh* function of the "spdep" *R* package (Bivand et al. 2016). The lag is defined as the distance between two neighbors when all observations are equally spaced out. As LDs have different shapes and sizes, here we defined lag 1 as the distance at which 95% of the LDs had at least one neighbor, i.e., 25 km (Figure 2.3a). Therefore, lag 2 refers to LDs within 50 km, lag 3 to LDs within 75 km, and so on.

Secondly, Li and Shepherd's residuals were extracted from the final ordinal logistic model. They are well adapted to measuring residuals correlation as they provide a single value per observation and contain directional information (i.e., under-or overestimation) between the observed value and the fitted distribution (Li and Shepherd 2012; Harrell 2016).

Thirdly, a spatial correlogram was built based on the distance matrix and the model residuals using the *sp.correlogram* function of the "spdep" *R* package (Bivand et al. 2016). The correlogram measures, for different lags, the spatial autocorrelation strength in the residuals with Moran's I (Legendre and Legendre 1998). Moran's I is an index ranging from -1 that indicates strong negative spatial autocorrelation, such as dispersion, to 1 that indicates strong positive spatial autocorrelation, such as clustering. A value of zero means a random pattern with no spatial autocorrelation (Cliff and Ord 1981). In order to test for the significance of the Moran's I for each lag distance, confidence intervals were computed using a progressive Bonferroni correction (Legendre and Legendre 1998). The Bonferroni-corrected significance level (α') of the *k*-th lag equals the significance level ($\alpha = 0.05$) divided by *k*, so that $\alpha' = \alpha/k$ (Legendre and Legendre 1998). This approach was applicable because it requires autocorrelation to be expected in the smallest distance classes.

Fourthly, an autocovariate was calculated for each lag at which the correlogram showed a significant spatial autocorrelation using the *autocov_dist* function of the "spdep" *R* package (Bivand et al. 2016). One RAC model was built per autocovariate. Finally, a pool of models was compiled, containing the final ordinal logistic model and all RAC models. The model having the lowest AIC value was kept as best model. Spatial autocorrelation in the RAC models' residuals was assessed to ensure that the inclusion of autocovariates led to residuals independency.

2.4.3.4 Goodness of fit

The goodness of fit of the final RAC model was determined using Nagelkerke's Pseudo-R^2. Moreover, its predictive capacity was assessed by calculating the Correct Classification Rate

(CCR) (Hosmer and Lemeshow 2000; Nur Aidi and Purwaningsih 2013). The CCR is expressed in percentage and was calculated for the accuracy of the overall model and of each class separately using the following equation (Hosmer and Lemeshow 2000):

$$CCR = \frac{number\ of\ correct\ predictions}{number\ of\ observations}\ x\ 100 \tag{2.1}$$

2.4.3.5 Partition of variance

Variance partitioning was used on the best RAC model to determine the relative importance of vegetation, physical environment, and climate in the BR variability. The calculation of exclusive and shared variance of the three groups of factors was derived from the method described by Legendre and Legendre (1998), after being adapted for three groups of factors instead of two. Variance was calculated with McFadden's R^2 (McFadden 1974).

2.5 Results

2.5.1 Model selection

The backward model selection showed that four ordinal logistic models, including the full model, were concurrent candidates to best explain the BR classes of LDs (Table 2.1). The final model, the most parsimonious, included one variable from the climate group (mean annual precipitation), all variables from the physical environment group (dominant relief, dominant SD and percentage of water), and the vegetation group variable (potential dominant vegetation). Analyses performed with current vegetation instead of potential vegetation produced a similar final ordinal logistic model (Table 2.5 in Supplementary material).

2.5.2 Performance of RAC models

The spatial correlogram indicated a significant spatial autocorrelation in the residuals of the final ordinal logistic model at lag one to lag three, i.e., within 25 to 75 km of the LDs' centroids (Figure 2.3). The correlation was strongest at lag one, weakening as lags increased. The AIC-based comparison between the final ordinal logistic model and the three RAC models (one for each lag at which spatial autocorrelation was significant) showed that the RAC model containing the first order autocovariate (i.e., autocovariate calculated at lag 1) performed best, both in terms of AIC and Nagelkerke's pseudo-R^2 (Table 2.2). RAC models' Nagelkerke's pseudo-R^2 were between 1.4 and 1.5 times higher than that of the final ordinal logistic model (Table 2.2). The CCR and CCR plus or minus one class of the first order RAC model are presented in Table 2.3. Analyses performed with current vegetation produced a similar final RAC model as those realized with potential vegetation. However, the AIC value of that model was greater by 19 than that of the first order RAC model factoring in potential vegetation, indicating that the latter performed best (Table 2.6 in Supplementary material).

2.5.3 Effect of climate, physical environment and vegetation on BRs

The variables' effects on BRs were extracted from the first order RAC model. They can be expressed either using odd ratios, i.e., the probability that the BR increases from one class to the next higher one (Table 2.4), or using the cumulative probability of minimally belonging to a non-null BR class, which is equivalent to the probability for an LD of having at least a low BR, at least a medium BR, or a high BR (Figure 2.4). All variables had a significant effect on BRs (Table 2.4).

First, the probability of belonging to any non-null BR class decreased with increasing precipitation, and precipitation became more limiting as the BR class increased (Figure 2.4d). The probability of having a high BR reached a near to zero value when precipitation exceeded 900 mm, while the probability of having at least a low BR was still close to 0.25 in LDs experiencing 1,200 mm of precipitation. Secondly, the probability of belonging to any non-null BR class varied with dominant SD (Figure 2.4a). LDs dominated by medium and coarse textures had the highest probabilities of belonging to any non-null BR class, followed by those dominated by bedrock, organic, and then fine texture. Thirdly, LDs dominated by low hills and hills had the highest probabilities of belonging to any non-null BR class, followed by those dominated by plains and valley bottoms and then high hills and mounts (Figure 2.4b). Fourthly, LDs covered with a high percentage of water tended to have a lower probability of belonging to any non-null BR class (Figure 2.4e). Lastly, in terms of vegetation, LDs dominated by spruce-moss forests had the highest probabilities of belonging to any non-null BR class, followed by those dominated by open forests, fir-dominated forests and then wetlands and mixed forests (Figure 2.4c). When factoring in current vegetation, LDs dominated by open forests had the highest probabilities of belonging to any non-null BR class. Next were those dominated by wetlands, mixed forests and coniferous-moss forests, all of which showing similar effects on BRs (Figure 2.8, Table 2.8 in Supplementary material).

2.5.4 Variance partitioning

Variance partitioning showed that climate, physical environment, and vegetation were responsible for 12.0%, 10.4%, and 11.0% of variance, respectively (Figure 2.5a). Both the vegetation and climate groups, as well as the vegetation and physical environment groups shared a fraction of variance. In contrast, the climate and physical environment groups did not – their shared fraction was negative and close to zero (-0.9%). This was also the case for the three groups altogether (-1.3%). A null value indicates that the groups of factors contain no redundant information on BRs, whereas a negative value indicates that the groups of factors together explain the BR better than the sum of the individual effects of these groups (Legendre and Legendre 1998). Therefore, the variance partitioning could be represented by a linear Venn diagram (Figure 2.5a). The Venn diagram of the RAC model using current vegetation was similar to that of the model using potential vegetation (Figure 2.5). However, the fractions of variance of vegetation alone and shared between vegetation and physical environment were smaller in the case of current vegetation than potential vegetation.

2.6 Discussion

2.6.1 Importance of taking spatial autocorrelation into account in fire studies

Although rarely accounted for, spatial autocorrelation represents a great issue in fire studies, mainly because fires have a contagious way of spreading (Reed et al. 1998). Consequently, regardless of the scale used in one's study, fires can spread over two or more units and connect them to each other. We used a smoothing process in the calculation of BRs at the LD level, as well as RAC models as a spatially explicit method in order to control for spatial autocorrelation. RAC models have demonstrated their excellent performance in other fields, such as species distribution modeling (Crase et al. 2012). Although more classic autocovariate models have been used in fire studies (e.g. Mishra et al. 2016), we here report the first use of this RAC method in such study. The RAC ordinal logistic models were found to be a great improvement compared to the corresponding simpler ordinal logistic model, thus underlining the need for taking spatial autocorrelation into account in fire studies (Reed et al. 1998; Mishra et al. 2016). Indeed, our method led to a pseudo-R^2 1.5 greater than that of the model that did not account for spatial autocorrelation.

Another advantage of using residuals autocovariates is that it also accounts for the spatial autocorrelation that remains in the explanatory variables after a model was built (Crase et al. 2012). Consequently, the variance partitioning analysis that was based on the first order RAC model was more likely to provide the unadulterated contribution of climate, physical environment and vegetation to the variability of BRs. For instance, we showed that climate and physical environment did not share any fraction of variance, although LDs close to each other were highly likely to share the same climatic and physical characteristics. Without controlling for spatial autocorrelation, a shared contribution – likely related to a type I error – could have been expected, as found by Grondin et al. (2014).

The inclusion of autocovariates calculated at several lags showed that accounting for spatial autocorrelation required to consider LDs that had their centroids up to 25 km apart. The area corresponding to that radius could fit 99.8% of all fire sizes, suggesting that the distribution of fire size is a good indicator of the extent to which data might be spatially correlated. This has great implications for future fire studies, where spatial scales could be partly determined based on the size of fires. For instance, using units larger than the maximum fire size of the study area could reduce the spatial autocorrelation between units. Moreover, fire size is expected to increase in the future in response to the facilitation of fire spread by a more intense and longer drought events (de Groot et al. 2013; Flannigan et al. 2016). As a result, spatial autocorrelation could become an even more important issue in the future, and consideration of the future fire size could be necessary in studies interested in future area burned.

2.6.2 Factors controlling the BR

Climate, physical environment and vegetation were found to equally contribute to the BR variability, supporting similar conclusions reached by a study conducted in a smaller portion of our study area (Cavard et al. 2015). This also reinforces the importance of considering all these factors together when attempting to predict area burned in boreal ecosystems (Cavard et al. 2015; Marchal et al. 2017). Indeed, exclusively focusing on climate and neglecting the effects of both vegetation (in terms of fuel) and physical environment on fire regimes could lead to highly misleading results (Marchal et al. 2017). While, as previously mentioned, climate and physical environment did not share any fraction of variance, vegetation shared some with both of them.

The fraction of variance shared between vegetation and physical environment was smaller in analyses performed with current vegetation than with potential vegetation. This could reflect the fact that physical environment is a greater determinant of potential vegetation than current vegetation, while the latter mainly results from the recent disturbance history (Leboeuf et al. 2012; Grondin et al. 2014). The fraction of variance brought by vegetation alone was greater and the fit of the model was better when using potential vegetation than current vegetation. This indicates that potential vegetation is a better predictor of the BR variability than current vegetation, partly because it better represents the vegetation that was present before the last fire events.

2.6.2.1 Climate

The importance of weather in driving fires has been demonstrated (e.g. Drever et al. 2008; Cavard et al. 2015), but its role is observed over shorter time periods and smaller spatial scales than those at which our study was conducted. Therefore, the effects of climate on BRs are discussed in this paper in terms of general climatic averages experienced in the LDs. Although different drought indices based on temperatures and precipitation were tested, only mean annual precipitation was retained in the analyses as a climatic variable influencing the BR. This suggests that climatically speaking, the spatial variability of BRs over the 1972-2015 period was mainly driven by precipitation. When falling during the fire season, precipitation leads to moister forest floors and fuel that are less prone to fire spread (Flannigan et al. 2016). On the other hand, high winter precipitation impacts fire regimes by remaining on site for a longer time in spring, taking longer to melt and therefore shortening fire seasons (Westerling et al. 2006).

This result has great implications in a climate change context. The north American boreal zone is expected to experience higher temperatures, changes in the distribution of precipitation throughout the year and increasing annual precipitation in the future (IPCC 2014). However, the increase in precipitation might not be able to compensate for the increasing fuel's evapotranspiration resulting from higher temperatures (Girardin and Mudelsee 2008; Bergeron et al. 2010; Flannigan et al. 2016). The limiting effect of precipitation being reduced, drier fuels could facilitate fire spread and lead to an important increase in BRs (Amiro et al. 2004; Flannigan et al. 2016). The fire regime could therefore gradually shift towards being controlled by temperatures instead of precipitation. This phenomenon may already be happening in the northwestern part of the study area where the fire regime has intensified since the 1980s (Erni et al. 2016).

2.6.2.2 Physical environment

Physical environment was shown to influence BRs through dominant SD, dominant relief and percentage of water. Previous studies at local scales in eastern Canada have shown that SDs influence fire cycles (Mansuy et al. 2010; Bélisle et al. 2016). At our larger scale, LDs dominated by SDs presenting a coarse or medium texture were the most likely to have a non-null BR, followed by LDs dominated by bedrock, and finally LDs dominated by fine texture SDs or organic deposits. Coarse and medium textures have a high drying potential which leads to dry forest floors that ease fire spread (Flannigan et al. 2016). Although bedrock also has a high drying potential, it usually presents a low vegetation cover due to the absence of soil

(Robitaille et al. 2015), and such a limited fuel continuity can reduce fire spread (Murray et al. 1998). Fine texture SDs and organic deposits have an excellent water retention potential and produce moderately to highly wet soils able to slow down or even stop fire spread.

Dominant relief was also shown to affect BRs, with LDs dominated by low hills and hills having the highest probabilities of belonging to any non-null BR class, followed by LDs dominated by plains and valley bottoms and finally by high hills and mounts. Low hills and hills are mostly found on thick till deposits with coarse or medium textures (Robitaille et al. 2015) that facilitate fire spread. In contrast, high hills and mounts are generally found on thin tills and bedrock in rugged landscapes that can act as firebreaks (Bélisle et al. 2016). Moreover, high hills and mounts most often have a higher elevation than the other two relief classes. High elevation areas tend to be subject to lower fire frequency (Rogeau and Armstrong 2017) as they experience shorter fire seasons resulting from lower temperatures and delayed snow melting (Westerling et al. 2006). In addition, there can be a cooling effect from orographic lifting of air masses, leading to increasing relative humidity and eventually precipitation (Rogeau and Armstrong 2017). Lastly, if a few plains and valleys are found in mid- to high elevation, most are located in the low elevation James Bay area. These landscapes are covered with extensive bogs and dominated by fine texture and organic SD (Robitaille et al. 2015), thus preventing fire spread.

2.6.2.3 Vegetation

Vegetation was shown to impact BRs, as suggested by previous studies (Cavard et al. 2015; Boulanger et al. 2017). LDs dominated by spruce-moss forests had the highest probability of belonging to any non-null BR class, followed by LDs dominated by open forests, fir-dominated forests, and then by wetlands and mixed forests. As this probability was lower for LDs dominated by open forests than for those dominated by the denser spruce-moss forests, this suggests that fires need a continuous forest cover for spreading (Murray et al. 1998; Senici et al. 2015). This also confirms previous findings suggesting that boreal forests present a resistance to high BRs, as when stands are open, fires cannot spread because of the lack of fuel, thus inducing a negative feedback between forest cover continuity and fire spread (Héon et al. 2014). Wetlands have an important water retention potential, and often reduce or stop fire spread (Senici et al. 2015; Erni et al. 2016). In the same way, deciduous species that are present in the mixed forests category have been shown to significantly reduce fire risk (Cumming 2001; Terrier et al. 2013).

One distinguishing feature of this study was the use of potential vegetation instead of current vegetation. In fact, we showed that using current vegetation could bias the interpretation of results, mainly because it is highly determined by the recent disturbance history (Grondin et al. 2014). First, recently burned LDs were classified as open in the current vegetation classification. As a result, open forests were suggested to lead to the highest probabilities of belonging to any non-null BR class, which is a misinterpretation of the current vegetation being a cause instead of a consequence of the BRs. This also contradicted the results obtained with potential vegetation which suggested that potential open forests could limit BRs because of their lack of fuel (Héon et al. 2014). Similarly, fir-dominated and spruce-moss forests are combined into a single coniferous-moss forest type in the current vegetation classification, a consequence of the impossibility of distinguishing spruce and fir from photointerpretation. This combined coniferous-moss forest type resulted in the lowest probabilities of belonging to any non-null BR class. However, fir-dominated and spruce-moss forests have been previously shown to be associated with very different fire regimes (Bouchard et al. 2008), corroborating our results from the analyses factoring in potential vegetation. These results reinforce the benefits of using potential vegetation over current vegetation to produce more reliable results concerning vegetation effects on BRs. Although considering the vegetation that burned (i.e. that was present prior to fires) would have been the best way to evaluate the effect of vegetation on BRs, such dataset does not exist. Potential vegetation seems to be the most adequate substitute despite the fact it only is a proxy and therefore could come with some biases.

2.7 Conclusion

We showed that RAC models are an efficient method to account for spatial autocorrelation in fire studies, and that fire size distribution can be used to assess the extent of the autocorrelation. Given the improvements to our models brought by this method, we insist that accounting for spatial autocorrelation in fire studies is highly necessary. Moreover, our results support those of other studies (e.g., Cumming 2001; Cavard et al. 2015; Marchal et al. 2017; Rogeau and Armstrong 2017) that showed that vegetation and physical environment are as important as climate to explain the BR variability in boreal ecosystems. All these factors should therefore be accounted for in fire regime studies, particularly in sight of climate change. For instance, studies attempting to predict future BRs should not only consider future climate, but also possible vegetation changes (Boulanger et al. 2017). Current policies regarding forest management in Canada encourage planners to take fire regime into account in decision making. Our results further support previous studies suggesting that forest management can be used to reduce fire risk (Terrier et al. 2013). Reforestation activities could favor, for example, vegetation less likely to increase BRs in an area already at high burning risk due to its physical environment and climate.

2.8 Acknowledgments

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2.9 Tables

Table 2.1 Ordinal logistic models within 2 Δ_{AIC} of best model resulting from the backward model selection process, as well as full and null models. The model used in the subsequent analyses is in bold type.

Ordinal logistic models			AIC	Δ_{AIC} with best model
Climate	**Physical environment**	**Vegetation**		
Precipitation	**Relief + SD texture + % water**	**Potential vegetation**	**2,255.4**	**0.0**
Precipitation + DC spring	Relief + SD texture + % water	Potential vegetation	2,255.5	0.1
Precipitation + DC July	Relief + SD texture + % water	Potential vegetation	2,255.6	0.2
	Full model			
Precipitation + DC spring + DC July	Relief + SD texture + % water	Potential vegetation	2,256.8	1.4
	Null model		2,735.7	480.3

Table 2.2 AIC and Nagelkerke's pseudo-R^2 of the final ordinal logistic model and of the RAC models. The best model used in the subsequent analyses is in bold type.

Models	AIC	Δ_{AIC} with best model	Nagelkerke's pseudo-R^2
1st order RAC model	**1,862.2**	**0.0**	**0.61**
2nd order RAC model	1,918.7	56.5	0.58
3rd order RAC model	1,971.7	109.5	0.56
Final ordinal logistic model	2,255.4	393.2	0.40

Table 2.3 CCR and CCR ± one class in percentage showing the accuracy of the overall model and of each BR class separately.

	BR class				
	Null	**Low**	**Medium**	**High**	**Overall**
CCR	67.1	74.9	48.4	25.6	63.9
CCR ± one class	100	99.6	99.1	91.0	99.0

Table 2.4 Odd ratios of variables from the first order RAC model and their 95% confidence intervals (95% CI).

Odd ratios represent the odds of going from one BR class to the next higher one. Their values are always positive. For instance, for an increase of 1 mm of precipitation, the odds of going from one BR class to the next are multiplied by 0.99, so precipitation decreases the odds of having a higher BR. For dummy variables, the odd ratios are given compared to a reference level. For example, the reference level of the relief variable is high hills and mounts. Therefore, the odds of plains and valley bottoms, and low hills and hills going up one class of BR are respectively 1.44 and 2.37 times greater than those of high hills and mounts. The 95% CI was obtained by bootstrap after 1,000 randomizations with replacement of the original dataset and computation of the upper and lower percentiles of the 1,000 resulting odd ratios of each variable.

	Variables		Odd ratios	95% CI	*p*-values
Climate	Precipitation *(for an increase of 1 mm)*		0.99	0.98 – 0.99	< 0.0001
Physical environment	Dominant SD *(reference level = Fine texture)*	Organic	1.80	0.71 – 5.00	< 0.0001
		Bedrock	4.61	1.81 – 12.49	
		Coarse texture	9.07	3.87 – 22.75	
		Medium texture	10.15	4.61 – 24.03	
	Relief *(reference level = High hills and mounts)*	Plains and valley bottoms	1.44	0.88 – 2.54	< 0.0001
		Low hills and hills	2.37	1.56 – 3.65	
	Percentage of water *(for an increase of 1%)*		0.99	0.97 – 1.00	0.0493
Vegetation	Potential vegetation *(reference level = Mixed)*	Wetlands	1.00	0.26 – 4.10	< 0.0001
		Fir-dominated	2.83	0.77 – 13.25	
		Open	3.94	1.18 – 15.83	
		Spruce-moss	6.67	2.13 – 27.19	

2.10 Figures

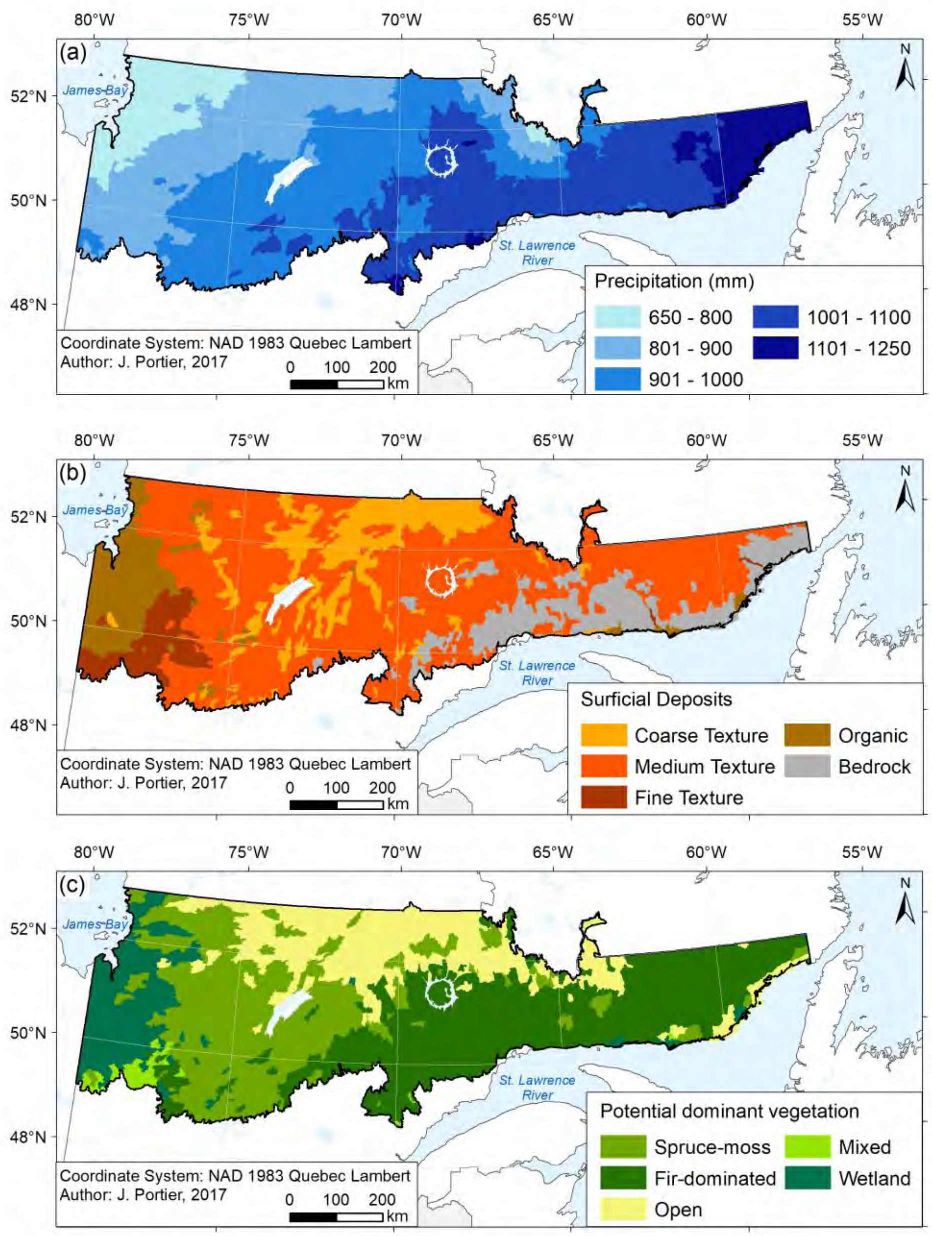

Figure 2.1 Maps of the study area showing distributions of (a) mean annual precipitation, (b) dominant SD texture, and (c) potential vegetation.

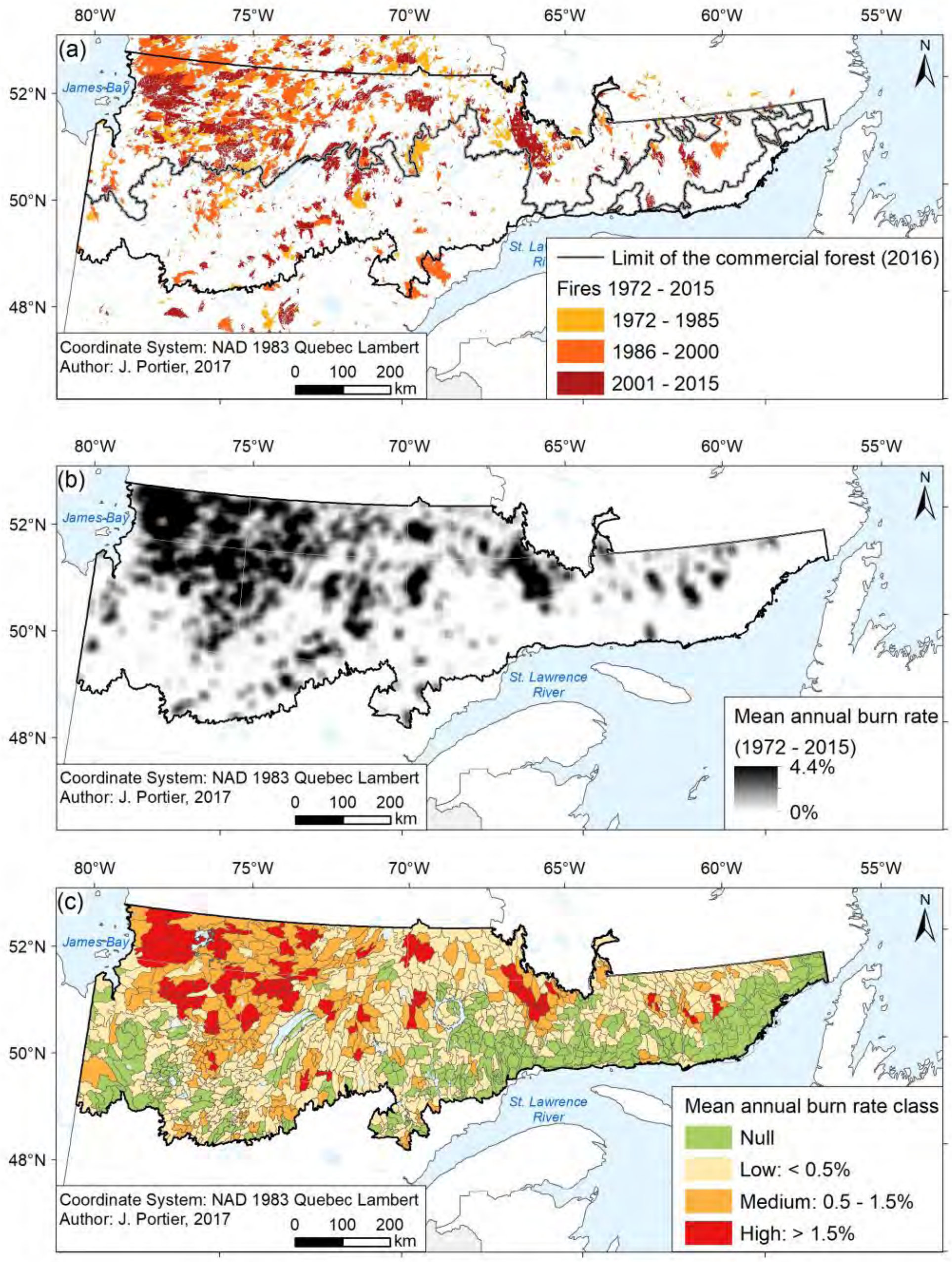

Figure 2.2 **Maps of (a) fires that occurred in the study area during the period 1972-2015; (b) smoothed BRs, and (c) final BR class of LDs.**

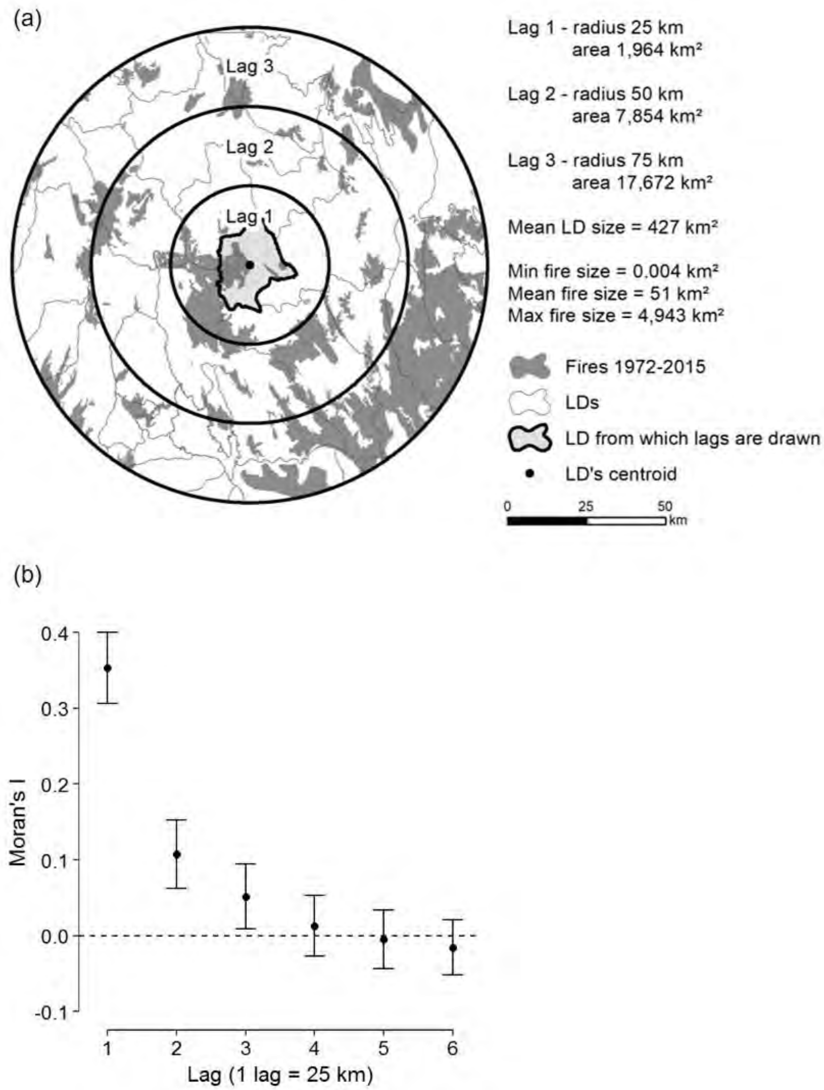

Figure 2.3 (a) Representation of lags one to three around an LD, as well as fires that occurred over the 1972-2015 period. The LD in this example was chosen because it was the same size as the mean size of LDs. (b) Spatial correlogram calculated on the residuals of the final ordinal logistic model.

The correlogram shows Moran's I associated with each lag as well as their respective Bonferroni-corrected confidence intervals.

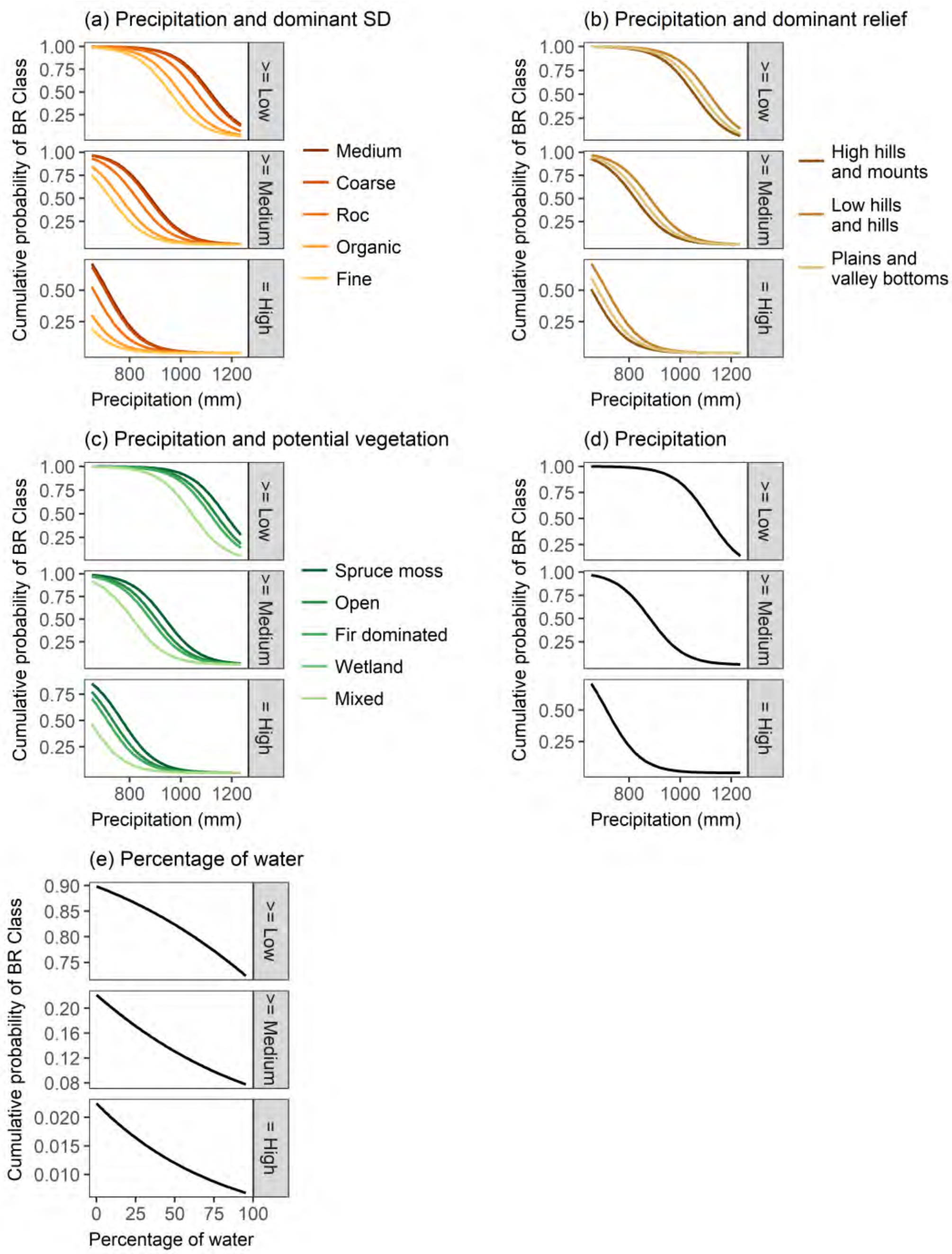

Figure 2.4 **Effects of precipitation and (a) dominant SD, (b) dominant relief, and (c) potential vegetation; as well as effects of (d) precipitation alone and (e) percentage of water alone on the cumulative probability of experiencing at least a low BR, at least a medium BR, or a high BR.**

In each panel, the continuous variables that are not represented were included in the model's predictions using their mean value. For dummy variables, the most represented class was used. In panel (c), the curve representing mixed forests is not visible because it is concealed by the curve representing wetlands.

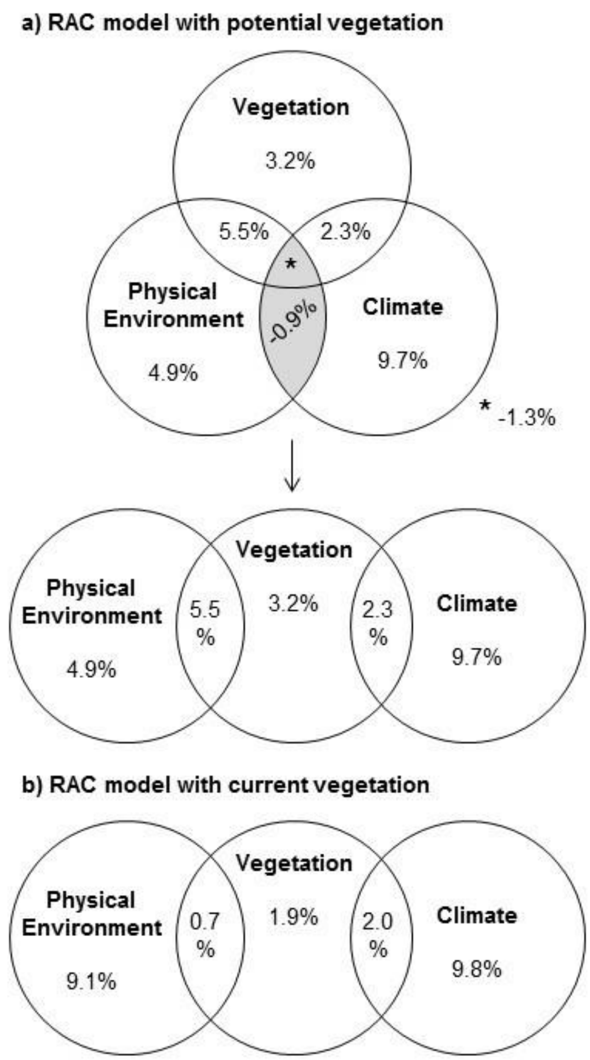

Figure 2.5 Venn diagrams of variance partitioning of the first order RAC models a) factoring in potential vegetation and b) factoring in current vegetation.

Variance is calculated as McFadden's R^2. The total percentage of variance explained by a given group of factors equals the sum of all percentages within the corresponding circle.

2.11 References

Amiro BD, Logan KA, Wotton BM, et al (2004) Fire weather index system components for large fires in the Canadian boreal forest. Int J Wildl Fire 13:391–400. doi: 10.1071/WF03066

Bélisle A, Leduc A, Gauthier S, et al (2016) Detecting local drivers of fire cycle heterogeneity in boreal forests: A scale issue. Forests 7:1–21. doi: 10.3390/f7070139

Bergeron Y, Cyr D, Drever CR, et al (2006) Past, current, and future fire frequencies in Quebec's commercial forests: implications for the cumulative effects of harvesting and fire on age-class structure and natural disturbance-based management. Can J For Res 36:2737–2744. doi: 10.1139/X06-177

Bergeron Y, Cyr D, Girardin MP, Carcaillet C (2010) Will climate change drive 21st century burn rates in Canadian boreal forest outside of its natural variability: collating global climate model experiments with sedimentary charcoal data. Int J Wildl Fire 19:1127. doi: 10.1071/WF09092

Bivand R, Altman M, Anselin L, et al (2016) Package "spdep." https://cran.r-project.org/web/packages/spdep/spdep.pdf. Accessed 10 Feb 2017

Bouchard M, Pothier D, Gauthier S (2008) Fire return intervals and tree species succession in the North Shore region of eastern Quebec. Can J For Res 38:1621–1633. doi: 10.1139/X07-201

Boulanger Y, Girardin MP, Bernier PY, et al (2017) Changes in mean forest age in Canada's forests could limit future increases in area burned but compromise potential harvestable conifer volumes. Can J For Res 47:755–764. doi: dx.doi.org/10.1139/cjfr-2016-0445

Cavard X, Boucher JF, Bergeron Y (2015) Vegetation and topography interact with weather to drive the spatial distribution of wildfires in the eastern boreal forest of Canada. Int J Wildl Fire 24:391–406. doi: 10.1071/WF13128

Cliff AD, Ord JK (1981) Spatial processes: models and applications. Pion, London, UK

Crase B, Liedloff AC, Wintle BA (2012) A new method for dealing with residual spatial autocorrelation in species distribution models. Ecography (Cop) 35:879–888. doi: 10.1111/j.1600-0587.2011.07138.x

Cumming SG (2001) Forest type and wildfire in the Alberta boreal mixedwood: what do fires burn? Ecol Appl 11:97–110. doi: 10.1890/1051-0761(2001)011[0097:FTAWIT]2.0.CO;2

de Groot WJ, Flannigan MD, Cantin AS (2013) Climate change impacts on future boreal fire regimes. For Ecol Manage 294:35–44. doi: 10.1016/j.foreco.2012.09.027

Dormann CF, McPherson JM, Araújo MB, et al (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography (Cop) 30:609–628. doi: 10.1111/j.2007.0906-7590.05171.x

Drever CR, Drever MC, Messier C, et al (2008) Fire and the relative roles of weather, climate and landscape characteristics in the Great Lakes-St. Lawrence forest of Canada. J Veg Sci 19:57–66. doi: 10.3170/2007-8-18313

Erni S, Arseneault D, Parisien M-A, Bégin Y (2016) Spatial and temporal dimensions of fire activity in the fire-prone eastern Canadian taiga. Glob Chang Biol. doi: 10.1111/gcb.13461

Flannigan MD, Wotton BM, Marshall GA, et al (2016) Fuel moisture sensitivity to temperature and precipitation: climate change implications. Clim Change 134:59–71. doi: 10.1007/s10584-015-1521-0

Gauthier S, Bernier P, Kuuluvainen T, et al (2015a) Boreal forest health and global change. Science (80-) 349:819–822. doi: 10.1126/science.aaa9092

Gauthier S, Raulier F, Ouzennou H, Saucier J (2015b) Strategic analysis of forest vulnerability to risk related to fire: an example from the coniferous boreal forest of Quebec. Can J For Res 45:553–565. doi: 10.1139/cjfr-2014-0125

Girardin MP, Mudelsee M (2008) Past and future changes in Canadian boreal wildfire activity. Ecol Appl 18:391–406. doi: 10.1890/07-0747.1

Girardin MP, Wotton BM (2009) Summer moisture and wildfire risks across Canada. J Appl Meteorol Climatol 48:517–533. doi: 10.1175/2008JAMC1996.1

Grondin P, Gauthier S, Borcard D, et al (2014) A new approach to ecological land classification for the Canadian boreal forest that integrates disturbances. Landsc Ecol 29:1–16. doi: 10.1007/s10980-013-9961-2

Grondin P, Noël J, Hotte D (2007) L'intégration de la végétation et de ses variables explicatives à des fins de classification et de cartographie d'unités homogènes du Québec méridional - Mémoire de recherche forestière n°150. Québec, QC, Canada

Harrell FEJ (2016) Package "rms." https://cran.r-project.org/web/packages/rms/rms.pdf. Accessed 10 Feb 2017

Héon J, Arseneault D, Parisien M-A (2014) Resistance of the boreal forest to high burn rates. Proc Natl Acad Sci 111:13888–13893. doi: 10.1073/pnas.1409316111

Hosmer DW, Lemeshow S (2000) Applied logistic regression - Second edition, John Wiley. New York, USA

Hu FS, Brubaker LB, Gavin DG, et al (2006) How climate and vegetation influence the fire regime of the Alaskan boreal biome: The Holocene perspective. Mitig Adapt Strateg Glob Chang 11:829–846. doi: 10.1007/s11027-005-9015-4

IPCC (2014) Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC: Geneva, Switzerland

Johnson EA, Miyanishi K, Weir JMH (1998) Wildfires in the western Canadian boreal forest: Landscape patterns and ecosystem management. J Veg Sci 9:603–610.

Jurdant M, Bélair JL, Gerardin V, Ducruc JP (1977) L'inventaire du capital nature: méthode de classification et de cartographie écologique du territoire. Québec, QC, Canada

Kasischke ES, Turetsky MR (2006) Recent changes in the fire regime across the North American boreal region-Spatial and temporal patterns of burning across Canada and Alaska. Geophys Res Lett 33:1–5. doi: 10.1029/2006GL025677

Larsen CPS (1997) Spatial and temporal variations in boreal forest fire frequency in northern Alberta. J Biogeogr 24:663–673. doi: 10.1111/j.1365-2699.1997.tb00076.x

Leboeuf A, Robitaille A, Létourneau J-P, et al (2012) Norme de cartographie écoforestière du programme d'inventaire écoforestier nordique (PIEN).

Legendre P, Legendre L (1998) Numerical Ecology, 2nd Edition. Amsterdam

Li C, Shepherd BE (2012) A new residual for ordinal outcomes. Biometrika 99:473–480. doi: 10.1093/biomet/asr073

Lichstein JW, Simons TR, Shriner SA, Franzreb KE (2002) Spatial autocorrelation and autoregressive models in ecology. Ecol Monogr 72:445–463. doi: 10.1890/0012-9615(2002)072[0445:SAAAMI]2.0.CO;2

Lord G (2013) Données climatiques. In: Ministère des Ressources Naturelles du Québec (ed) Rapport du Comité scientifique chargé d'examiner la limite nordique des forêts attribuables. Québec, QC, Canada, pp 17–19

Mansuy N, Gauthier S, Robitaille A, Bergeron Y (2010) The effects of surficial deposit-drainage combinations on spatial variations of fire cycles in the boreal forest of eastern Canada. Int J Wildl Fire 19:1083–1098. doi: 10.1071/WF09144

Marchal J, Cumming SG, McIntire EJB (2017) Land cover, more than monthly fire weather, drives fire-size distribution in Southern Québec forests: Implications for fire risk management. PLoS One 12:1–18. doi: 10.1371/journal.pone.0179294

McFadden D (1974) Conditional logit analysis of qualitative choice behavior. In: Zarembka P (ed) Frontiers in Econometrics. Academic Press, New York, New York, USA, pp 105–142

Mishra NB, Mainali KP, Crews KA (2016) Modelling spatiotemporal variability in fires in semiarid savannas: a satellite-based assessment around Africa's largest protected area. Int J Wildl Fire 25:730–741. doi: http://dx.doi.org/10.1071/WF15152

Murray MP, Bunting SC, Morgan P (1998) Fire history of an isolated subalpine mountain range of the Intermountain Region, United States. J Biogeogr 25:1071–1080. doi: 10.1046/j.1365-2699.1998.00241.x

Nur Aidi MMS, Purwaningsih TSS (2013) Modeling spatial ordinal logistic regression and the principal component to predict poverty ptatus of districts in Java Island. Int J Stat Appl 3:1–8. doi: 10.5923/j.statistics.20130301.01

R Core Team (2016) R: A language and environment for statistical computing.

Reed W, Larsen C, Johnson E, MacDonald G (1998) Estimation of temporal variations in historical fire frequency from time-since-fire map data. For Sci 44:465–475.

Régnière J, Saint-Amant R (2008) BioSIM 9 - User's Manual, Information Report LAU-X-134, Natural Re. Sainte-Foy, Quebec, Canada

Robitaille A, Saucier J-P (1996) Land distric, ecophysiographic units and areas: The landscape mapping of the Ministère des Ressources Naturelles du Québec. Environ Monit Assess 39:127–148. doi: 10.1007/BF00396141

Robitaille A, Saucier J-P, Chabot M, et al (2015) An approach for assessing suitability for forest management based on constraints of the physical environment at a regional scale. Can J For Res 45:529–539. doi: 10.1139/cjfr-2014-0338

Rogeau M-P, Armstrong GW (2017) Quantifying the effect of elevation and aspect on fire return intervals in the Canadian Rocky Mountains. For Ecol Manage 384:248–261. doi: 10.1016/j.foreco.2016.10.035

Senici D, Chen HYH, Bergeron Y, Ali AA (2015) The effects of forest fuel connectivity on spatiotemporal dynamics of Holocene fire regimes in the central boreal forest of North America. J Quat Sci 30:365–375. doi: 10.1002/jqs.2790

Stocks BJ, Mason JA, Todd JB, et al (2003) Large forest fires in Canada, 1959–1997. J Geophys Res. doi: 10.1029/2001JD000484

Terrier A, Girardin MP, Périé C, et al (2013) Potential changes in forest composition could reduce impacts of climate change on boreal wildfires. Ecol Appl 23:21–35. doi: 10.1890/12-0425.1

Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW (2006) Warming and earlier spring increase western U.S. forest wildfire activity. Science (80-) 313:940–943. doi: 10.1126/science.1128834

2.12 Supplementary material: Current vegetation

Method

Analyses have also been performed with current vegetation instead of potential vegetation in order to compare the results. Current vegetation was classified into four forest type – coniferous-moss forests, mixed forests, wetlands and open forests – and represented the dominant vegetation type in an LD in 2009 (Leboeuf et al. 2012). Contrary to potential vegetation, spruce-moss and fir-dominated forests were not distinguished as current vegetation was determined by photointerpretation, which is unable to differentiate spruce from fir. Some LDs were recently burned or cut. In the first case, they were reclassified as open. In the second case, they were reclassified as coniferous moss forest as this is the main type of forests aimed by forest management operations.

Table 2.5 Ordinal logistic models factoring in current vegetation within 2 Δ_{AIC} of best model resulting from the backward model selection process, as well as full and null models. The model used in the subsequent analyses is in bold type.

Ordinal logistic models			AIC	Δ_{AIC} with best model
Climate	**Physical environment**	**Vegetation**		
Precipitation	**Relief + SD texture + % water**	**Current vegetation**	**2,252.6**	**0.0**
Precipitation + DC July	Relief + SD texture + % water	Current vegetation	2,253.2	0.6
Precipitation + DC spring	Relief + SD texture + % water	Current vegetation	2,253.5	0.9
	Full model			
Precipitation + DC spring + DC July	Relief + SD texture + % water	Current vegetation	2,254.8	2.2
	Null model		2,735.7	483.1

Table 2.6 AIC of the final ordinal logistic model and of the RAC models factoring in current vegetation. The best model used in the subsequent analyses is in bold type.

The CCR of the first order RAC model is 62.9% and its CCR plus or minus one class of CR is 98.3%. Nagelkerke's pseudo-R^2 of the model is 0.60.

Models	AIC	Δ_{AIC} with best model	Δ_{AIC} with 1st order RAC model factoring in potential vegetation	Nagelkerke's pseudo-R^2
1st order RAC model	**1,881.2**	**0.0**	**19.0**	**0.60**
2nd order RAC model	1,885.5	4.3	23.3	0.58
3rd order RAC model	1,898.8	17.6	36.6	0.56
Final ordinal logistic model	2,252.6	371.4	390.4	0.40

Table 2.7 Odd ratios of variables from the first order RAC model factoring in current vegetation and their 95% confidence intervals (95% CI).

	BR class				
	Null	**Low**	**Medium**	**High**	**Overall**
CCR	64.6	74.5	47.0	28.2	62.9
CCR ± one class	99.4	99.2	99.1	85.9	98.3

Table 2.8 Odd ratios of variables from the first order RAC model factoring in current vegetation and their 95% confidence intervals (95% CI).

Odd ratios represent the odds of going from one BR class to the next higher one. Their values are always positive. For instance, for an increase of 1 mm of precipitation, the odds of going from one BR class to the next are multiplied by 0.99, so precipitation decreases the odds of having a higher BR. For dummy variables, the odd ratios are given compared to a reference level. For example, the reference level of the dominant relief variable is high hills and mounts. Therefore, the odds of plains and valley bottoms, and low hills and hills going up one class of BR are respectively 1.39 and 2.56 times greater than those of high hills and mounts. The 95% CI was obtained by bootstrap after 1,000 randomizations with replacement of the original dataset and computation of the upper and lower percentiles of the 1,000 resulting the odd ratios of each variable.

	Variables		Odd ratios	95% CI	*p*-values
Climate	Precipitation *(for an increase of 1 mm)*		0.99	0.98 – 0.99	< 0.0001
Physical environment	Dominant SD texture *(reference level = Fine texture)*	Organic	0.88	0.34 – 2.38	< 0.0001
		Bedrock	5.35	2.30 – 12.67	
		Coarse texture	12.53	6.33 – 27.28	
		Medium texture	13.86	7.74 – 28.75	
	Relief *(reference level = High hills and mounts)*	Plains and valley bottoms	1.39	0.84 – 2.21	< 0.0001
		Low hills and hills	2.56	1.73 – 3.84	
	Percentage of water *(for an increase of 1%)*		0.99	0.97 – 1.00	0.0468
Vegetation	Current vegetation *(reference level = Coniferous moss)*	Mixed	1.13	0.45 – 2.65	0.0001
		Wetlands	1.25	0.37 – 3.93	
		Open	2.02	1.49 – 2.69	

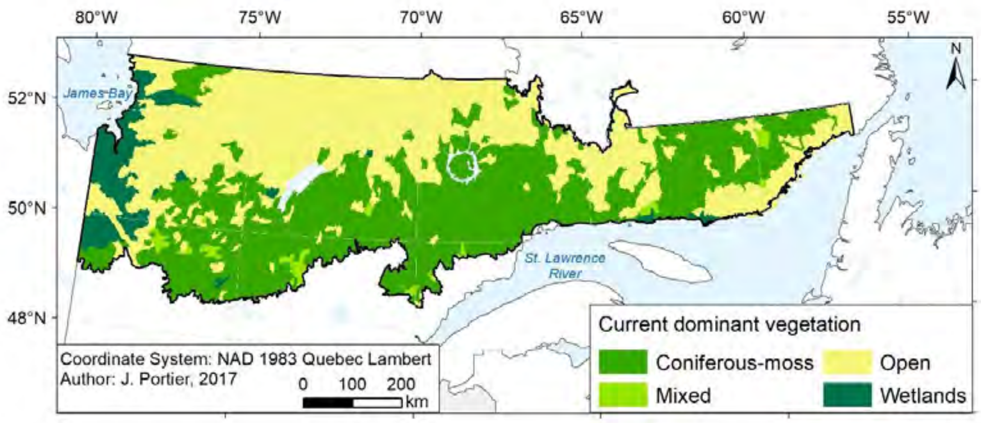

Figure 2.6 Map of current dominant vegetation.

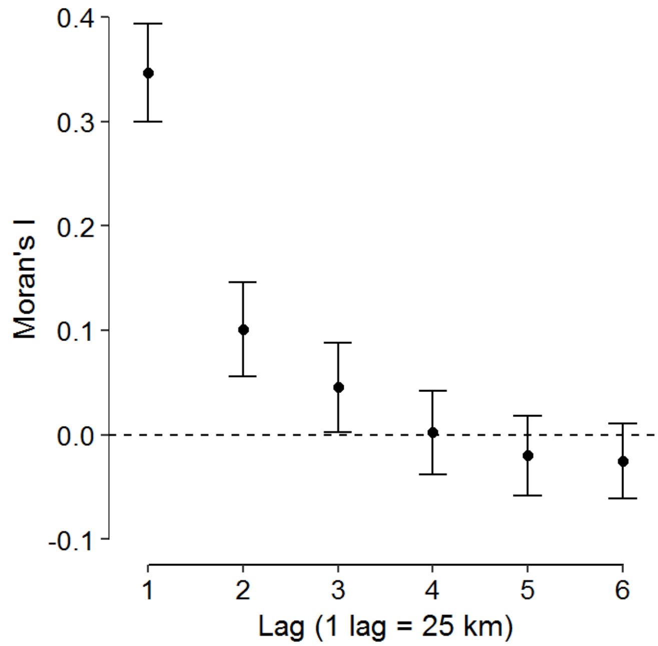

Figure 2.7 Spatial correlogram calculated on the residuals of the final ordinal logistic model factoring in current vegetation.

The correlogram shows Moran's I associated with each lag as well as their respective Bonferroni-corrected confidence intervals.

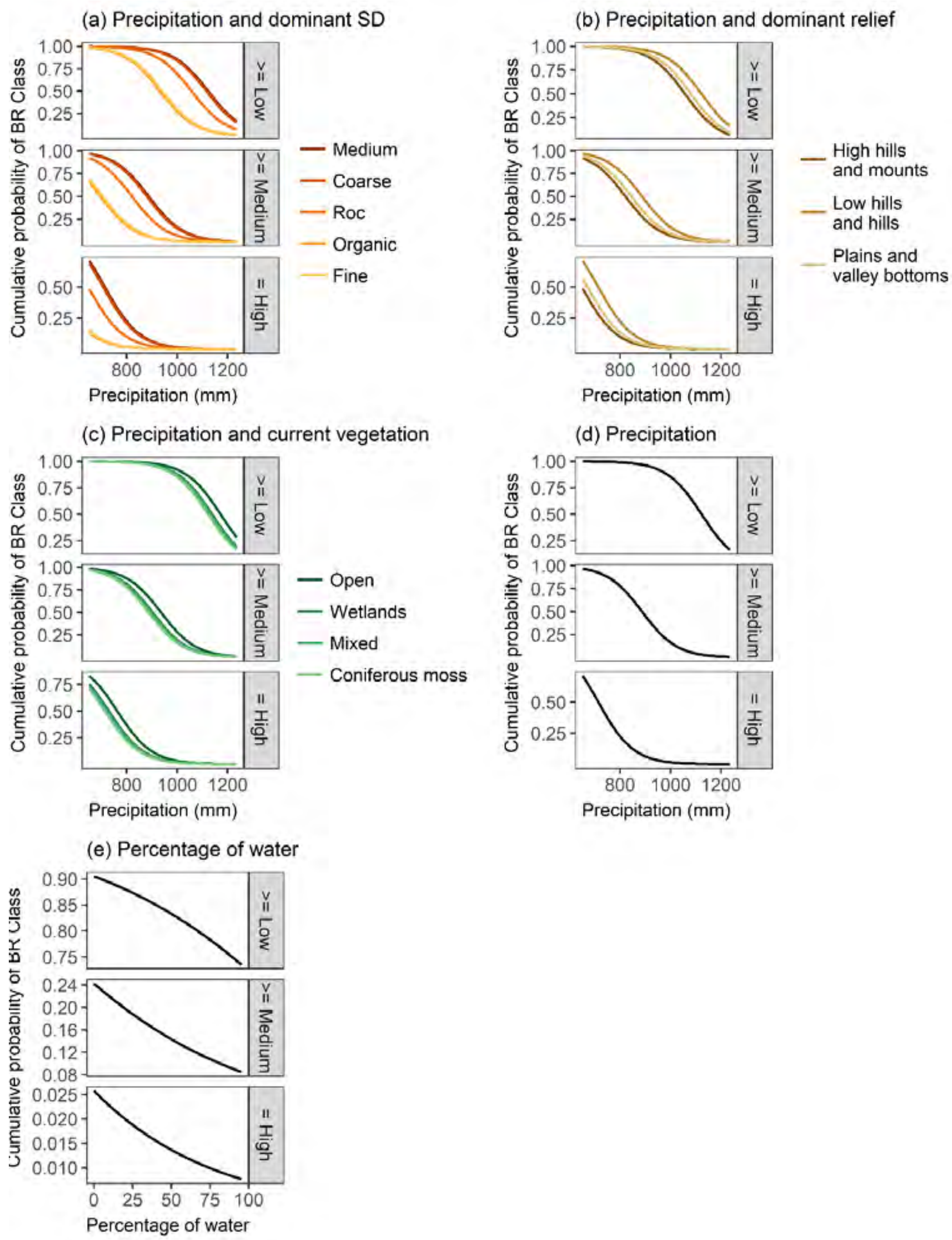

Figure 2.8 **Effects of precipitation and (a) dominant SD, (b) dominant relief, and (c) current vegetation, as well as effects of (d) precipitation alone and (e)**

percentage of water alone on the cumulative probability of experiencing at least a low BR, at least a medium BR, or a high BR.

In each panel, the continuous variables that are not represented were included in the model using their mean value. For dummy variables, the most represented class was used.

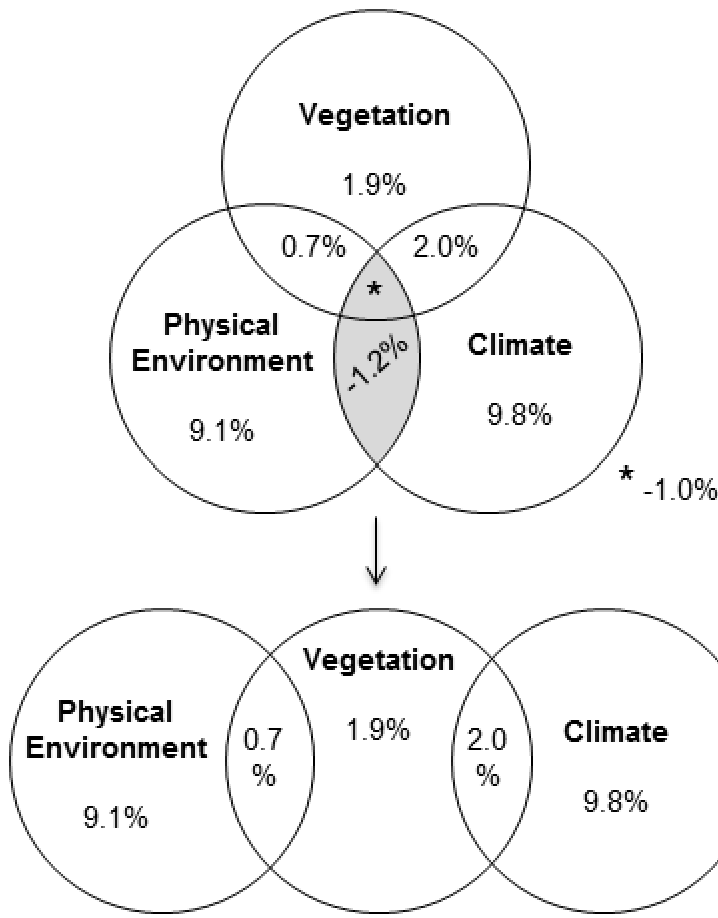

Figure 2.9 Venn diagrams of variance partitioning of the first order RAC model factoring in current vegetation.

Variance is calculated as McFadden's R^2. The total percentage of variance explained by a given group of factors equals the sum of all percentages within the corresponding circle.

CHAPITRE III

DOES TIME SINCE FIRE DRIVE LIVE ABOVEGROUND BIOMASS AND STAND STRUCTURE IN LOW FIRE ACTIVITY BOREAL FORESTS? IMPACTS ON THEIR MANAGEMENT

(EST-CE QUE LE TEMPS DEPUIS FEU DÉTERMINE LA BIOMASSE ARBORÉE VIVANTE ET LA STRUCTURE DES PEUPLEMENTS DANS LES FORÊTS BORÉALES À FAIBLE ACTIVITÉ DES FEUX ? IMPACTS POUR LEUR AMÉNAGEMENT)

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3.1 Abstract

Boreal forests subject to low fire activity are complex ecosystems in terms of structure and dynamics. They have a high ecological value as they contain important proportions of old forests that play a crucial role in preserving biodiversity and ecological functions. They also sequester important amounts of carbon at the landscape level. However, the role of time since fire in controlling the different processes and attributes of those forests is still poorly understood. The Romaine River area experiences a fire regime characterized by very rare but large fires and has recently been opened to economic development for energy and timber production. In this study, we aimed to characterize this region in terms of live aboveground biomass, merchantable volume, stand structure and composition, and to establish relations between these attributes and the time since the last fire. Mean live aboveground biomass and merchantable volume showed values similar to those of commercial boreal coniferous forests. They were both found to increase up to around 150 years after a fire and then to start declining. However, no significant relation was found between time since fire and stand structure and composition. Instead, they seemed to mostly depend on stand productivity and non-fire disturbances. Although in terms of merchantable volume these forests seemed profitable for the forest industry, a large proportion were old forests or presenting structures of old forests. Therefore, if forest management was to be undertaken in this region, particular attention should be given to these old forests in order to protect biodiversity and ecological functions. Moreover, non-fire disturbances should be monitored as they seemed to be an important driver of these forests' dynamics. Finally, the high amounts of carbon stored in these forests, resulting from the long fire cycles they experience, should be considered when undertaking activities that imply the flooding or harvesting of this carbon.

Keywords: Boreal forests; live aboveground biomass; stand structure; time since fire; low fire activity; forest management

3.2 Résumé

Les forêts boréales soumises à une faible activité de feux sont des écosystèmes complexes en termes de structure et de dynamique. Elles ont une valeur écologique importante puisqu'elles contiennent des proportions importantes de vieilles forêts qui jouent un rôle crucial dans la préservation de la biodiversité et des fonctions écologiques. Elles séquestrent aussi des quantités importantes de carbone à l'échelle du paysage. Cependant, le rôle du temps depuis feux dans le contrôle des différents attributs et processus de ces forêts est encore mal compris. Le secteur de la rivière Romaine est soumis à un régime de feux caractérisé par des feux rares mais de grande taille. Il a été récemment ouvert au développement économique pour la foresterie et la production d'énergie. Le but de cette étude est la caractérisation de cette région en termes de biomasse arborée vivante, de volume marchand, de structure et de composition des peuplements ; ainsi que l'établissement de relations entre ces attributs et le temps depuis feux. La biomasse arborée vivante et le volume marchand étaient similaires à ce que l'on retrouve en forêt boréale résineuse commerciale. Nous avons montré que tous deux augmentaient jusqu'environ 150 ans après un feu, puis déclinaient. Cependant, aucune relation n'a pu être démontrée entre le temps depuis feux et la structure et composition des peuplements. Ces attributs semblaient dépendre majoritairement de la productivité des sites et de l'occurrence de perturbations secondaires. Bien que le volume marchand de ces forêts semble être intéressant pour l'industrie forestière, une large proportion des peuplements étaient attribuable à des vieilles forêts, ou à des forêts présentant des structures de vieilles forêts. Ainsi, si l'aménagement forestier s'implantait dans cette région, une attention particulière devrait être portée à ces vieilles forêts afin d'en protéger la biodiversité et les fonctions écologiques. De plus, les perturbations secondaires devraient être suivies puisqu'elles semblent être un facteur déterminant important de la dynamique forestière. Enfin, les quantités importantes de carbone stockées dans ces forêts, résultant des longs cycles de

feux, devraient être considérées si des activités impliquant l'ennoiement ou la récolte de ce carbone devaient être entreprises.

Mots-clés : Forêt boréale, biomasse arborée vivante, structure des peuplements, temps depuis feux, faible activité de feux, aménagement forestier.

3.3 Introduction

North American boreal forests are shaped by disturbance regimes, most particularly wildfires (Johnson 1992; Payette 1992; Brandt 2009) whose activity generally decreases from West to East (Zhang and Chen 2007). Therefore, the North Shore region of Quebec, eastern Canada, experiences long fire cycles (Bouchard et al. 2008; Portier et al. 2016). In the absence of fires for several centuries, stands can become older than the mean longevity of tree species (Kneeshaw and Gauthier 2003; Boucher et al. 2006) and their dynamic gradually becomes driven by non-fire disturbances associated with gap dynamics, such as insect outbreaks and windthrows (Blais 1983; Pham et al. 2004; Waldron et al. 2013; Girard et al. 2014). Such regions are therefore characterized by complex age structures as new cohorts can establish below the old ones (Boucher et al. 2006; De Grandpré et al. 2008). If, as in the rest of the boreal zone of Quebec, black spruce (*Picea mariana* (Mill.) B.S.P.) is the most represented tree species in the coniferous boreal forests of the North Shore region, long fire cycles and high precipitation allow for a significant proportion of balsam fir (*Abies balsamea* (L.) Mill.) to develop in these forests (De Grandpré et al. 2000; Bouchard et al. 2008).

In the North Shore region of Quebec, the Romaine River area has recently been open to economic development for hydroelectric energy and forest products (Ministère des Ressources Naturelles du Québec 2013). However, areas experiencing long fire cycles come with various challenges in the context of such developments. First, they present an important proportion of old forests (De Grandpré et al. 2008; Bauhus et al.

2009; Bergeron and Fenton 2012) that are highly complex ecosystems playing a crucial role in preserving biodiversity and ecological functions (Kneeshaw and Gauthier 2003; Bergeron and Fenton 2012). Therefore, in a sustainable ecosystem management perspective, following recommendations considering old forests is essential. They promote the conservation of such forests, coupled with the implementation of sylvicultural strategies that reproduce attributes associated with late-successional forests (Bergeron et al. in press; Kneeshaw and Gauthier 2003; De Grandpré et al. 2008; Bauhus et al. 2009).

Secondly, boreal forests contain a large proportion of the stored terrestrial carbon stocks (De Groot et al. 2013; IPCC 2014; Bradshaw and Warkentin 2015). In a context of climate change, the importance of keeping this carbon stored is widely recognized (IPCC 2014). In areas subject to a high fire activity, a lot of this carbon is released into the atmosphere by fires (De Groot et al. 2007; Bond-Lamberty et al. 2007). However, areas subject to low fire activity can store large amounts of carbon at the landscape level as it is only rarely withdrawn by fires (Luyssaert et al. 2008).

Contrary to areas subject to short fire cycles (Harper et al. 2002; Rapanoela et al. 2015) and to a lesser extent, to the less fire prone western North Shore (Boucher et al. 2006; Bouchard et al. 2008; De Grandpré et al. 2008) that are relatively well documented, forest attributes and dynamics of the Romaine River area are still poorly known. Therefore, its potential in terms of live aboveground biomass and merchantable volume, as well as its composition and structure characteristics would now constitute valuable information for forest managers. Moreover, if forest live aboveground biomass and merchantable volume generally increase with time since the last fire (Paré and Bergeron 1995; Harper et al. 2005; Lecomte et al. 2006), this relation is still poorly understood in boreal forests subject to long fire cycles. Similarly, the role of fire versus non-fire disturbances in changes in structure and composition in these ecosystems needs to be further studied and understood, especially when forest management is involved. In addition, estimating carbon stocks is crucial to better understand the potential consequences of economically developing this region.

The goal of our study was to i) characterize the coniferous boreal forests of the Romaine River region in terms of live aboveground biomass, merchantable volume, structure and composition; ii) establish the relation between these attributes and the time since the last fire. First, field inventory plots were used to calculate the live aboveground biomass and merchantable volume and to characterize the stem size structure as well as the black spruce and balsam fir proportions in the study area. Secondly, the time since fire of the field plots was estimated to determine how long after a fire the live aboveground biomass and merchantable volume reached a peak and started to decline. The relation between time since fire and both structure and composition was also assessed. Thirdly, the field plots estimates were used to extrapolate live aboveground biomass and merchantable volume to the entire study area at the scale of forest polygons. To achieve this step, regression trees were built using various forest attributes, soil, topographic and remote sensing spectral variables.

3.4 Material and methods

3.4.1 Study area

The Romaine River is located in the eastern North Shore region of Quebec, eastern Canada, north of the St. Lawrence River. This region has recently been opened to economic development for hydroelectric energy and forest products (MMFPQ, 2013a). In particular, a portion of the forested landscape has been flooded permanently to produce electricity. The entire region is mainly characterized by a very low fire activity with rare but large fires. Fire cycles range from about 200 years in the north to 8,200 years in the south (Gauthier et al. 2015). Our study area is centered on Romaine River and is entirely located within the spruce-moss bioclimatic domain, except for the northernmost portion that lies in the spruce-lichen domain (MMFPQ, 2013b). It covers 72,681 km² and stretches between latitudes 50°N to 53°N, and between longitudes 66°W to 60°W (Fig. 1). This region is the one of the wettest in eastern Canada, with total mean annual precipitation ranging from 754 mm to 1,108 mm. Mean annual temperature varies from -4.2°C to 3.3°C (means of weather data extracted at the forest-stand level over the 1971-2000 period - Leboeuf et al. 2012; Ministère des Ressources Naturelles du Québec 2013). The topography is variable throughout the study area with flat, sea level areas in the south along the St. Lawrence River, gradually transiting to a highly fractured relief to the north, rising to nearly 1,000 m of elevation (Fig. 1). The southern half of the study area mainly sits on bedrocks with very thin mineral soil, while the northern half is largely dominated by thick till deposits. If, as in the rest of the boreal zone of Quebec, black spruce (*Picea mariana* (Mill.) B.S.P.) is the most represented tree species in the coniferous boreal forests of the North Shore region, the long fire cycles and high precipitation make it possible for a significant proportion of balsam fir (*Abies balsamea* (L.) Mill.) to develop in these forests (Bouchard et al., 2008; De Grandpré et al., 2000). Some other tree species, such as trembling aspen (*Populus tremuloides* Mich.), white birch (*Betula papyrifera* Marsh.) and white spruce (*Picea glauca* (Moench) Voss), can also be found in smaller proportions.

3.4.2 Field data and basal area calculation

The field campaign was conducted in 2014 along a 160-km-long road near Romaine River (Fig. 1). The road was divided into 32 consecutive 5-km-long by 750-m-wide cells (Portier et al., 2016). In each cell, two points located at a minimum distance of 100 m from the road were randomly generated and sampled. In the northern section of the road, a lower number of points were sampled because of access issues (total number of field plots = 54). The sampling plots were used for the estimation of tree basal area (BA) and organic layer thickness, and one out of two plots by cell was used for time since fire estimation. In addition, 164 plots from the Northern Forest Inventory

Program (NFIP; 2005 to 2009) of the Ministère des Forêts, de la Faune et des Parcs du Québec (MFFPQ), for which similar data was available, were added to the field dataset (Fig. 1).

In total, time since fire data was available for 200 plots: 44 field plots (Portier et al., 2016) and 156 inventory plots from the NFIP. Time since fire was determined by dendrochronology, so that the trees' age determined the time since the last fire in each stand. If this method allows the reconstruction of up to 350 years of fire history, time since fire estimates become less precise as they increase (Cyr et al., 2016; Portier et al., 2016). When a stand is older than the oldest tree on-site, assessing a precise stand age becomes impossible. In these cases, a minimum time since fire was attributed to the stand (Cyr et al., 2016; Portier et al., 2016).

In the 54 field plots, BA was assessed per species from the center of the plot using a factor-two wedge prism that selects trees meeting a certain size-distance threshold (Bruce, 1955). The BA of a given species equals two times the number of trees of that species that has been counted with the prism and is expressed in square meters per hectare. In the 164 NFIP inventory plots, BA was calculated from forest stand inventory data. The diameter at breast height (DBH) and height of all trees with a DBH ≥ 9 cm were measured in a 400 m² circle. In addition, the DBH of all saplings (DBH ≥ 3 cm and < 9 cm) was measured in a 100 m² circle from the same center. The BA of a tree or sapling in square meters was calculated as:

$$BA = \frac{\pi}{40\,000} * DBH^2 \tag{3.1}$$

The BA of a given species in square meters per hectare was then defined as:

$$BA_{species} = \sum BA_{tree} * 25 + \sum BA_{sapling} * 100 \tag{3.2}$$

In order to avoid biases related to the different field methods used, forest stand inventory was also carried out in 12 field plots using the same protocol as in the NFIP plots. BA estimates from those 12 field plots were compared with the prism estimates of the same plots, and a correction was then applied to all prism estimates.

3.4.3 Live aboveground biomass and merchantable volume

Live aboveground biomass was calculated from the allometric equations per species developed by Paré et al. (2013) which estimate the biomass of tree components (stemwood, foliage, branch, and bark). The biomass of all tree components was summed to obtain the biomass per species in tons per hectare for each plot. Finally, the biomass of all species was summed to obtain the total live aboveground biomass of each stand in tons per hectare.

The merchantable volume (i.e. volume in cubic meters per hectare of trees with a DBH ≥ 9 cm – Perron 2003; Newton 2012) was calculated for each forest inventory plot according to the per species equations developed from DBH and heights of trees (Perron, 2003). Plots in which biomass was estimated using wedge prism were removed for this calculation as DBH and height data are required (total number of plots in which merchantable volume was calculated = 168).

3.4.4 Composition and structure

Composition was assessed using the proportion of BA of merchantable trees attributed to black spruce and balsam fir in each plot. Four compositional types were defined: spruce-dominated, spruce-fir, fir-spruce, fir-dominated (Table 1a).

The stand structure of each plot was assessed from the proportion of density and BA of merchantable trees (DBH ≥ 9 cm) distributed in DBH classes. Plots that did not fall into the four compositional types presented in Table 1a were removed from this analysis. Two-centimeters DBH classes were defined, with “10” being the lowest class and containing trees with a DBH between 9 and 11 cm. The few trees presenting a DBH greater than 33 cm were grouped into a "34+" class. In each plot, the reversed cumulative proportions of trees and of BA in each class were calculated to identify groups of similar stand structures. Cumulative proportions were used because they smooth the DBH distributions and thus make it possible to avoid biases resulting from the use of classes, i.e. to avoid important differences between the proportions of two neighboring classes. For instance, consider two plots that contain the same number of trees distributed between two DBH classes, but one contains all the trees in one class while the other has the trees split equally between the two classes. With a continuous distribution, these two plots would be very similar, while they would be very different in a distribution by class.

A *k*-means clustering method was used to split the plots into homogeneous structure distribution groups (Nlungu-Kweta et al., 2016; Oksanen et al., 2017). The DBH distributions were first submitted to a Simple Structure Index (SSI) test using the *cascadeKM* function of the "vegan" *R* package (Oksanen et al., 2017). This test divides data into various numbers of clusters based on the distributions provided and produces an SSI value for each number of clusters tested. The highest value indicates the number of clusters into which the data should be divided. Two to five clusters were tested. Plots were then grouped based on their DBH distributions into the number of clusters obtained with the SSI test using the *kmeans* function of the "stats" R package.

3.4.5 Relation between live aboveground biomass, merchantable volume, organic layer thickness, time since fire, composition and structure

A piecewise regression method was used to determine how long after fire the live aboveground biomass peaked, and whether this peak was followed by a steady state or a decline (Harper et al., 2005). First, linear regression was used to test the effect of time since fire on biomass. Second, a Davies test was performed in order to test for a change of slope and to provide a first estimate of breakpoint (Muggeo, 2008). Third, a segmented regression was done using the *segmented* function of the *segmented* R package (Muggeo, 2008) based on the linear regression model. The breakpoint estimate returned by the Davies test was used as a starting value to search for the most likely breakpoint. The same process was repeated to test the effect of time since fire on the accumulation of merchantable volume and organic layer thickness.

To test for differences in live aboveground biomass, merchantable volume, time since fire and organic layer thickness between compositional types and structural clusters, one-way ANOVAs followed by Tukey's post-hoc tests were used. In addition, a chi-square test was conducted between structural clusters and compositional types.

3.4.6 Extrapolation of live aboveground biomass and merchantable volume to the Romaine River region at the scale of forest polygons

The extrapolation of live aboveground biomass and merchantable volume to the entire study area was done using regression trees. The analysis was carried out at the forest stand level (mean stand size = 17 ha). Forest stand maps were produced between 2005 and 2008 based on the analysis of Landsat satellite images confirmed with the use of aerial photographs (Leboeuf et al., 2012). Among other attributes, these maps contain information on forest stands' height, density and surficial deposits. All explanatory variables used in this analysis (Table 2) were compiled at the level of forest stands and are described in the sections below.

3.4.6.1 Rescaling of live aboveground biomass and merchantable volume

All plots (field plots and NFIP plots) were assigned to the forest stands in which they fell. Six stands contained two or more plots, in which cases the biomass and merchantable volume of those plots were averaged. Total live aboveground biomass and merchantable volume were split into five classes based on quantile intervals: biomass classes in tons per hectare: $0 \leq$ class $1 < 24.5 \leq$ class $2 < 42.5 \leq$ class $3 < 54 \leq$ class $4 < 71 \leq$ class $5 < 188$; merchantable volume in cubic meters per hectare: $0 \leq$ class $1 < 25.5 \leq$ class $2 < 61.5 \leq$ class $3 < 96.5 \leq$ class $4 < 138 \leq$ class $5 < 413$.

3.4.6.2 Forest, soil and topographic attributes data

Classes of stand height and density were reconverted into continuous variables using the median of their classes. The topographic variables considered were elevation, cosine of aspect (representing the north-south exposition of a stand), Terrain Ruggedness Index (TRI) and Topographic Position Index (TPI). Topographic variables were averaged using a weighted mean calculation for each forest stand. Surficial deposit drainage was defined based on the dominant surficial deposit of the forest stand and was classified as either xeric, mesic, subhydric, hydric or bare rock when the proportion of mineral soil covering the stand was too small.

3.4.6.3 Remote sensing spectral data

TERRA MODIS level 1B geolocated top of atmosphere radiance (MOD02) data for summer (July-August) and winter (January-February) 2008 were processed at the Canada Centre for Remote Sensing (Pouliot et al., 2009; Trishchenko et al., 2006). They produced orthorectified seasonal mosaics of composite surface reflectance at 250-m (Bands 1 and 2) and 500-m (Bands 3 and 6) resolutions, although different procedures were applied, including the downscaling of the 500-m resolution bands to 250 m (Trishchenko et al., 2006). We used the winter and summer reflectance data in bands 1 (red, 620-670 nm), 2 (near-infrared, 841-876 nm), 3 (blue, 459-479 nm) and 6 (shortwave infrared, 1628-1652 nm) at a 250-m resolution as well as six summer and winter spectral indices that were all derived from summer and winter reflectance data (bands 1, 2 and 3), i.e. Normalized Difference Vegetation Index (NDVI), Wide Dynamic Range Vegetation Index (WDVI), Soil Adjusted Vegetation Index (SAVI), Global Environment Monitoring Index (GEMI), Reduced Simple Ratio (RSR) and Normalized Difference Moisture Index (NDMI) (Pouliot et al., 2009). All spectral bands and indices were extracted for each forest stand using a weighted mean calculation.

3.4.6.4 Predicted live aboveground biomass and merchantable volume from regression trees

Regression trees are a nonlinear, nonparametric regression method that uses recursive partitioning of the data to model the response variable based on different explanatory variables. Regression trees are made of branches going through different explanatory variables and leading to terminal nodes that correspond to values of the response variable. Each terminal node forms a distinctive simple model only applicable to that particular node. Interior nodes in the branches of the tree constitute a test based on an explanatory variable's value (Breiman et al., 1984; De'ath and Fabricius, 2000). Regression trees of live aboveground biomass and merchantable volume were built using the *rpart R* package (Therneau et al., 2015). In order to avoid overfitting, the minimum size of the final nodes was set to 15 observations so that a node could not be built if it did not contain a reasonable number of observations.

A *k*-fold cross-validation was performed on both regression trees by randomly splitting the data set into *k* mutually exclusive subsets of approximately equal size (Kohavi, 1995). We used $k = 10$, as it has been suggested to be the most appropriate number of folds for real-world datasets (Kohavi, 1995). One of the subset was used for validation, while the other nine were used together as a training data set on which the regression tree was built. The cross-validation estimate of accuracy of a subset is the proportion of correct classifications in the validation subset. Those steps were repeated ten times so that each subset was used for validation. The mean value of the ten resulting estimates of accuracy provides the overall estimate of accuracy (Kohavi, 1995). This procedure was repeated in a bootstrap process in order to obtain a more precise overall estimate of accuracy, along with the corresponding 95% empirical confidence interval calculated using the lower and upper percentiles. The bootstrap was run using 1,000 iterations, after which the confidence interval's width tended to stabilize.

The regression trees were used to predict the live aboveground biomass and merchantable volume of the forest stands in the study area. For each forest stand, we extracted the probabilities of belonging to each class of biomass or merchantable volume that were estimated by the regression trees based on the values of the explanatory variables. The predicted live aboveground biomass and merchantable volume were then calculated based on the probability and median of each class as:

$$\text{Predicted value} = \sum_{class\,=\,1}^{class\,=\,5} class\ probability * class\ median \tag{3.3}$$

For the whole study area, mean live aboveground biomass and merchantable volume, as well as their 95% confidence interval, were calculated using the mean and the lower and upper percentiles of a 1,000-iteration bootstrap with replacement of the forest stands. In addition, carbon storage in living trees was estimated using a 0.5 conversion factor from live aboveground biomass (de Groot et al., 2007; Mathews, 1993). Mean predicted live aboveground biomass was also computed for each homogeneous fire zone located in the study area, which had been previously determined based on their fire cycle (Gauthier et al., 2015).

3.5 Results

Mean live aboveground biomass of all plots was 49.7 $t.ha^{-1}$ (standard deviation = 29.4), while mean merchantable volume was 94.2 $m^3.ha^{-1}$ (standard deviation = 78.3). The most represented compositional type was spruce-dominated, followed by spruce-fir, fir-spruce and finally fir-dominated (Table 3.1a). The SSI test led to splitting the data into three structural clusters: the “inverted J” structure, dominated by small stems; the “intermediate” structure, showing stems of intermediate DBH; and the “flat” structure, presenting a wider range of stem sizes and containing the largest ones (Table 3.1b, Figure 3.2).

3.5.1 Time since fire

The Davies tests performed on the linear model of live aboveground biomass and time since fire, as well as on the linear model of merchantable volume and time since fire, were both significant (*p*-value = 0.013 and 0.004, respectively) and both provided a starting breakpoint value at 146 years. The segmented regressions returned a breakpoint value of 149 years (95% CI: 107-192) for live aboveground biomass, and of 150 years (95% CI: 118-183) for merchantable volume (Figure 3.3a and 3.3b). Estimates of all segments were significant (Table 3.3a and 3.3b).

The Davies test performed on the linear model of organic layer thickness and time since fire was not significant (p-value = 0.665), suggesting that no breakpoint could be found. Consequently, the segmented regression was not performed. Instead, the initial linear model was kept and showed that organic layer thickness significantly increased with time since fire (Table 3.3c, Figure 3.3c).

The ANOVA tests did not show any significant difference between structural clusters and between compositional types in terms of time since fire (Figure 3.4). Nevertheless, Figure 3.5 shows that the “inverted J” structure tended to have a younger median time since fire than the other structures. In order to better understand why no significant relation was found, the relation between mean tree volume and tree density was plotted to visually estimate the sites' productivity (Newton, 2012), depending on their time since fire and structural clusters (Figure 3.6). Younger stands with an intermediate or flat structure were mostly productive (high tree density and high mean tree volume), while older stands with an "inverted J" structure were mostly found in unproductive sites.

3.5.2 Structure and composition

ANOVAs followed by Tukey's post-hoc tests showed significant differences in terms of live aboveground biomass and merchantable volume between structural clusters and between compositional types. On the opposite, no significant differences were found in terms of organic layer thickness (Figure 3.4). The chi-square test showed a significant relation between structural clusters and compositional types (Figure 3.7).

3.5.3 Predicted live aboveground biomass and merchantable volume

The regression trees that partitioned forest stands based on their live aboveground biomass and merchantable volume had eight and seven final nodes, respectively, and used five and four explanatory variables, respectively (Figure 3.8). The 10-fold cross-validation showed an estimate of accuracy of the regression trees of live aboveground biomass and merchantable volume of 0.35 (95% CI: 0.30-0.40) and 0.39 (95% CI: 0.34-0.44), respectively.

Predicted live aboveground biomass and merchantable volume were extracted for all forest stands from the regression trees and mapped over our study area (Figure 3.9). On average, forest stands presented a predicted live aboveground biomass of 58.0 $t.ha^{-1}$ (95% CI: 57.8-58.2) and a merchantable volume of 129.0 $m^3.ha^{-1}$ (95% CI: 128.5-129.3). Furthermore, we estimated from the values of live aboveground biomass that carbon storage in living trees was 29.0 $t.ha^{-1}$ (95% CI: 28.9-29.1). In comparison, live aboveground biomass estimates from Beaudoin et al. (2014) extracted at the forest stand level predicted a mean live aboveground biomass of 57.0 $t.ha^{-1}$ (95% CI: 56.9-57.1). Predicted live aboveground biomass was higher in areas subject to long fire cycles than in areas subject to short fire cycles (Figure 3.10).

3.6 Discussion

3.6.1 Characterization of forests in a boreal region with low fire activity

Forests in the Romaine River region were mostly dominated by black spruce, although a high proportion of balsam fir was also found. This composition is similar to that previously observed in the western half of the North Shore region of Quebec, just east of our study area (Boucher et al., 2006). Stands were split into three structural types – "inverted J", intermediate and flat - that matched those previously determined by other studies (Boucher et al., 2003; Moussaoui et al., 2016; Nlungu-Kweta et al., 2016).

Live aboveground biomass and merchantable volume significantly increased from the "inverted J" structure to the intermediate structure and finally to the flat structure. The flat structure presented a wide range of stem sizes, representative of the irregular structures that characterize old forests. The complexity of those structures and of the disturbances occurring in such old forests are recognized to be responsible for their high biodiversity (Bergeron and Fenton, 2012; Fenton and Bergeron, 2008; Kneeshaw and Gauthier, 2003; Lindenmayer and Franklin, 2002).

We estimated the live aboveground biomass and merchantable volume of the study area to be 57.96 $t.ha^{-1}$ (95% CI: 57.75-58.16) and 129.03 $m^3.h^{-1}$ (95% CI: 128.51-129.28), respectively. These values are consistent with estimates obtained at larger scales in forested boreal areas – i.e. without considering recently burned areas – using different methods (Beaudoin et al., 2014; Boudreau et al., 2008). Boudreau et al. (2008) found that the moderately open coniferous boreal forests of Quebec (density between 26 and 60%) presented an aboveground biomass of 50.2 $t.ha^{-1} \pm 1.4$ in non-commercial forests and of 58.3 $t.ha^{-1} \pm 1.6$ in commercial forests. Moreover, the merchantable volume we estimated fell into the upper range of what had been observed in stands dominated by black spruce in northcentral Quebec (Rapanoela et al., 2015). Therefore, we suggest that the forests of the Romaine River area would be mostly akin to commercial boreal forests.

3.6.2 Biomass accumulation with time since fire

Our analyses regarding the pattern of change in live aboveground biomass and merchantable volume with time since fire showed an aggradation phase that lasted up to about 150 years, followed by a phase of slow decline. This breakpoint is consistent with other studies conducted in Quebec (Garet et al., 2009; Gauthier et al., 2010; Harper et al., 2005) and Ontario (Gao et al., 2017). Other studies found an earlier breakpoint in the western North Shore region (~ 90 years – Bouchard et al. 2008) and in western Quebec (~ 100 years – Harper et al. 2002). However, the western North Shore has been experiencing stronger and more frequent spruce budworm outbreaks than our study area, as well as some hemlock looper outbreaks (MFFP, 2013; De Grandpré et al. 2008). These insect disturbances could change the slope of the aggradation phase into a fluctuating pattern by inducing high mortality rates and lowering tree growth (Bouchard et al., 2005).

The decline phases most likely resulted from two processes. First, senescence of trees eventually leads to mortality of the oldest dominant trees. In fact, the mean longevity of canopy trees for black spruce and balsam fir is 100-200 and 60-100 years, respectively (Burns and Honkala, 1990), and balsam fir is a shade-tolerant species that is rarely present in the first decades after fire (Bouchard et al., 2008; De Grandpré et al., 2000). Second, non-fire disturbances often occur in areas subject to long fire intervals (McCarthy, 2001; Pham et al., 2004), and they lead to high mortality rates in mature stands (Bouchard et al., 2005; Girard et al., 2014; Pham et al., 2004). Insect outbreaks, such as spruce budworm or hemlock looper outbreaks, are the main secondary disturbance in the North Shore region (MFFP, 2013; De Grandpré et al. 2000), followed by windthrows (Girard et al., 2014; Waldron et al., 2013).

However, decline phases in live aboveground biomass and merchantable volume often stabilize eventually (Bond-Lamberty et al., 2004; Garet et al., 2009; Harper et al., 2005; Irulappa Pillai Vijayakumar et al., 2016). Although not entirely compensating for increasing tree mortality with time since fire, young tree regeneration can allow the upkeep of a certain level of live aboveground biomass and merchantable volume (Garet et al., 2009). In our study, this was also supported by the fact that the decline phase in merchantable volume which did not consider saplings (DBH < 9 cm), was steeper than that in live aboveground biomass. In other particular cases, as in the Clay Belt area of western Quebec, paludification can lead to the continuous decline of biomass by lowering site productivity, regeneration success and tree growth (Lecomte et al., 2006; Simard et al., 2007).

Similarly, paludification has impacts on organic layer thickness. When a stand ages, tree mortality leads to increasing dead wood biomass, which eventually decomposes and thickens the organic layer (Luyssaert et al., 2008; Terrier et al., 2016). However, organic layer thickness in our study area did not reach depths observed in the paludified Clay Belt area. For example, 200 years after fire, the organic layer in the western North Shore region (Ward et al., 2014) as well as in the Romaine River area was approximately 20 cm thick, while it could reach 50 cm in the Clay Belt area (Simard et al., 2009, 2007). Ward et al. (2014) concluded that contrary to these paludified regions, the organic layer accumulation observed in the North Shore region did not lead to a strong decrease in productivity. Furthermore, important quantities of dead biomass and, consequently, of carbon are contained in the organic layer, which in boreal ecosystems often surpass live aboveground biomass and carbon (Bradshaw and Warkentin, 2015; Yuan et al., 2008). This confirms that old forests are important carbon sinks (Luyssaert et al., 2008) and, therefore, that the Romaine River region most likely contains important quantities of carbon stored in its soils.

3.6.3 At the landscape level: biomass and fire cycle

At the landscape level, low fire activity areas contain more above- and belowground biomass and therefore more carbon stored than regions with shorter fire cycles (Luyssaert et al., 2008). This is consistent with our results showing that in our study area, total predicted aboveground biomass increased between regions experiencing the shortest to the longest fire cycles. While areas subjected to long fire cycles will mostly be covered by forested lands, regions experiencing short fire cycles will present an important proportion of recently burned areas (Gauthier et al., 1996). At the landscape level, the mean age of the forest will also be lower, which is associated with a lower biomass. In addition, large amounts of carbon are released into the atmosphere by fires burning living and dead biomass in both above- and belowground forest compartments (Bond-Lamberty et al., 2007; Bradshaw and Warkentin, 2015; de Groot et al., 2007), although productive young forests can partly compensate for these carbon stock losses.

Biomass and carbon differences at the landscape level between high and low fire activity areas should be considered when planning economic development. On the one hand, forest management harvests large amounts of biomass and leads to a rejuvenation of forests (Cyr et al., 2009) and to the exportation of important quantities of carbon. On the other hand, the flooding of terrestrial ecosystems for energy production affects carbon stocks in two different ways, although the balance between them is still poorly understood. First, the flooded biomass eventually releases carbon into the atmosphere, although in such cold ecosystems this phenomenon can take centuries to millennia (Gennaretti et al., 2014; St. Louis et al., 2000; Teodoru et al., 2012; Tremblay et al., 2004). Second, flooded forests no longer fix carbon, and thus lose their role of carbon sequesters.

3.6.4 Relation between time since fire and stand structure

Contrary to what we expected, time since fire did not explain structural nor compositional differences between stands. Several hypotheses can be formulated to explain this lack of relation. First, as we demonstrated, stand productivity can affect stand structure (Boucher et al., 2006; Moussaoui et al., 2016; Newton, 2012). Relatively young stands with a flat structure can be observed when stands are highly productive, as trees can reach large DBHs over a relatively short time. On the contrary, old stands can sometimes present an “inverted J” structure when they are located on poor, unproductive sites. Indeed, unproductive sites usually present a very low tree density and remain in this condition regardless of time since the last fire (Boucher et al., 2006).

Second, the increasing prevalence of non-fire disturbances with time since fire can gradually alter stand structure (McCarthy, 2001). As this region is subject to long fire cycles (Gauthier et al., 2015; Portier et al., 2016), structural differences between stands could result from mortality caused either by senescence of old stands or by insect outbreaks and/or windthrows that induce gap dynamics (De Grandpré et al., 2000; Girard et al., 2014; Kneeshaw and Gauthier, 2003; Pham et al., 2004). In particular, a stand with a flat structure containing both small and large stems could be attributable to a multi-cohort old forest experiencing gap dynamics driven by small-scale disturbances (Kneeshaw and Gauthier, 2003). On the other hand, if this stand is subject to strong non-fire disturbances inducing high mortality rates, it could rapidly go back to an “inverted J” structure. Large stems would have died and small stems would represent the new trees regenerating from beneath.

Finally, time since fire estimates are not always precise, especially when stands are not composed of the first post-fire trees (Cyr et al., 2016), which can complicate the determination of relations between time since fire and composition or structure. Indeed, stands having a time since fire greater than 150 years are necessarily old, regardless of the precision of the estimate. However, a stand in which the estimated time since fire is short could be considered young, although it might be an unproductive stand or an old stand that suffered from non-fire disturbances and in which only young trees are still alive.

3.6.5 Relation between time since fire and stand structure

The coniferous boreal forests of the Romaine River region present a live aboveground biomass and a merchantable volume that are similar to those found in commercial boreal forests. However, at the landscape level, regions with low fire activity present two main characteristics. First, long fire cycles lead to large proportions of old forests. If forest management had to be undertaken in a sustainable way in those forests, particular attention should be given to old stands as they are associated with high biodiversity (Bergeron and Fenton, 2012; Drapeau et al., 2009; Kneeshaw and Gauthier, 2003; Saint-Germain et al., 2007). Many studies propose forest management options, either to preserve old forests or to manage stands so as to maintain or recreate old forest attributes (Bauhus et al., 2009; Burton et al., 1999; Shorohova et al., 2011). In particular, ecosystem-based management provides recommendations regarding silvicultural treatments that reproduce the structural patterns of natural forests (Bergeron et al., 2017; Burton et al., 1999; Gauthier et al., 2008; Newton, 2012).

Second, even though the total merchantable volume, live aboveground biomass and carbon stored are more important at the landscape level than in high fire activity areas, a certain number of stands could be unavailable to the forest industry. This could be the case when stands are old, when they have been subjected to important damage due to non-fire disturbances, or when they are unproductive. If clear-cut harvesting should be avoided in these stands, partial harvesting could be an option in some cases (Bauhus et al., 2009; Burton et al., 1999), although this treatment is rarely used because it is usually not economically profitable.

Finally, our results suggest that stand structure could result from the interaction between time since fire, non-fire disturbances and site productivity. As a consequence, stand structure could be a more integrative and complete indicator of the ecosystem's condition than stand age. As an example, an old but unproductive stand would have a minor ecological interest compared to a younger, more productive one. In terms of stand structure and biodiversity, the latter could be more similar to that of an old forest than the first. For this reason, forest management should base its strategies on stand structure, to which biodiversity largely responds (Fenton and Bergeron, 2008), rather than on stand age or merchantable volume.

In conclusion, economic development in low fire activity areas in general, and in the Romaine River region in particular, should pay particular attention to the large amounts of stored carbon resulting from long fire cycles, as well as to the highly ecologically valuable old forests that are largely represented in these ecosystems. Not only useful to the forest industry, our study also brings valuable information to assess the potential effects of flooding forests in low fire activity regions.

3.7 Acknowledgements

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3.8 Tables

Table 3.1 Description and repartition of compositional types (a). Repartition of structural clusters (b).

Only plots corresponding to the four compositional types presented in a) were used in the analyses.

a) Compositional types

	Spruce	**Spruce-Fir**	**Fir-Spruce**	**Fir**
Description (percentages relative to the merchantable BA of the stands)	Spruce ≥ 75 %	Spruce: 50-75 % Fir: Second most represented species	Fir: 50-75 % Spruce: Second most represented species	Fir ≥ 75 %
Percentage of sites	66.1 %	12.8 %	10.1 %	4.1 %

b) Structural clusters

	Inverted J	**Intermediate**	**Flat**
Percentage of sites	27.2 %	50.6 %	22.2 %

Table 3.2 Variables used in the analyses and their description

Variables	Description and range	Ref
Forest polygon attributes		
Height class	Classes: 1: > 22m; 2: 17 to 21m; 3: 12 to 16m; 4: 7 to 11m; 5: 4 to 6m; 6: 2 to 3m; 7: < 2m	(Leboeuf et al. 2012)
Density class	Classes: A: > 81%; B: 61 to 81%; C: 41 to 60%; D: 26 to 40%; L: 10 to 25%	
Topographic variables		
Elevation	Range: 1 to 996 m	
Cosine of aspect	Equivalent to the north-south exposure of a stand. Range: from -1 = facing south to 1 = facing north	
TPI	Topographic Position Index < 0 tends towards valleys > 0 tends towards hilltops Range: - 82 to 90	
TRI	Terrain Ruggedness Index Increases with ruggedness of terrain (0 = level) Range: 0 to 138 m	
Soil variable		
Drainage	Classes: xeric, mesic, subhydric, hydric or bare rock	
MODIS spectral variables		
Band 1 (red) Band 2 (near-infrared) Band 3 (blue) Band 6 (shortwave infrared)	Winter and summer surface reflectance bands at 250 m resolution Range B1: 286 to 1398 – Range B2: 215 to 3633 Range B3: 867 to 1720 – Range B4: 89 to 2370	(Trishchenko et al. 2006; Pouliot et al. 2009)
Winter and summer GEMI	Global Environment Monitoring Index Range winter: -15251 to 5942 Range summer: 1795 to 7809	
Winter and summer NDMI	Normalized Difference Moisture Index Range winter: 3160 to 9064 Range summer: -3602 to 5566	
Winter and summer NDVI	Normalized Difference Vegetation Index Range winter: -823 to 4630 Range summer: -1932 to 7709	
Winter and summer RSR	Reduced Simple Ratio Range winter: 424 to 1386 Range summer: 378 to 3263	
Winter and summer SAVI	Soil Adjusted Vegetation Index Range winter: -685 to 292 Range summer: -279 to 5152	
Winter and summer WDVI	Wide Dynamic Range Vegetation Index Range winter: -7088 to -2942 Range summer: -7618 to 2151	

Table 3.3 Segmented regression estimates and *p*-values (significance level = 0.05) for a) live aboveground biomass and b) merchantable volume; c) linear regression estimates and *p*-value for organic layer thickness.

a) Live aboveground biomass and time since fire

	Coefficient	***p*-value**
Intercept	28.63	6.85×10^{-4}
Time since fire – segment 1 (< 149 years)	0.20	1.18×10^{-2}
Time since fire – segment 2 (> 149 years)	-0.14	1.28×10^{-2}

b) Merchantable volume and time since fire

	Coefficient	***p*-value**
Intercept	30.21	1.22×10^{-1}
Time since fire – segment 1 (< 150 years)	0.64	6.16×10^{-3}
Time since fire – segment 2 (> 150 years)	-0.62	3.29×10^{-3}

c) Organic layer thickness and time since fire

	Coefficient	***p*-value**
Intercept	11.46	1.88×10^{-4}
Time since fire – segment 1	0.04	2.48×10^{-2}

3.9 Figures

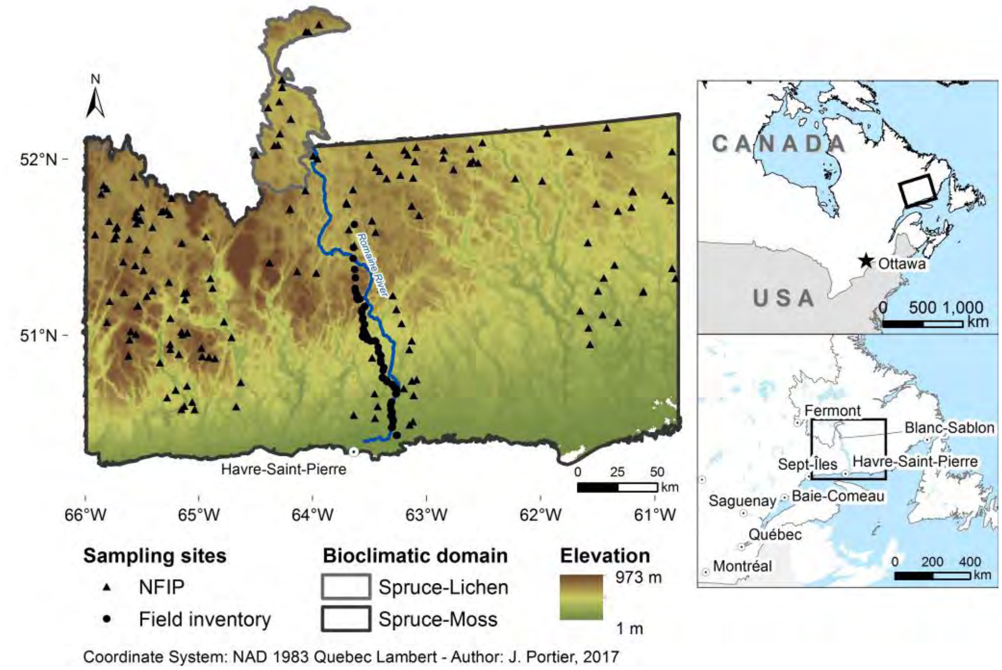

Figure 3.1 **Map of study area showing the location of sampling sites, elevation profile and bioclimatic domains.**

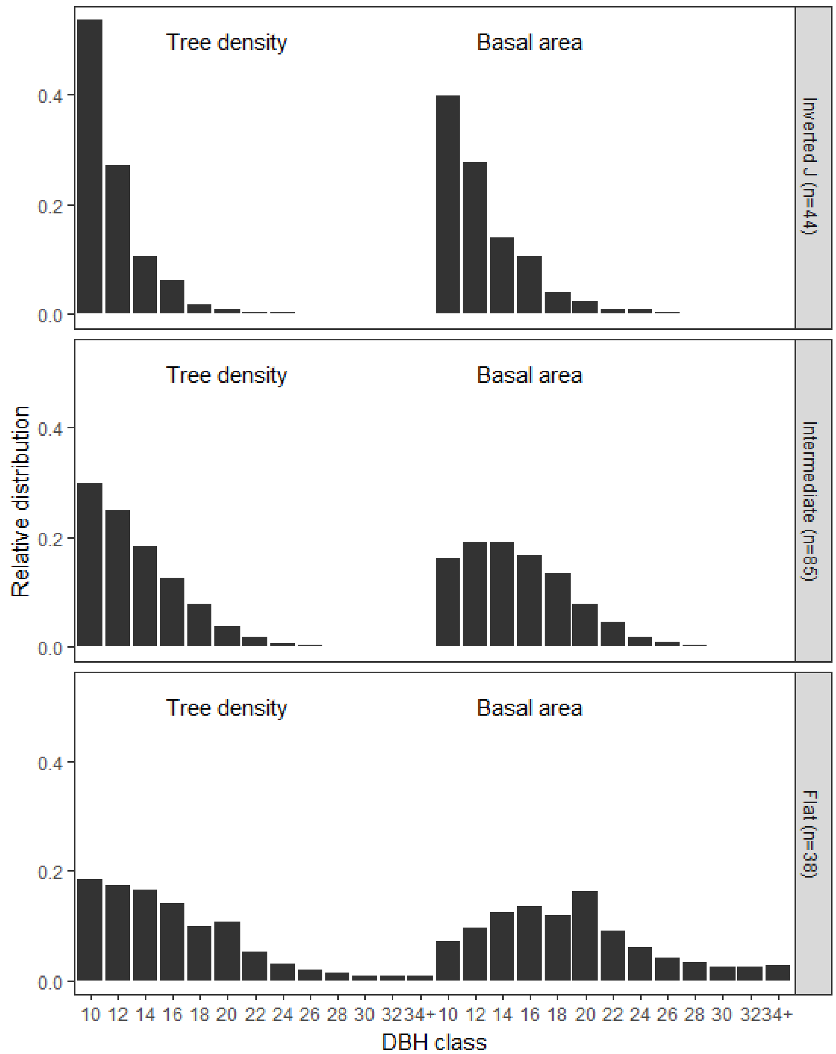

Figure 3.2 **DBH distributions in terms of merchantable tree density and merchantable BA in each structural cluster.**

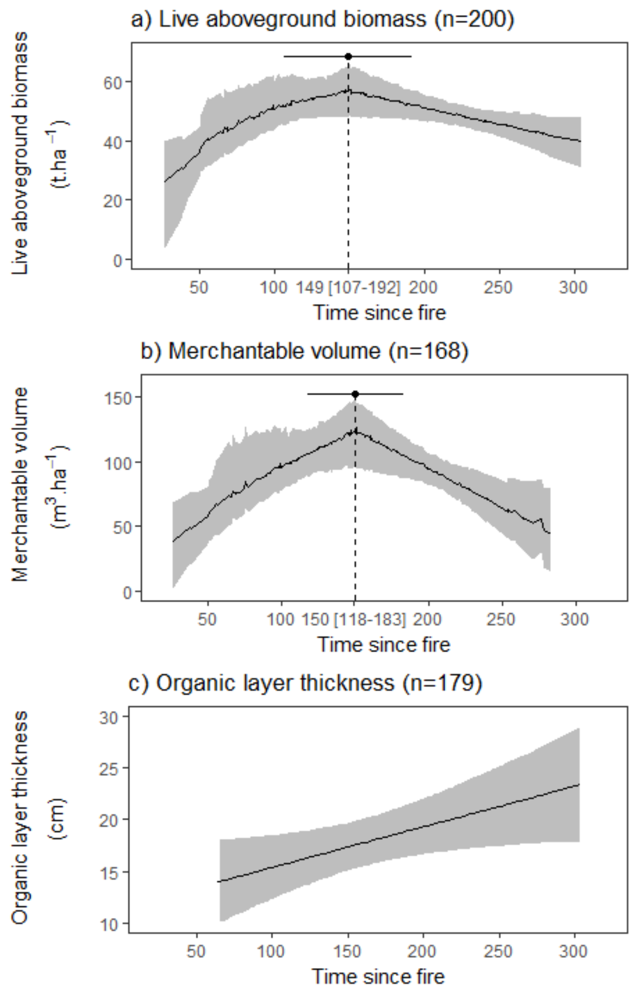

Figure 3.3 Live aboveground biomass (a); merchantable volume (b) and organic matter accumulation (c) with time since fire.

Shaded areas represent the 95% confidence interval of the effect of time since fire on live aboveground biomass, merchantable volume and organic layer thickness. For a) and b), curves and confidence intervals were obtained by bootstrap after 1,000 randomizations with replacement of the original dataset and computation of the predicted biomass and merchantable volume values for each time since fire value from the segmented regression. The mean values were used for the curves and for the upper and lower percentiles for the confidence intervals. The 95% confidence interval on the time since fire breakpoint estimate is represented by the horizontal black line.

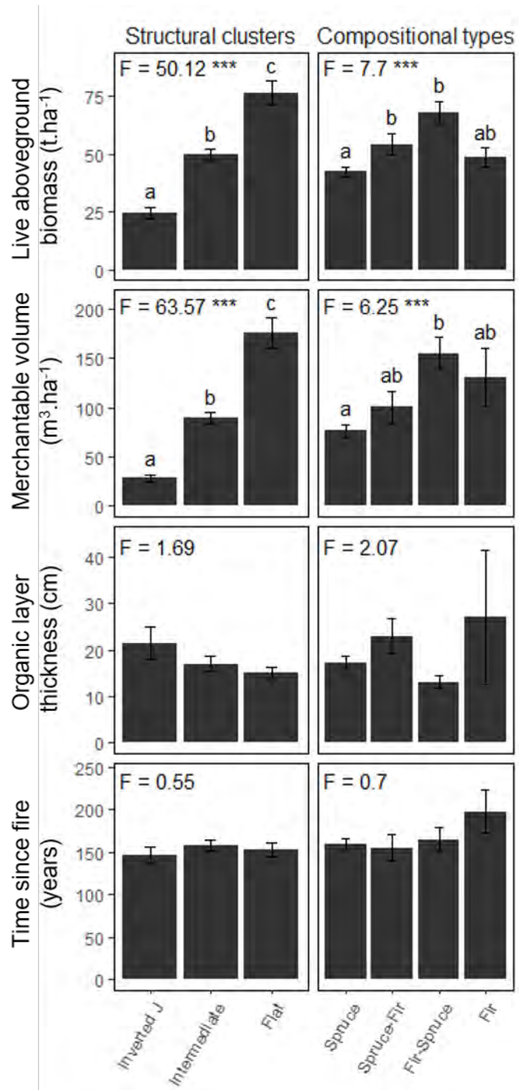

Figure 3.4 Mean and standard error of live aboveground biomass, merchantable volume and organic layer thickness per structural cluster and per compositional type.

ANOVA *F*-tests are shown on the top left corner of each panel along with the significance of the test (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). Tukey's post-hoc tests were used for pairwise comparisons when the ANOVA -*F*-test was significant. Unique letters within each panel reflect significant differences.

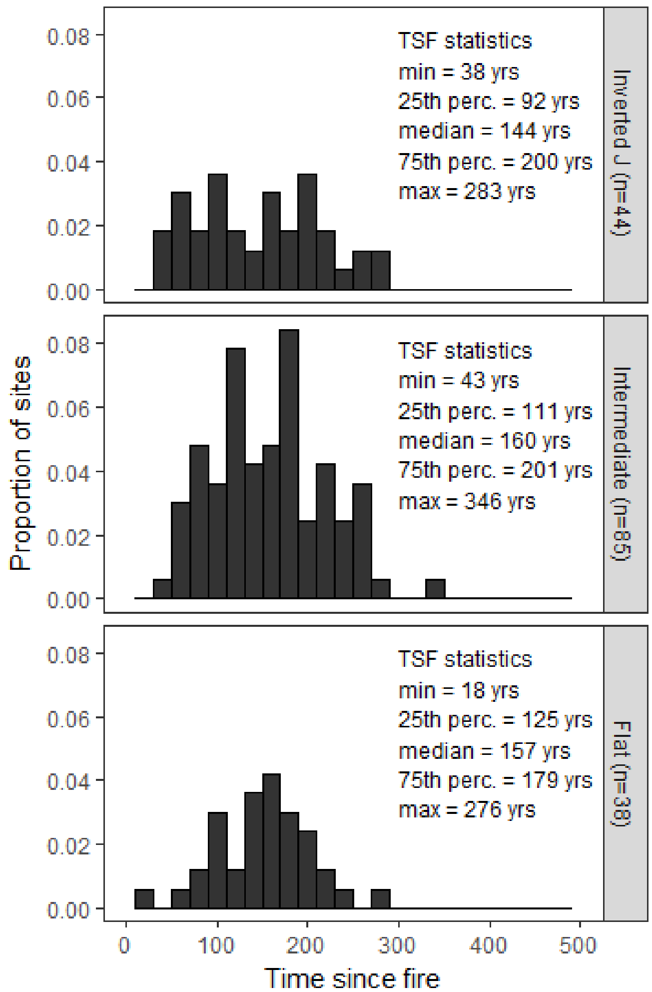

Figure 3.5 **Time since fire structure of each structural cluster. Time since fire statistics (minimum, 25th percentile, median, 75th percentile and maximum values) are also presented for each structural cluster.**

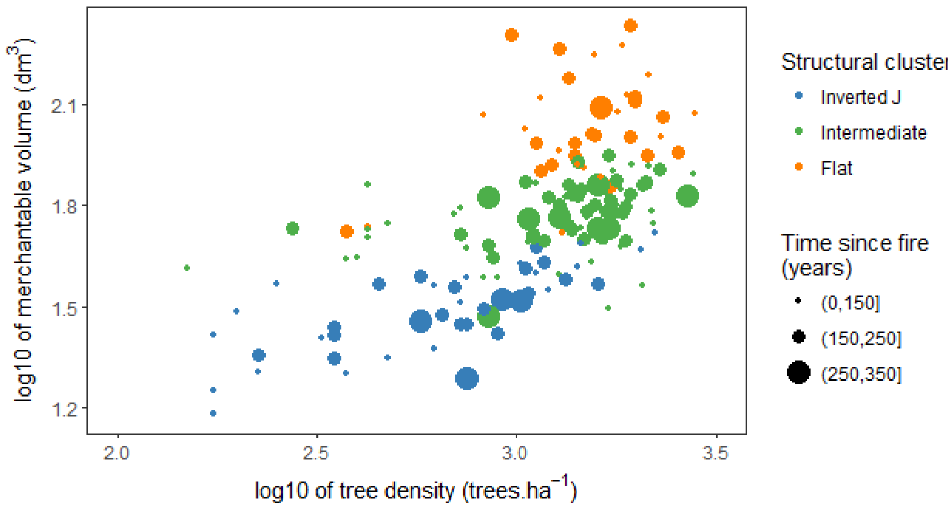

Figure 3.6 **Relation between mean tree volume and tree density of sites according to structural clusters and time since fire.**

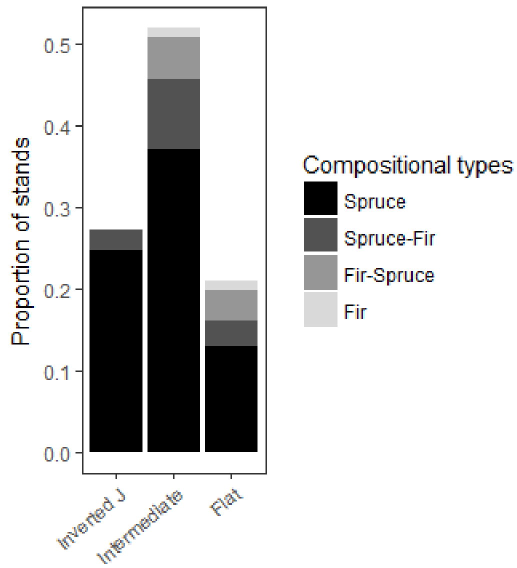

Figure 3.7 Repartition of compositional types into each structural cluster.

Chi-square test: $\chi^2 = 13.37$ (df = 6; *p*-value = 0.04).

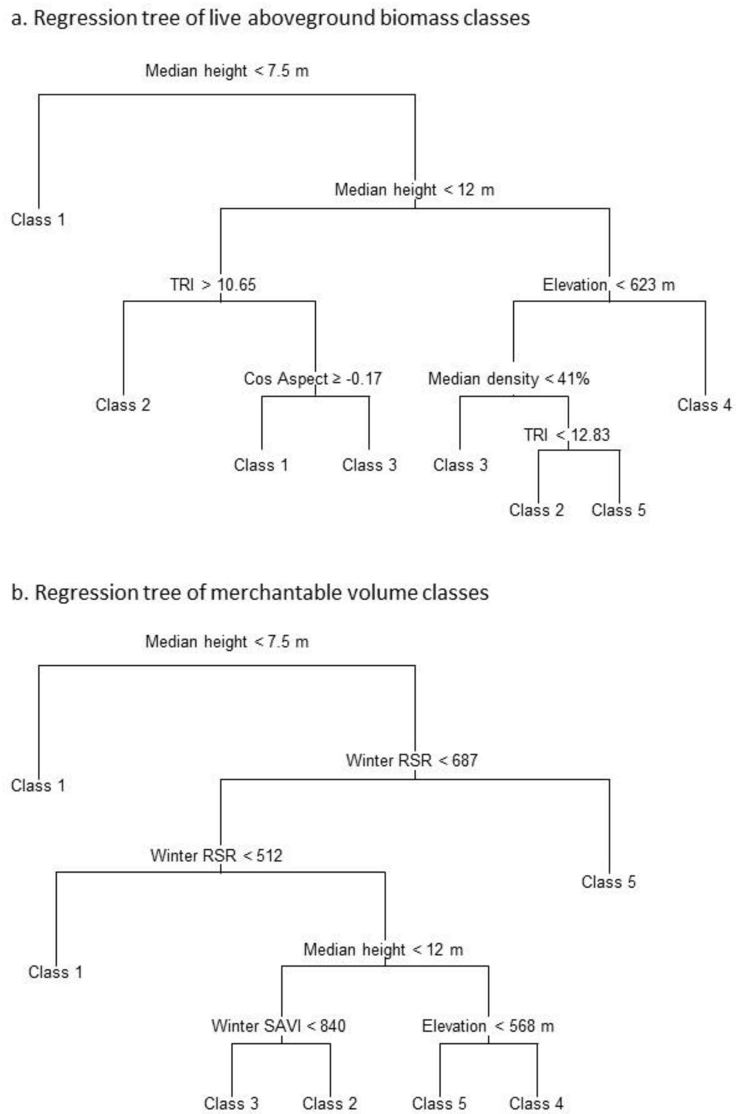

Figure 3.8 Regression tree of live aboveground biomass (a) classes and merchantable volume classes (b).

Each interior node constitutes a test with a yes/no answer. The “yes” branch is on the left, while the “no” branch is on the right. Live aboveground biomass classes ($t.ha^{-1}$) : $0 \leq$ class 1 $< 24.4 \leq$ class 2 $< 42.4 \leq$ class 3 $< 53.9 \leq$ class 4 $< 70.8 \leq$ class 5 < 188; merchantable volume ($m^3.ha^{-1}$) classes : $0 \leq$ class 1 $< 25.4 \leq$ class 2 $< 61.3 \leq$ class 3 $< 96.5 \leq$ class 4 $< 138.1 \leq$ class 5 < 412.7.

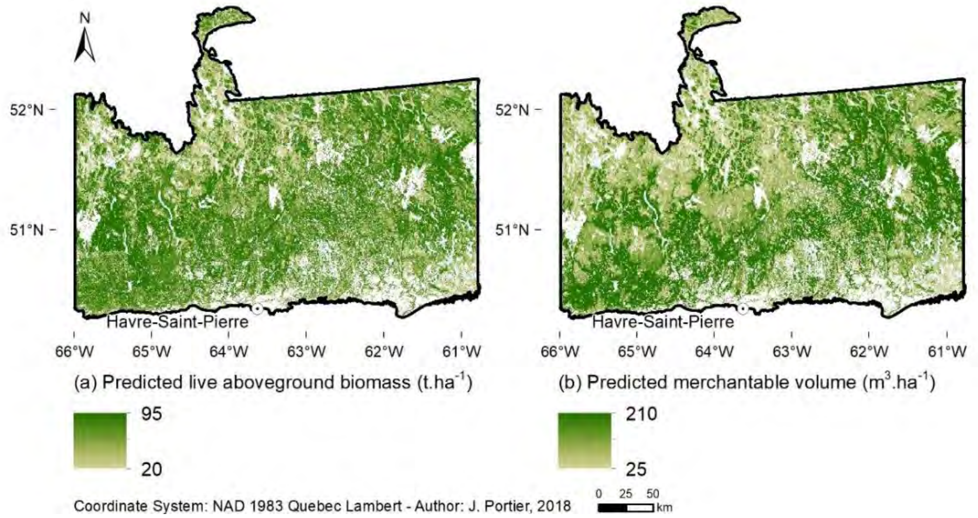

Figure 3.9 Map of predicted live aboveground biomass in tons per hectare (a) and predicted merchantable volume in m^3 per hectare (b).

White areas represent zones where no data (explanatory variables) was available.

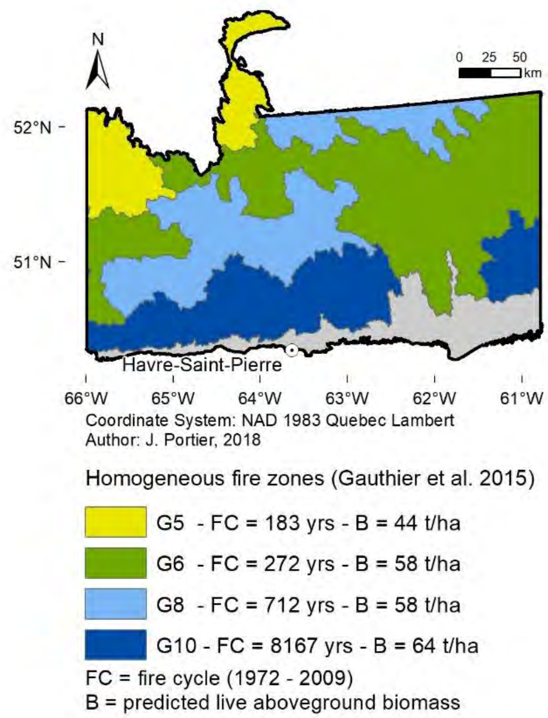

Figure 3.10 Homogeneous fire zones in the study area (Gauthier et al., 2015), with fire cycles calculated over the 1972-2009 period.

3.10 References

Bauhus, J., Puettmann, K., Messier, C., 2009. Silviculture for old-growth attributes. For. Ecol. Manage. 258, 525–537. doi:10.1016/j.foreco.2009.01.053

Beaudoin, A., Bernier, P.Y., Guindon, L., Villemaire, P., Guo, X.J., Stinson, G., Bergeron, T., Magnussen, S., Hall, R.J., 2014. Mapping attributes of Canada's forests at moderate resolution through kNN and MODIS imagery. Can. J. For. Res. 44, 521–532. doi:dx.doi.org/10.1139/cjfr-2013-0401

Bergeron, Y., Fenton, N.J., 2012. Boreal forests of eastern Canada revisited: old growth, nonfire disturbances, forest succession, and biodiversity. Botany 90, 509–523. doi:10.1139/B2012-034

Bergeron, Y., Irulappa Pillai Vijayakumar, D.B., Ouzennou, H., Raulier, F., Leduc, A., Gauthier, S., 2017. Projections of future forest age class structure under the influence of fire and harvesting: implications for forest management in the boreal forest of eastern Canada. Forestry 0, 1–11. doi:doi:10.1093/forestry/cpx022 Projections

Blais, J.R., 1983. Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. Can. J. For. Res. 13, 539–547.

Bond-Lamberty, B., Peckham, S.D., Ahl, D.E., Gower, S.T., 2007. Fire as the dominant driver of central Canadian boreal forest carbon balance. Nature 450, 89–92. doi:10.1038/nature06272

Bond-Lamberty, B., Wang, C., Gower, S.T., 2004. Net primary production and net ecosystem production of a boreal black spruce wildfire chronosequence. Glob. Chang. Biol. 10, 473–487. doi:10.1111/j.1529-8817.2003.0742.x

Bouchard, M., Kneeshaw, D., Bergeron, Y., 2005. Mortality and stand renewal patterns following the last spruce budworm outbreak in mixed forests of western Quebec. For. Ecol. Manage. 204, 297–313. doi:10.1016/j.foreco.2004.09.017

Bouchard, M., Pothier, D., Gauthier, S., 2008. Fire return intervals and tree species succession in the North Shore region of eastern Quebec. Can. J. For. Res. 38, 1621–1633. doi:10.1139/X07-201

Boucher, D., De Grandpré, L., Gauthier, S., 2003. Développement d'un outil de classification de la structure des peuplements et comparaison de deux territoires de la pessiere à mousses du Québec. For. Chron. 79, 318–328.

Boucher, D., Gauthier, S., De Grandpré, L., 2006. Structural changes in coniferous stands along a chronosequence and a productivity gradient in the northeastern boreal forest of Québec. Ecoscience 13, 172–180. doi:10.2980/i1195-6860-13-2-172.1

Boudreau, J., Nelson, R.F., Margolis, H.A., Beaudoin, A., Guindon, L., Kimes, D.S., 2008. Regional aboveground forest biomass using airborne and spaceborne LiDAR in Québec. Remote Sens. Environ. 112, 3876–3890. doi:10.1016/j.rse.2008.06.003

Bradshaw, C.J.A., Warkentin, I.G., 2015. Global estimates of boreal forest carbon stocks and flux. Glob. Planet. Change 128, 24–30. doi:10.1016/j.gloplacha.2015.02.004

Brandt, J.P., 2009. The extent of the North American boreal zone. Environ. Rev. 17, 101–161. doi:10.1139/A09-004

Breiman, L., Friedman, J., Stone, C.J., Olshen, R.A., 1984. Classification and Regression Trees. CRC Press, Boca Raton, FL.

Bruce, D., 1955. A new way to look at trees. J. For. 53, 163–167.

Burns, R.M., Honkala, B.H., 1990. Silvics of North America. Volume 1: Conifers, Agriculture Handbook 654. USDA Forest Service, Washington, DC.

Burton, P.J., Kneeshaw, D.D., Coates, K.D., 1999. Managing forest harvesting to maintain old growth in boreal and sub-boreal forests. For. Chron. 75, 623–631. doi:10.5558/tfc75623-4

Cyr, D., Gauthier, S., Bergeron, Y., Carcaillet, C., 2009. Forest management is driving the eastern North American boreal forest outside its natural range of variability. Front. Ecol. Environ. 7, 519–524. doi:10.1890/080088

Cyr, D., Gauthier, S., Boulanger, Y., Bergeron, Y., 2016. Quantifying fire cycle from dendroecological records using survival analyses. Forests 7, 1–21. doi:10.3390/f7070131

De'ath, G., Fabricius, K.E., 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81, 3178–3192. doi:10.2307/177409

De Grandpré, L., Gauthier, S., Allain, C., Cyr, D., Périgon, S., Thu Phan, A., Boucher, D., Morissette, J., Reyes, G., Aakala, T., Kuuluvainen, T., 2008. Vers un aménagement écosystémique de la forêt boréale de la Côte Nord, in: Aménagement Écosystémique En Forêt Boréale. Les Presses de l'Université du Québec, Québec, QC, Canada, pp. 241–268.

De Grandpré, L., Morisette, J., Gauthier, S., 2000. Long-term post-fire changes in the northeastern boreal forest of Quebec. J. Veg. Sci. 11, 791–800.

de Groot, W.J., Cantin, A.S., Flannigan, M.D., Soja, A.J., Gowman, L.M., Newbery, A., 2013. A comparison of Canadian and Russian boreal forest fire regimes. For. Ecol. Manage. 294, 23–34. doi:10.1016/j.foreco.2012.07.033

de Groot, W.J., Landry, R., Kurz, W.A., Anderson, K.R., Englefield, P., Fraser, R.H., Hall, R.J., Banfield, E., Raymond, D.A., Decker, V., Lynham, T.J., Pritchard, J.M., 2007. Estimating direct carbon emissions from Canadian wildland fires. Int. J. Wildl. Fire 16, 593–606. doi:10.1071/WF06150

Drapeau, P., Nappi, A., Imbeau, L., Saint-Germain, M., 2009. Standing deadwood for keystone bird species in the eastern boreal forest: Managing for snag dynamics. For. Chron. 85, 227–234.

Fenton, N.J., Bergeron, Y., 2008. Does time or habitat make old-growth forests species rich? Bryophyte richness in boreal Picea mariana forests. Biol. Conserv. 141, 1389–1399. doi:10.1016/j.biocon.2008.03.019

Gao, B., Taylor, A.R., Searle, E.B., Kumar, P., Ma, Z., Hume, A.M., Chen, H.Y.H., 2017. Carbon storage declines in old boreal forests irrespective of succession pathway. Ecosystems. doi:10.1007/s10021-017-0210-4

Garet, J., Pothier, D., Bouchard, M., 2009. Predicting the long-term yield trajectory of black spruce stands using time since fire. For. Ecol. Manage. 257, 2189–2197. doi:10.1016/j.foreco.2009.03.001

Gauthier, S., Boucher, D., Morissette, J., De Grandpré, L., 2010. Fifty-seven years of composition change in the eastern boreal forest of Canada. J. Veg. Sci. 21, 772–785. doi:10.1111/j.1654-1103.2010.01186.x

Gauthier, S., Leduc, A., Bergeron, Y., 1996. Forest dynamics modelling under natural fire cycles: a tool to define natural mosaic diversity for forest management. Environ. Monit. Assess. 39, 417–434.

Gauthier, S., Raulier, F., Ouzennou, H., Saucier, J., 2015. Strategic analysis of forest vulnerability to risk related to fire: an example from the coniferous boreal forest of Quebec. Can. J. For. Res. 45, 553–565. doi:10.1139/cjfr-2014-0125

Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpré, L., Kneeshaw, D.D., Morin, H., Drapeau, P., Bergeron, Y., 2008. Aménagement écosystémique en forêt boréale. Les Presses de l'Université du Québec, Québec, QC, Canada.

Gennaretti, F., Arseneault, D., Bégin, Y., 2014. Millennial stocks and fluxes of large woody debris in lakes of the North American taiga. J. Ecol. 102, 367–380. doi:10.1111/1365-2745.12198

Girard, F., De Grandpre, L., Ruel, J.C., 2014. Partial windthrow as a driving process of forest dynamics in old-growth boreal forests. Can. J. For. Res. 44, 1165–1176. doi:10.1139/cjfr-2013-0224

Harper, K.A., Bergeron, Y., Drapeau, P., Gauthier, S., De Grandpré, L., 2005. Structural development following fire in black spruce boreal forest. For. Ecol. Manage. 206, 293–306. doi:10.1016/j.foreco.2004.11.008

Harper, K.A., Bergeron, Y., Gauthier, S., Drapeau, P., 2002. Post-fire development of canopy structure and composition in black spruce forests of Abitibi, Québec: a landscape scale study. Silva Fenn. 36, 249–263.

IPCC, 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.

Irulappa Pillai Vijayakumar, D.B., Raulier, F., Bernier, P., Paré, D., Gauthier, S., Bergeron, Y., Pothier, D., 2016. Cover density recovery after fire disturbance controls landscape aboveground biomass carbon in the boreal forest of eastern Canada. For. Ecol. Manage. 360, 170–180. doi:10.1016/j.foreco.2015.10.035

Johnson, E.A., 1992. Fire and Vegetation Dynamics - Studies from the North American Boreal Forest. Cambridge University Press, Cambridge, UK. doi:10.1046/j.1469-8137.1997.00703-3.x

Kneeshaw, D., Gauthier, S., 2003. Old growth in the boreal forest: A dynamic perspective at the stand and landscape level. Environ. Rev. 11, 99–114. doi:10.1139/A03-010

Kohavi, R., 1995. A study of cross-validation and bootstrap for accuracy estimation and model selection, in: International Joint Conference on Artificial Intelligence. Morgan Kaufmann Publishers, San Francisco, pp. 1137–1145. doi:10.1067/mod.2000.109031

Leboeuf, A., Robitaille, A., Létourneau, J.-P., Morneau, C., Bourque, L., 2012. Norme de cartographie écoforestière du programme d'inventaire écoforestier nordique (PIEN). Ministère des Ressources naturelles, Secteur des forêts, Québec, QC, Canada.

Lecomte, N., Simard, M., Fenton, N., Bergeron, Y., 2006. Fire severity and long-term ecosystem biomass dynamics in coniferous boreal forests of eastern Canada. Ecosystems 9, 1215–1230. doi:10.1007/s10021-004-0168-x

Lindenmayer, D.B., Franklin, J.F., 2002. Conserving Forest Biodiversity: A Comprehensive Multiscaled Approach. Island Press, Washington, DC.

Luyssaert, S., Schulze, E.-D., Börner, A., Knohl, A., Hessenmöller, D., Law, B.E., Ciais, P., Grace, J., 2008. Old-growth forests as global carbon sinks. Nature 455, 213–215. doi:10.1038/nature07276

Mathews, G., 1993. The carbon content of trees. Forestry Commission Technical Paper 4. Edinburgh, Scotland.

McCarthy, J., 2001. Gap dynamics of forest trees: A review with particular attention to boreal forests. Environ. Rev. 9, 1–59. doi:10.1139/a00-012

MFFPQ (Ministère de la Forêt, de la Faune et des Parcs du Québec), 2013a. Rapport du Comité scientifique chargé d'examiner la limite nordique des forêts attribuables. Québec, QC, Canada.

MFFPQ (Ministère de la Forêt, de la Faune et des Parcs du Québec), 2013b. Cartographie numérique des niveaux supérieurs du Système hiérarchique de classifcation écologique et banque de données descriptives des districts écologiques. Québec, QC, Canada.

Moussaoui, L., Fenton, N.J., Leduc, A., Bergeron, Y., 2016. Can retention harvest maintain natural structural complexity? A comparison of post-harvest and post-fire residual patches in boreal forest. Forests 7, 1–17. doi:10.3390/f7100243

Muggeo, V.M.R., 2008. segmented: An R package to fit regression models with broken-line relationships. R News 8, 20–25. doi:10.1159/000323281

Newton, P.F., 2012. A decision-support system for forest density management within upland black spruce stand-types. Environ. Model. Softw. 35, 171–187. doi:10.1016/j.envsoft.2012.02.019

Nlungu-Kweta, P., Leduc, A., Bergeron, Y., 2016. Climate and disturbance regime effects on aspen (Populus tremuloides Michx.) stand structure and composition along an east–west transect in Canada's boreal forest. Forestry 90, 70–81. doi:10.1093/forestry/cpw026

Oksanen, J.F., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Gavin L. Simpson, Peter Solymos, M. Henry H. Stevens, E.S., Wagne, H., 2017. Package "vegan" [WWW Document]. URL https://cran.r-project.org/web/packages/vegan/vegan.pdf (accessed 3.23.17).

Paré, D., Bergeron, Y., 1995. Above-ground biomass accumulation along a 230-year chronosequence in the southern portion of the Canadian boreal forest. J. Ecol. 83, 1001–1007. doi:10.2307/2261181

Paré, D., Bernier, P., Lafleur, B., Titus, B.D., Thiffault, E., Maynard, D.G., Guo, X., 2013. Estimating stand-scale biomass, nutrient contents, and associated uncertainties for tree species of Canadian forests. Can. J. For. Res. 43, 599–608. doi:dx.doi.org/10.1139/cjfr-2012-0454

Payette, S., 1992. Fire as a controlling process in the North American boreal forest, in: Shugart, H.H., Leemans, R., Bonan, G.B. (Eds.), A System Analysis of the Global Boreal Forest. Cambridge University Press, Cambridge, UK, pp. 144–169. doi:http://dx.doi.org/10.1017/CBO9780511565489.006

Perron, J.-Y., 2003. Tarif de cubage général - volume marchand brut, 3e édition. Ministère des Ressources naturelles, de la Faune et des Parcs, Direction des inventaires forestiers, Québec, QC, Canada.

Pham, A.T., De Grandpré, L., Gauthier, S., Bergeron, Y., 2004. Gap dynamics and replacement patterns in gaps of the northeastern boreal forest of Quebec. Can. J. For. Res. 34, 353–364. doi:10.1139/x03-265

Portier, J., Gauthier, S., Leduc, A., Arseneault, D., Bergeron, Y., 2016. Fire regime along latitudinal gradients of continuous to discontinuous coniferous boreal forests in eastern Canada. Forests 7, 211. doi:10.3390/f7100211

Pouliot, D., Latifovic, R., Fernandes, R., Olthof, I., 2009. Evaluation of annual forest disturbance monitoring using a static decision tree approach and 250 m MODIS data. Remote Sens. Environ. 113, 1749–1759. doi:10.1016/j.rse.2009.04.008

Rapanoela, R., Raulier, F., Gauthier, S., Ouzennou, H., Saucier, J., Bergeron, Y., 2015. Contrasting current and potential productivity and the influence of fire and species composition in the boreal forest: a case study in eastern Canada. Can. J. For. Res. 45, 541–55. doi:10.1139/cjfr-2014-0124

Saint-Germain, M., Drapeau, P., Buddle, C.M., 2007. Host-use patterns of saproxylic phloeophagous and xylophagous Coleoptera adults and larvae along the decay gradient in standing dead black spruce and aspen. Ecography. 30, 737–748. doi:10.1111/j.2007.0906-7590.05080.x

Shorohova, E., Kneeshaw, D., Kuuluvainen, T., Gauthier, S., 2011. Variability and dynamics of old-growth forests in the circumboreal zone: implications for conservation, restoration and management. Silva Fenn. 45, 785–806.

Simard, M., Bernier, P.Y., Bergeron, Y., Paré, D., Guérine, L., 2009. Paludification dynamics in the boreal forest of the James Bay Lowlands: effect of time since fire and topography. Can. J. For. Res. 39, 546–552. doi:10.1139/X08-195

Simard, M., Lecomte, N., Bergeron, Y., Bernier, P.Y., Paré, D., 2007. Forest productivity decline caused by successional paludification of boreal soils. Ecol. Appl. 17, 1619–1637.

St. Louis, V.L., Kelly, C.A., Duchemin, E., Rudd, J.W.M., Rosenberg, D.M., 2000. Reservoir surfaces as sources of greenhouse gases to the atmosphere: A global estimate. Bioscience 50, 766–775.

Teodoru, C.R., Bastien, J., Bonneville, M.-C., del Giorgio, P.A., Demarty, M., Garneau, M., Hélie, J.-F., Pelletier, L., Prairie, Y.T., Roulet, N.T., Strachan, I.B., Tremblay, A., 2012. The net carbon footprint of a newly created boreal hydroelectric reservoir. Global Biogeochem. Cycles 26, 1–14. doi:10.1029/2011GB004187

Terrier, A., Paquette, M., Gauthier, S., Girardin, M.P., Pelletier-Bergeron, S., Bergeron, Y., 2016. Influence of fuel load dynamics on carbon emission by wildfires in the Clay Belt boreal landscape. Forests 8, 1–20. doi:10.3390/F8010009

Therneau, T., Atkinson, B., Ripley, B., 2015. Package "rpart" [WWW Document]. URL http://cran.r-project.org/web/packages/rpart/rpart.pdf. (accessed 1.1.17).

Tremblay, A., Lambert, M., Gagnon, L., 2004. Do hydroelectric reservoirs emit greenhouse gases? Environ. Manage. 33, 509–517. doi:10.1007/s00267-003-9158-6

Trishchenko, A.P., Luo, Y., Khlopenkov, K.V., 2006. A method for downscaling MODIS land channels to 250 m spatial resolution using adaptive regression and normalization, in: Ehlers, M., Michel, U. (Eds.), SPIE Proceedings Vol. 6366: Remote Sensing for Environmental Monitoring, GIS Applications, and Geology VI. International Society for Optics and Photonics, Ottawa, ON, Canada. Article No. 636607. doi:10.1117/12.689157

Waldron, K., Ruel, J.-C., Gauthier, S., 2013. Forest structural attributes after windthrow and consequences of salvage logging. For. Ecol. Manage. 289, 28–37. doi:10.1016/j.foreco.2012.10.006

Ward, C., Pothier, D., Paré, D., 2014. Do boreal forests need fire disturbance to maintain productivity? Ecosystems 17, 1053–1067. doi:10.1007/s10021-014-9782-4

Yuan, F., Arain, M.A., Barr, A.G., Black, T.A., Bourque, C.P.-A., Coursolle, C., Margolis, H.A., McCaughey, J.H., Wofsy, S.C., 2008. Modeling analysis of primary controls on net ecosystem productivity of seven boreal and temperate coniferous forests across a continental transect. Glob. Chang. Biol. 14, 1765–1784. doi:10.1111/j.1365-2486.2008.01612.x

Zhang, Q., Chen, W., 2007. Fire cycle of the Canada's boreal region and its potential response to global change. J. For. Res. 18, 55–61. doi:10.1007/s11676-007-0010-3

CONCLUSION GÉNÉRALE

L’objectif général de cette thèse était d’améliorer les connaissances et la compréhension des régimes de feux, de leurs facteurs déterminants et de leurs conséquences dans la forêt boréale résineuse du Québec. Ce territoire se situe de part et d’autre de la limite nordique des forêts attribuables, à l’interface forêts fermées – forêts ouvertes. Dans un premier temps, cette conclusion générale revient sur les principales conclusions de chacun des trois chapitres. Dans un deuxième temps, une synthèse plus globale des trois chapitres est réalisée afin de mieux répondre à l’objectif général, puis d’en dégager les implications dans un contexte de changements climatiques ainsi que pour l’aménagement forestier. Enfin, des pistes de recherche pour le futur sont proposées.

4.1 Variabilité latitudinale des régimes de feux passés – Influence du climat (chapitre 1)

Le premier chapitre se basait sur la reconstruction, à partir d’analyses dendrochronologiques, de l’historique des feux des 150-300 dernières années le long de quatre transects orientés nord-sud, également répartis le long de l’axe est-ouest de la zone boréale résineuse du Québec. Si de nombreuses études se sont intéressées à la reconstruction dendrochronologique de l’historique passé des feux dans certaines régions de la pessière fermée québécoise (Bergeron et al. 2004; Cyr et al. 2007;

Bouchard et al. 2008; Girardin 2010; Bélisle et al. 2011), très peu se sont concentrées sur des zones en pessière à lichens au nord de la limite nordique (voir Héon et al. 2014; Erni et al. 2016). De plus, à notre connaissance aucune étude ne s'était encore basée sur des données récoltées à l'échelle de l'ensemble de la zone boréale résineuse québécoise, ce qui permet d'appréhender la variabilité spatiale passée de façon plus robuste.

Les transects ont permis d'une part de mettre en évidence et de quantifier la variabilité latitudinale du régime de feux passé de part et d'autre de la limite nordique des forêts attribuables du Québec, et d'autre part de déterminer l'influence du climat sur cette variabilité. Nos résultats ont montré une claire délimitation entre des zones à haut risque de feux dans les parties nord des transects, et à faible risque dans les parties sud. Dans certaines zones, comme par exemple au nord du réservoir Manicouagan (transect C) ou dans le secteur de la rivière Romaine (transect D), nos résultats apportent les premières estimations dendrochronologiques des cycles de feux passés. Ailleurs, les cycles de feux que nous avons calculés étaient similaires à ceux estimés par d'autres études (Bergeron et al. 2004; Bergeron et al. 2006; Bouchard et al. 2008; Bélisle et al. 2011), validant par conséquent notre méthode d'estimation ainsi que les cycles de feux calculés dans les zones où aucun estimé n'était encore disponible. Les cycles de feux passés particulièrement courts observés dans les parties nord des transects (de 5 à 60 ans) expliquent en partie la présence des pessières à lichens qui souvent résultent d'une activité des feux accrue menant à des accidents de régénération (Payette et al. 2000; Jasinki and Payette 2005; Girard et al. 2009; Mansuy et al. 2013).

Notre étude témoigne cependant de la difficulté d'estimation des cycles de feux dans deux cas opposés : lorsque l'activité des feux est extrêmement importante comme dans le nord de la Baie James (transect A) ou au contraire, lorsque les régimes de feux sont définis par des feux très rares mais de grande taille comme dans le secteur de la rivière Romaine (transect D). Dans le premier cas, de grands feux survenant à des intervalles rapprochés effacent rapidement les traces des feux passés, rendant difficile la détermination du régime de feux passé (Cyr et al. 2016). De plus, cela entraîne des estimés de cycles de feux très courts, comme le cycle de 5 ans calculé au nord de la Baie James, qui ne sont pas nécessairement représentatifs de la région dans laquelle ils sont calculés. Dans ce cas, il serait nécessaire d'utiliser des zones d'étude plus grandes, adaptées à un régime de grands feux très fréquents dans un territoire pouvant être en déséquilibre. Dans le deuxième cas, l'estimation d'un cycle de feux peut être très sensible à l'occurrence d'un unique grand feu survenant dans une zone où l'activité des feux est très faible. Ainsi, il est délicat d'associer ce cycle à toute une zone lorsque celle-ci est majoritairement composée de vieilles forêts qui peuvent ne pas avoir brûlé pendant plusieurs siècles. De même, retirer ces rares grands feux dans le calcul du cycle n'est pas une solution idéale, puisque qu'ils définissent malgré tout le régime de feux de la zone en question. Dans ce cas, le régime pourrait être appréhendé par d'autres attributs du régime de feux relatifs à la taille ou au nombre de feux au lieu du cycle de feux.

Par ailleurs, ce chapitre a démontré l'influence du climat sur la variabilité latitudinale des risques de feux passés. En particulier, l'indice de sécheresse a pu expliquer la variabilité latitudinale des risques de feux de trois des quatre transects, témoignant de l'importance des conditions de sécheresse dans le déterminisme des risques de feux passés. Cela a d'ailleurs été démontré par diverses études au Québec comme au Canada (Amiro et al. 2004; Girardin et al. 2004; Girardin et al. 2009). Cependant, d'autres facteurs agissant à des échelles plus locales semblaient influencer la variabilité du risque de feux puisque dans certains transects (A et C), la topographie (présence de monts) ou la présence de grands lacs semblaient jouer un rôle de protecteurs de feux, le long desquels le risque de feux diminuait de façon importante. De même, le rôle du climat dans le secteur de la rivière Romaine (transect D) n'a pas pu être démontré. Bien que le transect puisse avoir été trop court pour détecter l'effet du climat, ce résultat témoigne néanmoins de l'influence d'autres facteurs sur le risque de feux. Cette région étant complexe tant en termes de régime de feux (feux rares mais de grande taille) qu'en termes topographique et de variabilité des dépôts de surface, ces pistes pourraient être poursuivies afin d'acquérir une meilleure compréhension de cette région.

Les résultats de ce chapitre, lorsque comparé à ceux de Gauthier et al. (2015) sur la régionalisation des cycles de feux contemporains, montrent que la zonation des régimes de feux est restée stable au cours du temps. Pourtant, les cycles contemporains (chapitre 2, Gauthier et al. 2015) sont plus longs que les cycles passés. Malgré des changements temporels dans l'activité des feux, la stabilité de cette zonation constitue un résultat important puisqu'il témoigne d'une certaine inertie de la limite entre les zones de risque de feux. Puisqu'on s'attend à une augmentation de l'activité des feux dans le futur (Zhang and Chen 2007; Girardin et al. 2009; Flannigan et al. 2016), les régimes de feux futurs pourraient retrouver l'amplitude des régimes de feux passés. Ainsi, les limites entre les zones de risque de feux ne devraient pas être déplacées. De plus, ces limites correspondent à l'emplacement de la limite nordique des forêts attribuables de 2002. Ainsi, la limite nordique, basée en partie sur la variabilité spatiale des risques de feux, devrait elle-même rester stable dans le futur malgré une intensification de l'activité des feux.

Ce chapitre fournit donc de nouvelles connaissances sur les régimes de feux passés de part et d'autre de la limite nordique des forêts attribuables du Québec, et a des implications quant à la délimitation future de cette limite. Il met aussi en perspective l'importance des conditions de sécheresse sur la variabilité latitudinale des risques de feux passés, bien qu'il apporte de nouvelles questions sur le rôle des facteurs environnementaux plus locaux, en particulier dans le secteur de la Rivière Romaine soumis à une activité faible de feux.

4.2 Variabilité spatiale contemporaine des taux de brûlage dans la forêt boréale résineuse du Québec – Contribution du climat, de l'environnement physique et de la végétation (chapitre 2)

Ce chapitre avait pour objectif de déterminer la contribution relative du climat, de l'environnement physique et de la végétation dans la détermination de la variabilité spatiale des taux de brûlage contemporains dans la zone boréale résineuse du Québec. En effet, certaines études sur les régimes de feux testent les effets uniques d'un seul de ces facteurs, ou encore de plusieurs à des échelles beaucoup plus locales (Hu et al. 2006; Girardin et al. 2009; Mansuy et al. 2010; Cavard et al. 2015), mais leur contribution relative à l'échelle d'un vaste territoire boréal est encore mal comprise. Par ailleurs, ce chapitre utilise une méthode statistique spatiale performante basée sur des modèles RAC. Cette méthode permet de parer aux difficultés méthodologiques relatives au caractère spatial (autocorrélation) des feux et des facteurs environnementaux. Celles-ci doivent en effet être correctement traitées afin d'obtenir des résultats robustes (Dormann et al. 2007), ce qui constitue souvent une faiblesse des études sur les facteurs déterminants des feux.

Ce chapitre démontre que le climat, l'environnement physique et la végétation contribuaient de façon égale à la variabilité spatiale des taux de brûlage, ce qui confirme les résultats d'une étude réalisée à une échelle plus locale dans une région du Québec (Cavard et al. 2015). En termes climatiques, si l'on s'attendait à un contrôle venant principalement d'indices dérivés des températures et des précipitations comme l'indice de sécheresse (Amiro et al. 2004; Girardin et al. 2004), nos résultats indiquent que la variabilité spatiale des précipitations était à l'origine de la variabilité spatiale des taux de brûlage entre 1972 et 2015. Cela a d'importantes répercussions puisque dans un futur proche, l'on s'attend à une augmentation des températures, accompagnée d'une augmentation plus modeste des précipitations (IPCC 2014; Flannigan et al. 2016). Les changements climatiques devraient ainsi engendrer une augmentation des épisodes de sécheresse extrême (Wang et al. 2015). Dans ce chapitre, nous discutons de la possibilité, dans le futur, d'un retour à un système contrôlé par les températures, où les précipitations ne seraient plus capables de compenser pour les hausses de températures et leurs effets sur l'évapotranspiration du combustible (Girardin and Mudelsee 2008; Bergeron et al. 2010; Flannigan et al. 2016). Un tel revirement de situation pourrait mener rapidement à une augmentation importante et possiblement soudaine des taux de brûlage (Amiro et al. 2004; Flannigan et al. 2005; Flannigan et al. 2016), ce qui pourrait déjà être le cas dans la partie nord-ouest du Québec où l'on observe d'ors et déjà une augmentation des aires brûlées annuelles depuis les années 1980 (Erni et al. 2016).

Dans ce chapitre, nous démontrons également l'importance du choix de variables en termes de végétation. En effet, nous avons comparé nos résultats en utilisant d'une part la végétation potentielle, indépendante de l'effet des feux, et d'autre part la végétation actuelle qui elle constitue en partie une conséquence des régimes de perturbation. La végétation potentielle est utilisée comme un proxy de la végétation présente avant feu qui est une information très souvent non disponible dans les études sur les feux. Nos résultats indiquent très clairement la nécessité d'utiliser la végétation potentielle dans de telles études afin d'éviter les biais associés aux différentes rétroactions des systèmes feux-végétation.

Globalement, ce chapitre apporte de nouvelles connaissances concernant les facteurs déterminants des taux de brûlage dans la zone boréale québécoise, et montre qu'il est indispensable de prendre en compte non seulement les facteurs agissant du haut vers le bas (« top-down ») comme le climat mais aussi les facteurs agissant du bas vers le haut (« bottom-up ») comme l'environnement physique et la végétation dans les études sur les feux. D'un point de vue méthodologique, nous insistons sur la nécessité d'utilisation de méthodes spatialement explicites qui permettent de contrôler les difficultés liées à l'autocorrélation spatiale. De même, à défaut de connaître pour chaque feu la végétation pré-feu sur une longue période temporelle, l'utilisation de la végétation potentielle, détachée des effets des feux sur la végétation, au lieu de la végétation actuelle est nécessaire dans les études visant à mieux comprendre les effets de la végétation sur les régimes de feux.

4.3 Biomasse arborée et structure des peuplements dans une région à faible activité de feux – Liens avec le temps depuis feu (chapitre 3)

Le troisième chapitre se focalisait sur un territoire caractérisé par des feux très rares mais grands. Cette région de l'est du Québec, centrée sur la rivière Romaine, a été nouvellement ouverte au développement économique pour les secteurs forestier et énergétique (MFFPQ 2013). Il visait à caractériser cette région en termes de biomasse arborée, de volume marchand, de structure des peuplements et de composition, ainsi qu'à déterminer l'effet du temps depuis le dernier feu sur ces attributs. En effet, les effets du temps depuis feu sur l'accumulation de biomasse et la dynamique forestière sont aujourd'hui encore peu connus dans les zones comme la Côte Nord soumises à une faible activité des feux.

Ce chapitre a permis de montrer que les peuplements du secteur de la rivière Romaine, dominés par des systèmes épinette noire – sapin baumier, s'apparentaient à des peuplements en forêt boréale commerciale en termes de biomasse arborée et de volume marchand. Cependant, à l'échelle du paysage, la quantité de biomasse arborée et de carbone stocké devrait être plus importante que dans des régions soumises à une activité plus importante des feux, où une large proportion du carbone stocké dans le paysage peut être prélevée par les feux. L'âge de bris, c'est-à-dire l'âge à partir duquel la biomasse forestière arborée cesse de s'accumuler et commence à décliner, a été estimé à environ 150 ans après un feu. Ce seuil est en accord avec les résultats de précédentes études (Harper et al. 2005; Garet et al. 2009; Gauthier et al. 2010). On s'attend cependant à ce que la phase de déclin se stabilise. Ces résultats témoignent de l'importance des feux dans l'accumulation de biomasse arborée et de volume marchand de ces écosystèmes, malgré la rareté de leur occurrence.

Nous avons également montré que la structure des peuplements n'était pas directement liée au temps depuis feux. En effet, si l'on s'attendait à ce que les peuplements jeunes présentent une structure en J inversé et les peuplements plus vieux une structure plus étalée avec la présence de larges tiges, nos résultats indiquent que les situations inverses se produisent également. La productivité des peuplements explique en partie ce résultat, puisque nous avons montré que certains vieux peuplements peu productifs présentaient effectivement une structure en J inversé, alors que certains jeunes peuplements productifs présentaient déjà une structure étalée. En effet, un peuplement s'établissant sur un site de faible productivité ne permettra pas la croissance de grosses tiges et restera avec une structure dominée par de petites tiges, indépendamment du temps depuis le dernier feu. Au contraire, un site très productif permettra la croissance de grosses tiges rapidement après un feu.

Par ailleurs, les perturbations secondaires comme les épidémies d'insectes ou les chablis occupent une place importante dans les forêts soumises à une activité faible de feux (De Grandpré et al. 2000; Kneeshaw and Gauthier 2003; Pham et al. 2004; Waldron et al. 2013). Ces perturbations secondaires sont connues pour affecter de façon importante la structure des peuplements (Pham et al. 2004; Waldron et al. 2013), et ainsi effacent graduellement les traces du temps depuis feux. Ces perturbations constituent une autre raison pour laquelle nous n'avons pas pu mettre en évidence de liens significatifs entre le temps depuis feux et la structure et composition des peuplements.

Ce chapitre apporte de nouvelles connaissances sur la dynamique forestière du secteur de la rivière Romaine et sur son lien avec le temps depuis le dernier feu, jusqu'ici encore mal documenté. En dépit de la rare occurrence des feux, le rôle du temps depuis feux est important dans l'accumulation de biomasse arborée et de volume marchant. Cependant, la productivité des peuplements et les perturbations secondaires semblent être les principales déterminantes de la structure et la composition des peuplements.

4.4 Synthèse générale des trois chapitres

4.4.1 Régimes de feux passés et contemporains dans la zone boréale résineuse québécoise

Les régimes de feux dans la forêt boréale résineuse québécoise sont très variables spatialement. Les cycles de feux s'allongent graduellement d'ouest en est, et de façon plus soudaine du nord vers le sud. Cette variabilité spatiale s'observe sur les régimes de feux passés comme contemporains, en dépit de la variabilité temporelle observée entre les deux périodes. L'une des conclusions importantes de cette thèse réside dans la démonstration que malgré la variabilité temporelle des régimes de feux, leur zonation spatiale semble rester constante à travers le temps. Cela indique une certaine inertie de la répartition spatiale des zones de feux homogènes (Oris et al. 2014)

Si l'on compare les 150-300 dernières années (chapitre 1) à une période plus récente à partir de 1972 (Annexe A, Gauthier et al. 2015), on observe un allongement des cycles de feux. Par exemple, au nord du lac Mistassini qui est une zone soumise à une activité des feux relativement importante, le cycle passé était de 33 ans (chapitre 1), alors que le cycle calculé sur la période 1972-2015 était de 80 à 179 ans (Annexe A). Dans la section sud du secteur de la rivière Romaine, une des régions les moins touchées par les feux, le cycle passé était de 732 ans (chapitre 1) pour un cycle contemporain de 2917 ans (Annexe A). Cependant, dans la région de la Baie James au nord-ouest de la zone d'étude, l'activité des feux s'est intensifiée depuis les années 1980 (Héon et al. 2014; Erni et al. 2016). Selon nos résultats, la différence entre le cycle avant et après 1972 y est d'ailleurs très faible (44 et 50 ans, respectivement), contrairement à toutes les autres zones. Kasischke et Turetsky (2006) ont montré que dans l'ensemble de la forêt boréale nord-américaine, l'aire brûlée par décade ainsi que la fréquence des grands feux ne cessent d'augmenter depuis les années 1960, doublant même entre les années 1960/70 et 1980/90. Ce phénomène serait cependant plus important dans l'ouest du Canada que dans l'est. Ainsi, la Baie James, se situant à l'ouest du Québec, pourrait être l'une des premières zones touchées par cette augmentation de la fréquence des grands feux et de l'aire brûlée dans l'est du Canada. On pourrait donc s'attendre à ce que ces augmentations se propagent rapidement vers l'est du Québec, retrouvant possiblement des régimes de feux similaires à ceux observés dans les 150-300 dernières années.

4.4.2 Facteurs climatiques passés et contemporains déterminants des régimes de feux

A l'échelle de la forêt boréale résineuse du Québec, nous avons montré que l'indice de sécheresse contrôlait la variabilité latitudinale du risque de feux des 150-300 dernières années (chapitre 1). Par contre, les résultats du chapitre 2 indiquent que seules les précipitations influençaient la variabilité spatiale des taux de brûlage contemporains. Cette différence indique que si d'un point de vue climatique, les régimes de feux sont contrôlés par les conditions de sécheresse, c'est-à-dire l'adéquation de la température et des précipitations, le rôle de chacun a évolué à travers le temps. Les régimes de feux actuels seraient plutôt contrôlés par les précipitations, alors que les températures auraient joué un rôle plus important dans le passé. Au cours du XX^{ème} siècle, le Canada a été soumis à une forte augmentation des précipitations (Zhang et al. 2000). Cela explique très bien les changements de régimes de feux et de leurs contrôles climatiques entre la période passée et contemporaine. En effet, nos résultats indiquent également que les cycles de feux passés étaient plus courts que les cycles de feux contemporains. Ainsi, l'augmentation des précipitations au cours du dernier siècle a pu mener à une réduction de l'évapotranspiration du combustible, réduisant ainsi la capacité de propagation des feux (Girardin et al. 2009; Flannigan et al. 2016), et expliquant pourquoi les régimes de feux contemporains sont plus contrôlés par les précipitations que les régimes de feux passés.

Il est cependant important de noter que dans le premier chapitre concernant les régimes de feux passés, l'influence climatique était testée selon des gradients latitudinaux. Dans le chapitre 2, l'effet du climat était recherché à l'échelle de toute la zone d'étude sans restriction directionnelle. Or, les précipitations au Québec suivent un gradient nord-ouest à sud-est, qui est plus difficilement décelable lorsque l'on se positionne selon un gradient purement latitudinal. Les différences de contrôles climatiques entre les deux périodes pourraient donc avoir en partie été influencées par cette distinction méthodologique.

4.4.3 Facteurs déterminants hors climat de la variabilité des régimes de feux passés et contemporains

Outre le climat, nos résultats indiquent que d'autres facteurs environnementaux sont responsables de la variabilité spatiale des régimes de feux passés et contemporains. En particulier, le chapitre 2 a démontré que sur la période contemporaine, l'environnement physique et le combustible apportaient chacun une contribution équivalente à celle du climat dans la détermination de la variabilité spatiale des taux de brûlage. Dans le chapitre 1, bien que seul l'effet du climat fût testé, nous avons également mis en évidence que la présence de monts ou de grands plans d'eau menait à une diminution des risques de feux passés. Cela est en accord avec les résultats du chapitre 2 qui a démontré que les monts connaissaient des taux de brûlage faibles, et que la proportion du territoire couverte par de l'eau était liée négativement aux taux de brûlage. Ces conclusions sont importantes dans un contexte où de nombreuses études tentent de prévoir les régimes de feux futurs à partir des changements du climat. Alors qu'une quantité grandissante de travaux démontrent également les effets de l'environnement physique et de la végétation sur les régimes de feux (Hu et al. 2006; Girardin et al.

2013; Parisien et al. 2014; Cavard et al. 2015; Rogeau and Armstrong 2017), nous insistons sur la nécessité de prendre en compte ces facteurs environnementaux, en plus du climat, dans les travaux de modélisation des régimes de feux.

Concernant la végétation, nos résultats témoignent de l'importance de l'utilisation de la végétation potentielle par rapport à la végétation actuelle lorsque l'on teste son effet sur les régimes de feux. Il est en effet crucial de se détacher de l'effet de la végétation comme conséquence des feux qui peut masquer ou biaiser l'effet causal de cette végétation. L'utilisation de la végétation potentielle dans le chapitre 2 a permis de démontrer que les peuplements ouverts, majoritaires dans les pessières à lichens et souvent présents dans des zones qui brûlent de façon importante, n'engendraient pas nécessairement des taux de brûlage importants. Ce résultat appuie les conclusions récentes de Héon et al. (2014) qui suggèrent que la forêt boréale est capable de résister aux forts taux de brûlage, ce qui lui permet de persister dans des paysages soumis à une forte occurrence de grands feux. En effet, nous avons montré dans le chapitre 1 que sur les 150-300 dernières années, les cycles de feux dans la Baie James étaient déjà très courts, et bien qu'on y trouve aujourd'hui une proportion importante de peuplements ouverts, la forêt boréale y est toujours présente.

L'environnement physique est lui aussi important dans la détermination des régimes de feux (Mansuy et al. 2010; Bélisle et al. 2016; Rogeau and Armstrong 2017). En particulier, nous avons montré dans le chapitre 2 que le relief et la texture des dépôts de surface, déterminante de la capacité de drainage des sols, pouvaient avoir un effet important sur les taux de brûlage à l'échelle des districts écologiques. Dans le chapitre 1, la variation latitudinale des risques de feux dans le secteur de la rivière Romaine, à l'est du Québec, n'a pas pu être liée au climat. Cette région étant très variable d'un point de vue physique, il se pourrait que la variabilité des régimes de feux dans ce secteur soit plus sensible à l'environnement physique qu'à des facteurs climatiques ou de végétation. Ainsi, la contribution relative de chacun des facteurs environnementaux pourrait varier d'une région à l'autre.

4.4.4 Conséquences des régimes de feux pour la forêt boréale résineuse québécoise

L'importante variabilité des régimes de feux en forêt boréale résineuse du Québec entraîne diverses conséquences sur les types de peuplements et la dynamique forestière. Dans les régions soumises à une activité très importante des feux, comme au nord de la limite nordique des forêts commerciales, ces feux à répétitions entraînent souvent une ouverture des peuplements liée à des accidents de régénération, menant souvent à l'obtention de pessières à lichens (Jasinki and Payette 2005; Girard et al. 2009). Ces pessières à lichens sont généralement improductives (Mansuy et al. 2013), et leur état est considéré irréversible naturellement (Jasinki and Payette 2005). Elles sont toutefois capables de perdurer dans le paysage, la rétroaction de la végétation sur les régimes de feux permettant leur résilience (Héon et al. 2014). Toutefois, dans le secteur de la Baie James, l'activité des feux s'intensifie depuis déjà quelques décennies, et la perduration des pessières à lichens dans un milieu soumis à une telle pression des feux pourrait être remise en question dans le futur. En termes de composition, une forte activité des feux mène souvent à une proportion importantes de pin gris, espèce très bien adaptée aux feux (Gauthier et al. 1993; Le Goff and Sirois 2004).

À l'opposé, les effets des régimes de feux sur la forêt sont bien différents dans des zones soumises à des régimes caractérisés par des feux très rares, bien que de grande taille. Le secteur de la rivière Romaine sur lequel on s'est penché au chapitre 3 en est un excellent exemple. Si le fait d'échapper aux feux pendant parfois plusieurs siècles permet aux peuplements d'accumuler une biomasse arborée et un volume marchand importants, s'apparentant à des valeurs retrouvées en forêts boréales résineuse commerciales, la dynamique forestière y est bien plus complexe. Contrairement à des forêts soumises à des régimes de feux plus actifs où la structure des peuplements est majoritairement régie par le temps depuis feu (Harper et al. 2002), nos résultats indiquent que dans le secteur de la rivière Romaine la structure dépend principalement de la productivité des sites ainsi que des perturbations secondaires. En effet, les régions soumises à une faible activité de feux comportent une proportion importante de vieilles forêts (Van Wagner 1978), dans lesquelles les perturbations secondaires telles que les épidémies d'insectes ou le vent sont importantes et régissent la dynamique de ces peuplements (De Grandpré et al. 2000; Kneeshaw and Gauthier 2003; Waldron et al. 2013). De plus, l'importante proportion de vieilles forêts résultant des longs cycles de feux permet à cette région de stocker des quantités importantes de carbone (Luyssaert et al. 2008). Par ailleurs, la rare occurrence de feux permet l'apparition en proportion abondante du sapin baumier, espèce tolérante à l'ombre qu'on ne retrouve que rarement dans les zones soumises à une plus forte activité des feux.

4.5 Implications des résultats de cette thèse

4.5.1 Dans un contexte de changements climatiques

Nos résultats ont des implications importantes dans un contexte de changements climatiques, découlant principalement de l'influence du climat sur les régimes de feux. En effet, nous avons montré que climatiquement, la variabilité spatiale des risques de feux passés était contrôlée par l'indice de sécheresse, basé sur les températures et précipitations (Amiro et al. 2004), alors que les taux de brûlage contemporains étaient eux régis principalement par les précipitations. Nous avons émis l'hypothèse que ce changement de contrôles climatiques était dû à l'augmentation importante des précipitations au cours du XX$^{\text{ème}}$ siècle (Zhang et al. 2000), qui aurait également mené à une diminution de l'activité des feux au cours de la deuxième moitié de ce siècle (Kasischke and Turetsky 2006).

Dans le futur, l'augmentation prévue des précipitations ne devrait pas permettre de compenser l'augmentation des températures, c'est-à-dire que l'évapotranspiration du combustible devrait, malgré l'augmentation des précipitations, être plus importante qu'elle ne l'est aujourd'hui (Girardin et al. 2009; Bergeron et al. 2010; Flannigan et al. 2016). Dans ce contexte, on peut s'attendre à ce que le système devienne à nouveau contrôlé par les températures, comme il l'était dans le passé. En effet, l'augmentation des températures devrait entraîner un combustible globalement plus sec facilitant le départ et la propagation des feux (Amiro et al. 2004; Flannigan et al. 2016). L'augmentation de l'occurrence des feux en réponse à de meilleures chances de succès des départs de feux, ainsi que l'occurrence de plus grands feux en réponse à la facilité de propagation, devraient entraîner une augmentation des risques de feux et des taux de brûlage. Les capacités de suppression des feux dans toute la zone boréale pourraient ainsi être poussées au-delà d'un seuil ne permettant plus de contrôler ces feux, ce qui participerait à l'augmentation importante des grands feux et ainsi que des taux de brûlage (de Groot et al. 2013b).

Par ailleurs, nous avons montré que malgré les changements de régimes de feux entre la période passée et la période contemporaine, leur zonation était restée relativement stable. Si le système feux – climat redevient contrôlé non seulement par les précipitations, mais aussi par les températures, il reste des questionnements quant au dépassement de la variabilité naturelle passée des régimes de feux. En effet, si les régimes de feux futurs se maintiennent dans la gamme de variabilité passée comme suggéré par Bergeron et al. (2010), on peut s'attendre à ce que la zonation de ces régimes reste stable et conserve son inertie. Cependant, si les régimes futurs dépassent la variabilité passée, alors la stabilité de leur zonation pourrait être remise en question. La quantité/qualité de combustible pourrait néanmoins tempérer ce basculement, puisque nous avons montré qu'elle jouait un rôle important dans la détermination des taux de brûlage. De plus, il a été démontré qu'elle serait potentiellement capable de réduire les effets des changements climatiques sur les régimes de feux (Hély et al. 2001; Girardin et al. 2013; Terrier et al. 2013).

Toutefois, l'effet d'une intensification des régimes de feux futurs sur l'ouverture des peuplements au nord n'est pas à négliger. En effet, le basculement de pessières à mousses denses en pessières à lichens ouvertes est majoritairement dû à l'occurrence de feux à répétition, engendrant des échecs de régénération (Jasinki and Payette 2005; Girard et al. 2009; Mansuy et al. 2013). Les changements climatiques, en agissant sur l'activité des feux, pourraient donc engendrer rapidement une expansion des pessières à lichens vers le sud (Girard et al. 2008), bien qu'une certaine résistance des forêts aux forts taux de brûlage pourrait également être observée (Héon et al. 2014).

Dans des secteurs aujourd'hui soumis à une activité faible des feux, comme la Côte Nord, les répercussions des changements climatiques pourraient être différentes. Tout d'abord, l'augmentation de l'activité des feux pourrait y être moindre puisqu'on s'attend à une augmentation des précipitations plus marquée dans cette région (Flannigan et al. 2016). Cependant, durant les années de sécheresse extrême, les impacts pourraient être importants. En effet, bien que les feux y soient rares, ils sont néanmoins de grande taille. Un combustible plus sec pourrait donc rendre rapidement ces feux incontrôlables, d'autant plus considérant la quantité importante de biomasse présente dans ces peuplements du fait de l'occurrence rare des feux. Puisque ces régions contiennent des stocks importants de carbone, une augmentation de l'activité des feux dans ce secteur signifierait nécessairement des émissions importantes de carbone dans l'atmosphère (de Groot et al. 2007; Terrier et al. 2016).

4.5.2 Pour l'aménagement forestier

Nos résultats ont également des implications pour l'aménagement forestier. La première se situe au niveau de la limite nordique des forêts attribuables, qui sépare principalement les forêts ouvertes au nord des forêts fermées commerciales au sud. En effet, nous avons montré que la zonation des régimes de feux était relativement stable dans le temps malgré des changements de régimes de feux. Nous avons aussi montré dans le premier chapitre que cette zonation correspondait à la limite nordique des forêts attribuables. Si la variabilité future des taux de brûlage se maintient à l'intérieur de la variabilité passée (Bergeron et al. 2010), on peut donc s'attendre à ce que la limite entre les forêts ouvertes et les forêts fermées reste stable elle aussi. Bien qu'une réévaluation régulière de la limite nordique est souhaitable afin de monitorer les éventuels changements de végétation et les critères hors feux la définissant (MFFPQ 2013), nos résultats indiquent qu'elle devrait démontrer une certaine inertie face aux changements futurs de régimes des feux.

Deuxièmement, l'aménagement forestier va devoir faire face aux effets des changements climatiques et de l'augmentation des taux de brûlage, qui font concurrence aux récoltes forestières (Bergeron et al. 2017). En effet, dans un contexte d'aménagement écosystémique, la différence entre les taux de brûlage passés (plus importants) et présents (plus faibles) peut être comblée par l'aménagement forestier. En se maintenant à l'intérieur la variabilité naturelle des régimes de perturbations, la structure d'âge des paysages n'est ainsi pas affectée (Bergeron et al. 2002; Gauthier et al. 2008a; Cyr et al. 2009). Avec les changements climatiques, cette différence pourrait devenir nulle, voire négative, ce qui implique l'implantation de nouvelles mesures pour permettre à l'aménagement forestier durable de s'adapter aux conditions futures (Bergeron et al. 2017). Par exemple, nos résultats appuient de précédentes études démontrant que la végétation, en particulier les espèces feuillues qui sont moins inflammables que les espèces résineuses, pourrait réduire le risque de feux et ainsi les taux de brûlage (Hély et al. 2001; Girardin et al. 2013; Terrier et al. 2013). Cela permet de réduire la capacité de propagation des feux, et ainsi de conserver une portion plus importante du territoire pour l'aménagement (Hirsch et al. 2004; Girardin et al. 2013; Terrier et al. 2013).

Troisièmement, cette thèse apporte de nouvelles connaissances sur le secteur de la rivière Romaine, nouvellement ouvert au développement économique pour les secteurs forestier et énergétique. Nos résultats indiquent que si le volume marchand des peuplements de cette région est assimilable à celui de forêts commerciales, la proportion de peuplements s’apparentant à des vieilles forêts en termes d’âge ou de structure y est très importante. La protection de ce type de peuplements est un des principaux enjeux en aménagement écosystémique, puisqu’ils permettent le maintien de la biodiversité et des fonctions écologiques (Kneeshaw and Gauthier 2003; Bergeron and Fenton 2012), mais aussi des importants stocks de carbone qu’ils contiennent (Luyssaert et al. 2008). Ainsi, les stratégies d’aménagement qui pourraient être implantées dans cette région devraient tenir compte de l’importance de ces vieilles forêts ou des peuplements présentant des attributs de vieilles forêts (Bergeron et al. 2017). Dans la littérature, plusieurs stratégies sont proposées comme la conservation de massifs complets de vieilles forêts ou encore une sylviculture adaptée à ce type de peuplements, permettant parfois de recréer des attributs de vieilles forêts (Kneeshaw and Gauthier 2003; Bauhus et al. 2009; Galatowitsch et al. 2009; Bergeron and Fenton 2012; Bergeron et al. 2017). Par ailleurs, le chapitre 3 démontre que la biomasse arborée et le volume marchand s’accumulent jusqu’à environ 150 ans après un feu, puis déclinent. Ce chiffre donne un renseignement important aux aménagistes qui peuvent ainsi prévoir l’âge auquel la récolte est idéale. Cependant, nous avons montré que la structure et la composition des peuplements dépendaient plus de la productivité du site et des perturbations secondaires que du temps depuis le dernier feu. Or, les pertes de bois annuelles dues à ce type de perturbations peuvent être plus importantes que celles engendrées par les feux dans certaines régions (Volney and Fleming 2000). L’aménagement forestier dans ce secteur pourrait ainsi miser davantage sur la variabilité de structure des peuplements de laquelle la biodiversité dépend en grande partie (Fenton and Bergeron 2008), plutôt que sur l’âge de ces peuplements. Par ailleurs le développement économique engendrant la récolte ou l’ennoiement de biomasse forestière dans cette région devrait tenir compte des quantités importantes de carbone y étant stockées.

4.6 Pistes pour des recherches futures

Cette thèse apporte de nouvelles connaissances sur les régimes de feux en forêt boréale, mais nos conclusions entraînent toutefois d'autres questionnements, et permettent de cibler de potentielles pistes de recherches à suivre dans le futur. Tout d'abord, dans les zones soumises à une activité importante des feux, comme le nord-ouest du Québec, la résilience des forêts face aux changements climatiques et aux changements de régimes de feux qu'ils impliquent pourrait être approfondie. En particulier, les risques d'ouverture des peuplements face à une augmentation des risques de feux et des taux de brûlage sont encore peu connus. Ensuite, il serait nécessaire d'évaluer si comme nous en faisons l'hypothèse, le système climat-feux est en train de passer d'un contrôle par les précipitations à un contrôle par les températures au nord-ouest du Québec, menant à une augmentation des taux de brûlage, et si ce phénomène risque de se propager à toute la zone boréale québécoise.

Le secteur de la rivière Romaine apporte lui aussi de nombreux questionnements. Premièrement, les facteurs déterminants de son régime de feux mériteraient d'être plus amplement étudiés. Si nous n'avons pas pu mettre en évidence le rôle du climat dans cette région, il serait nécessaire de mieux comprendre comment l'environnement physique, localement, agit sur la variabilité des risques de feux. Ensuite, nous avons montré que le système forestier de cette région était complexe, avec un effet du temps depuis feux sur l'accumulation de biomasse arborée, et une structure et composition des peuplements majoritairement dépendantes de la productivité des sites et des perturbations secondaires. Ces derniers résultats devraient être approfondis, afin de mieux comprendre les liens productivité – structure, et perturbations secondaires – structure dans cette région. Les raisons pour lesquelles certains peuplements sont improductifs pourraient également être mieux documentées. Le fait que cette région renferme des quantités importantes de carbone pourrait lui aussi être approfondi, afin de mieux évaluer les conséquences du développement économique de cette région sur son bilan de carbone.

ANNEXE A

CARACTÉRISTIQUES DU RÉGIME DE FEUX EN FORÊT BORÉALE RÉSINEUSE QUÉBÉCOISE

Cette annexe vise à décrire le régime de feux en termes de distributions de taille et de nombre de feux dans la forêt boréale résineuse du Québec (aire d'étude du chapitre 2). Les données de feux utilisées proviennent de la base de données de feux du MFFP, qui est considérée complète et précise depuis 1972 au sud de la limite des forêts attribuables établie en 2002. Au nord de cette limite, les contours de certains feux ont été délimités à l'aide de techniques de télédétection, et leur taille est estimée. Ces feux ont également été datés par des intervalles de 5 ans, et le milieu de ces intervalles a été utilisé comme date de feux dans les analyses. Les caractéristiques du régime de feux sont décrites sur la période 1972-2015 à l'échelle des zones homogènes de feux (Figure A1) qui ont été précédemment définies par Gauthier et al. (2015) en se basant sur les cycles de feux de la période 1972-2009. La zone G11, qui avait été retirée des analyses de Gauthier et al. (2015) dû à l'absence de feu dans leur période d'étude, a été rajoutée dans nos calculs.

Les cycles de feux ont été calculés comme l'inverse de la proportion annuelle moyenne de la surface qui a brulé (Johnson et al. 1998) dans l'unité territoriale étudiée. En dehors des calculs sur les cycles de feux, lorsqu'un feu chevauchait plusieurs zones, il était attribué à la zone contenant la plus grande aire brûlée par ce même feu.

Les principaux attributs du régime de feux de chaque zone sont présentés dans le tableau A1, et les distributions de taille et de nombre sont présentés dans les tableaux A2 et A3. Ces tableaux montrent par exemple que dans chaque zone, l'aire brûlée totale est majoritairement le résultat de quelques grands feux. En effet, dans toute les zones la majorité des feux sont petits en comparaison à la taille des feux nécessaires de considérer pour obtenir une petite portion de l'aire brûlée totale. La figure A1 représente cartographiquement les cycles de feux des différentes zones, et les tailles de chaque feu à l'intérieur de chaque zone en fonction de leur année d'occurrence sont présentées sur la figure A2.

Tableau A1 Caractéristiques principales du régime de feux de chaque zone homogène de feux entre 1972 et 2015.

Zone de feux*	% de la zone d'étude couverte par la zone	Aire (kha)	Cycle de feux* (95% IC) 1972-2009 (ans)	Cycle de feux (95% IC)** (ans)	Nombre moyen annuel de feux par 1000 km²	Nombre total de feux	Taille moyenne de feux (ha)	Taille médiane de feux (ha)	Taille du plus grand feu (ha)
G1	4.7	2,169	44 (34-61)	50 (34-82)	0.17	162	13,087	867	406,446
G2	1.0	483	59 (46-81)	72 (50-116)	0.16	33	7,096	1,836	36,167
G3	8.3	3,825	67 (57-82)	80 (65-104)	0.18	305	6,936	1,065	194,484
G4	9.3	4,305	94 (85-105)	95 (68-131)	0.19	364	5,886	593	494,341
G5	21.3	9,884	183 (155-221)	179 (128-258)	0.12	534	5,379	546	459,250
G6	15.1	7,021	272 (239-312)	275 (203-397)	0.08	260	5,306	331	225,826
G7	4.6	2,332	395 (343-463)	513 (357-756)	0.09	83	2,142	283	34,436
G8	17.9	8,530	712 (636-816)	743 (576-989)	0.07	249	1,703	183	29,741
G9	4.3	1,999	1,668 (1,286-2,380)	1,478 (834-3,429)	0.04	37	1,613	152	19,384
G10	9.1	4,219	8,167 (5,904-12,990)	2,917 (1,499-9,421)	0.02	34	2,359	137	43,390
G11	4.3	2,009	/	3,790 (1,390-41,294)	0.02	18	211	52	1,228

* Les zones homogènes de feux et les cycles de feux couvrant la période 1972-2009 proviennent de Gauthier et al. (2015).

** IC 95% des cycles de feux couvrant la période 1972-2015 ont été obtenus par rééchantillonnage (bootstrap) après 1000 randomisations avec remplacement de tous les feux ayant eu lieu dans une zone donnée, et la compilation des plus haut et bas percentiles des 1000 cycles de feux obtenus.

Tableau A2 Pour chaque zone homogène de feux, distributions sur la période 1972-2015 de la taille des feux et de la taille pour laquelle un certain pourcentage de l'aire brûlée a été observé.

Zone de feux	Distribution de taille des feux (percentiles 0.25, 0.5 et 0.75) (ha) Taille à partir de laquelle x% de l'aire brûlée cumulée est observée (ha)		
	25%	**50%**	**75%**
G1	200 53,719	867 111,005	4,899 168,290
G2	572 9,090	1,836 17,758	11,191 26,425
G3	186 18,455	1,065 38,759	5,412 59,063
G4	100 16,404	593 33,822	3,467 51,241
G5	114 21,924	546 46,233	2,365 70,541
G6	77 19,963	331 41,216	2,357 62,469
G7	95 4,081	283 8,316	2,221 12,551
G8	38 5,373	183 11,222	914 17,072
G9	72 4,601	152 9,597	1,018 14,592
G10	17 7,181	137 14,529	538 21,876
G11	4 271	52 521	388 771

Exemple dans la zone G1 : Considérant les feux ordonnés en ordre croissant de taille, 25% des feux font 200 ha ou moins, 50% font 867 ha ou moins, et 75% font 4,899 ha ou moins. Par contre, pour obtenir 25% de l'aire brûlée totale, il faut considérer tous les feux faisant 53,719 ha ou moins, pour 50% les feux faisant 111,005 ha ou moins, pour 75% les feux faisant 168,290 ha ou moins.

Tableau A3 Pour chaque zone homogène de feux, distributions sur la période 1972-2015 de la taille de feux et du nombre de feux selon différentes classes de taille, exprimées en pourcentage de l'aire totale brûlée et du nombre total de feux.

Zone de feux	**% du nombre de feux par classe de taille % responsable de l'aire brûlée totale par classe de taille**					
	0-10 ha	**10-100 ha**	**100-1,000 ha**	**1,000-10,000 ha**	**10,000-50,000 ha**	**>= 50,000 ha**
G1	3.70	12.96	**36.42**	28.40	11.11	7.41
	0.00	0.04	1.05	7.90	16.16	**74.84**
G2	0.00	6.06	36.36	**30.30**	27.27	-
	0.00	0.06	2.89	19.50	**77.54**	-
G3	1.31	15.74	31.48	**35.41**	13.44	2.62
	0.00	0.11	1.72	19.51	**42.53**	36.13
G4	2.75	22.25	**33.24**	28.02	12.64	1.10
	0.00	0.16	2.28	17.13	**46.09**	34.34
G5	1.69	20.97	**38.20**	27.72	9.36	2.06
	0.00	0.20	2.94	16.37	**33.78**	46.72
G6	0.77	27.69	**36.54**	23.08	9.62	2.31
	0.00	0.25	2.60	14.33	**40.07**	42.75
G7	7.23	18.07	**39.76**	30.12	4.82	-
	0.01	0.35	6.25	**50.94**	42.44	-
G8	6.83	32.53	**36.55**	19.68	4.42	-
	0.01	0.81	8.75	**40.66**	49.77	-
G9	5.41	32.43	**35.14**	21.62	5.41	-
	0.02	1.03	6.39	34.80	**57.77**	-
G10	20.59	23.53	**32.35**	14.71	8.82	-
	0.03	0.29	3.25	12.50	**83.43**	-
G11	33.33	**27.78**	33.33	5.56	**-**	
	0.45	5.35	**61.81**	32.39	**-**	-

Les valeurs en gras représentent les classes de taille à partir desquelles 50% du nombre total de feux ou de l'aire brûlée totale sont cumulativement atteints.

Exemple dans la zone G1 : 3.70% des feux sont plus petits que 10 ha, 12.96% font entre 10 et 100 ha, etc. Considérant les feux ordonnés par ordre croissant de taille, 50% du nombre total de feux est atteint en additionnant les feux des trois premières classes de taille. Les feux entre 100 et 1,000 ha sont responsables de 1.05% de l'aire brûlée totale, les feux entre 1,000 et 10,000 ha de 7.90%, etc. Considérant les feux ordonnés par ordre croissant de taille, 50% de l'aire brûlée totale est atteinte avec les feux de la plus grande classe de taille.

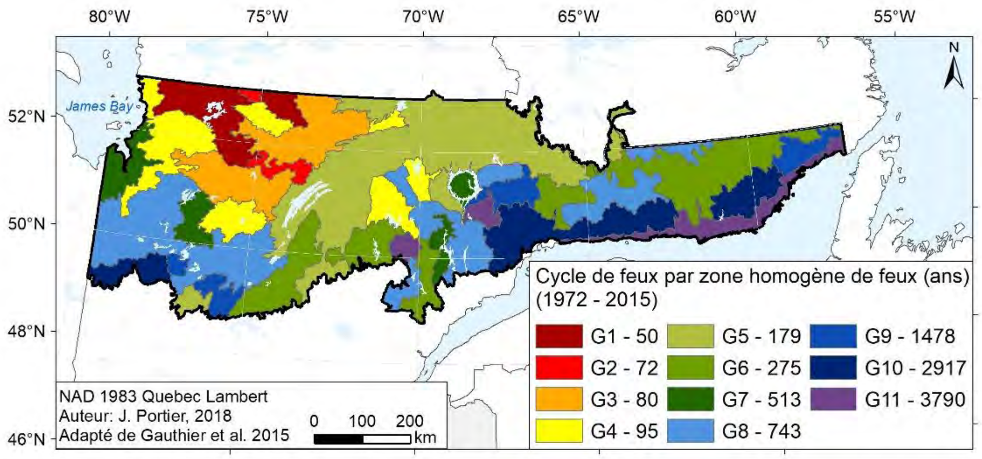

Figure A1 **Cycles de feux calculés sur la période 1972-2015 des zones homogènes de feux définies par Gauthier et al. (2015).**

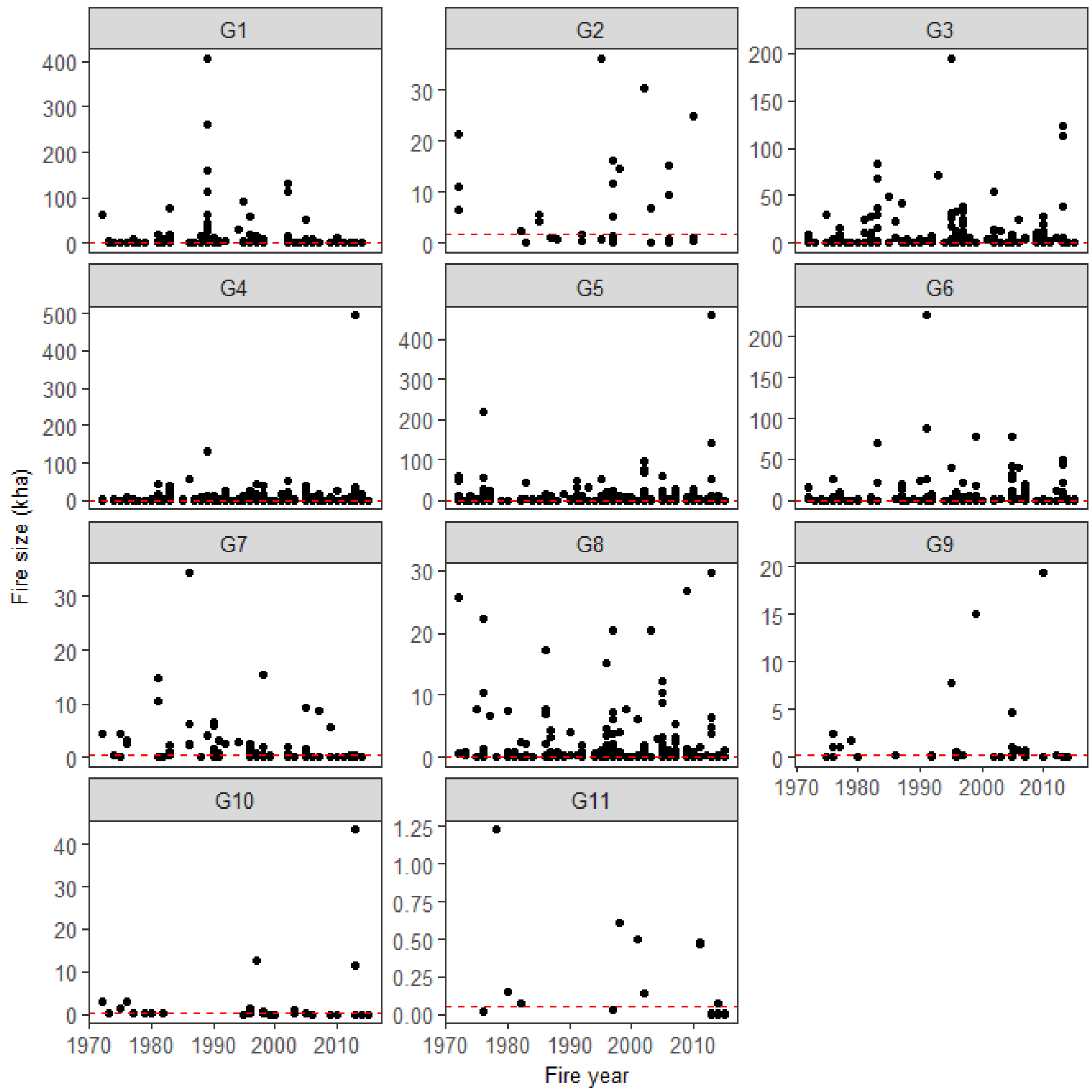

Figure A2 Taille de chaque feu enregistré entre 1972 et 2015 par zone homogène de feux.

L'axe représentant la taille des feux est exprimé en 10^3 ha et l'échelle varie d'une zone à l'autre. Chaque point représente un feu et les lignes pointillées rouges représentent la taille médiane des feux de chaque zone.

Références

Gauthier S, Raulier F, Ouzennou H, Saucier J (2015) Strategic analysis of forest vulnerability to risk related to fire: an example from the coniferous boreal forest of Quebec. Can J For Res 45:553–565. doi: 10.1139/cjfr-2014-0125

Johnson EA, Miyanishi K, Weir JMH (1998) Wildfires in the western Canadian boreal forest: Landscape patterns and ecosystem management. J Veg Sci 9:603–610.

RÉFÉRENCES GÉNÉRALES

Amiro BD, Logan KA, Wotton BM, et al (2004) Fire weather index system components for large fires in the Canadian boreal forest. Int J Wildl Fire 13:391–400. doi: 10.1071/WF03066

Bauhus J, Puettmann K, Messier C (2009) Silviculture for old-growth attributes. For Ecol Manage 258:525–537. doi: 10.1016/j.foreco.2009.01.053

Beck PS, Goetz SJ, Mack MC, et al (2011) The impacts and implications of an intensifying fire regime on Alaskan boreal forest composition and albedo. Glob Chang Biol 17:2853–2866. doi: 10.1111/j.1365-2486.2011.02412.x

Bélisle A, Leduc A, Gauthier S, et al (2016) Detecting local drivers of fire cycle heterogeneity in boreal forests: A scale issue. Forests 7:1–21. doi: 10.3390/f7070139

Bélisle AC, Gauthier S, Cyr D, et al (2011) Fire regime and old-growth boreal forests in central Quebec, Canada: An ecosystem management perspective. Silva Fenn 45:889–908.

Bergeron Y, Archambault S (1993) Decreasing frequency of forest fires in the southern boreal zone of Quebec and its relation to global warming since the end of the "Little Ice Age." The Holocene 3:255–259. doi: 10.1177/095968369300300307

Bergeron Y, Cyr D, Drever CR, et al (2006) Past, current, and future fire frequencies in Quebec's commercial forests: implications for the cumulative effects of harvesting and fire on age-class structure and natural disturbance-based management. Can J For Res 36:2737–2744. doi: 10.1139/X06-177

Bergeron Y, Cyr D, Girardin MP, Carcaillet C (2010) Will climate change drive 21st century burn rates in Canadian boreal forest outside of its natural variability: collating global climate model experiments with sedimentary charcoal data. Int J Wildl Fire 19:1127. doi: 10.1071/WF09092

Bergeron Y, Drapeau P, Gauthier S, Lecomte N (2007) Using knowledge of natural disturbances to support sustainable forest management in the northern Clay Belt. For Chron 83:326–337.

Bergeron Y, Fenton NJ (2012) Boreal forests of eastern Canada revisited: old growth, nonfire disturbances, forest succession, and biodiversity. Botany 90:509–523. doi: 10.1139/B2012-034

Bergeron Y, Gauthier S, Flannigan M, Kafka V (2004) Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec. Ecology 85:1916–1932.

Bergeron Y, Irulappa Pillai Vijayakumar DB, Ouzennou H, et al (2017) Projections of future forest age class structure under the influence of fire and harvesting: implications for forest management in the boreal forest of eastern Canada. For An Int J For Res 90:485–495. doi: doi:10.1093/forestry/cpx022 Projections

Bergeron Y, Leduc A, Harvey BD, Gauthier S (2002) Natural fire regime: a guide for sustainable management of the Canadian boreal forest. Silva Fenn 36:81–95.

Blais JR (1983) Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. Can J For Res 13:539–547.

Bogdanski BEC (2008) Canada's boreal forest economy: economic and socioeconomic issues and research opportunities. Natural Resources Canada - Canadian Forest

Service, Victoria, BC, Canada

Bond-Lamberty B, Peckham SD, Ahl DE, Gower ST (2007) Fire as the dominant driver of central Canadian boreal forest carbon balance. Nature 450:89–92. doi: 10.1038/nature06272

Bouchard M, Pothier D, Gauthier S (2008) Fire return intervals and tree species succession in the North Shore region of eastern Quebec. Can J For Res 38:1621–1633. doi: 10.1139/X07-201

Boulanger Y, Gauthier S, Gray DR, et al (2013) Fire regime zonation under current and future climate over eastern Canada. Ecol Appl 23:904–923.

Bradshaw CJA, Warkentin IG (2015) Global estimates of boreal forest carbon stocks and flux. Glob Planet Change 128:24–30. doi: 10.1016/j.gloplacha.2015.02.004

Brandt JP (2009) The extent of the North American boreal zone. Environ Rev 17:101–161. doi: 10.1139/A09-004

Brandt JP, Flannigan MD, Maynard DG, et al (2013) An introduction to Canada's boreal zone: ecosystem processes, health, sustainability, and environmental issues. Environ Rev 21:207–226. doi: 10.1139/er-2013-0040

Burton PJ, Kneeshaw DD, Coates KD (1999) Managing forest harvesting to maintain old growth in boreal and sub-boreal forests. For Chron 75:623–631. doi: 10.5558/tfc75623-4

Burton PJ, Messier C, Smith DW, Adamowicz WL (2003) Toward Sustainable Management of the Boreal Forest. NRC Research Press, Ottawa, Ontario, Canada

Carcaillet C, Bergeron Y, Richard PJH, et al (2001) Change of fire frequency in the eastern Canadian boreal forests during the Holocene: does vegetation composition or climate trigger the fire regime? J Ecol 89:930–946.

Cavard X, Boucher JF, Bergeron Y (2015) Vegetation and topography interact with weather to drive the spatial distribution of wildfires in the eastern boreal forest of Canada. Int J Wildl Fire 24:391–406. doi: 10.1071/WF13128

CCMF (2008) Politiques en matière d'aménagement durable des forêts au Canada.

Chabot M, Blanchet P, Drapeau P, et al (2009) Le feu en milieu forestier. In: Manuel de foresterie., MultiMonde. Ordre des ingénieurs forestiers du Québec., Québec (Québec), pp 1037–1090

Comité d'experts sur l'aménagement écosystémique des forêts et les changements climatiques (2017) L'aménagement écosystémique des forêts dans le contexte des changements climatiques - Rapport du comité d'experts. Québec, QC, Canada

Cyr D, Gauthier S, Bergeron Y (2007) Scale-dependent determinants of heterogeneity in fire frequency in a coniferous boreal forest of eastern Canada. Landsc Ecol 22:1325–1339. doi: 10.1007/s10980-007-9109-3

Cyr D, Gauthier S, Bergeron Y, Carcaillet C (2009) Forest management is driving the eastern North American boreal forest outside its natural range of variability. Front Ecol Environ 7:519–524. doi: 10.1890/080088

Cyr D, Gauthier S, Boulanger Y, Bergeron Y (2016) Quantifying fire cycle from dendroecological records using survival analyses. Forests 7:1–21. doi: 10.3390/f7070131

De Grandpré L, Morisette J, Gauthier S (2000) Long-term post-fire changes in the northeastern boreal forest of Quebec. J Veg Sci 11:791–800.

de Groot WJ, Cantin AS, Flannigan MD, et al (2013a) A comparison of Canadian and

Russian boreal forest fire regimes. For Ecol Manage 294:23–34. doi: 10.1016/j.foreco.2012.07.033

de Groot WJ, Flannigan MD, Cantin AS (2013b) Climate change impacts on future boreal fire regimes. For Ecol Manage 294:35–44. doi: 10.1016/j.foreco.2012.09.027

de Groot WJ, Landry R, Kurz WA, et al (2007) Estimating direct carbon emissions from Canadian wildland fires. Int J Wildl Fire 16:593–606. doi: 10.1071/WF06150

Dormann CF, McPherson JM, Araújo MB, et al (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography (Cop) 30:609–628. doi: 10.1111/j.2007.0906-7590.05171.x

Drapeau P, Nappi A, Imbeau L, Saint-Germain M (2009) Standing deadwood for keystone bird species in the eastern boreal forest: Managing for snag dynamics. For Chron 85:227–234.

Drever CR, Peterson G, Messier C, et al (2006) Can forest management based on natural disturbances maintain ecological resilience? Can J For Res 36:2285–2299. doi: 10.1139/X06-132

Erni S, Arseneault D, Parisien M-A, Bégin Y (2016) Spatial and temporal dimensions of fire activity in the fire-prone eastern Canadian taiga. Glob Chang Biol. doi: 10.1111/gcb.13461

Fenton NJ, Bergeron Y (2008) Does time or habitat make old-growth forests species rich? Bryophyte richness in boreal Picea mariana forests. Biol Conserv 141:1389–1399. doi: 10.1016/j.biocon.2008.03.019

Flannigan M, Cantin AS, De Groot WJ, et al (2013) Global wildland fire season severity in the 21st century. For Ecol Manage 294:54–61. doi: 10.1016/j.foreco.2012.10.022

Flannigan MD, Harrington JB (1988) A study of the relation of meteorological variables to monthly provincial area burned by wildfire in Canada (1953–80). J Appl Meteorol 27:441–452.

Flannigan MD, Logan KA, Amiro BD, et al (2005) Future area burned in Canada. Clim Change 72:1–16. doi: 10.1007/s10584-005-5935-y

Flannigan MD, Stocks B, Turetsky M, Wotton M (2009) Impacts of climate change on fire activity and fire management in the circumboreal forest. Glob Chang Biol 15:549–560. doi: 10.1111/j.1365-2486.2008.01660.x

Flannigan MD, Wotton BM, Marshall GA, et al (2016) Fuel moisture sensitivity to temperature and precipitation: climate change implications. Clim Change 134:59–71. doi: 10.1007/s10584-015-1521-0

Franklin JF, Spies TA, Van Pelt R, et al (2002) Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For Ecol Manage 155:399–423. doi: 10.1016/S0378-1127(01)00575-8

Galatowitsch S, Frelich L, Phillips-Mao L (2009) Regional climate change adaptation strategies for biodiversity conservation in a midcontinental region of North America. Biol Conserv 142:2012–2022. doi: 10.1016/j.biocon.2009.03.030

Garet J, Pothier D, Bouchard M (2009) Predicting the long-term yield trajectory of black spruce stands using time since fire. For Ecol Manage 257:2189–2197. doi: 10.1016/j.foreco.2009.03.001

Gauthier S, Bergeron Y, Simon J-P (1993) Cone serotiny in jack pine: ontogenetic, positional, and environmental effects. Can J For Res 23:394–401.

Gauthier S, Bernier P, Burton PJ, et al (2014) Climate change vulnerability and adaptation in the managed Canadian boreal forest. Environ Rev 30:1–30. doi: dx.doi.org/10.1139/er-2013-0064

Gauthier S, Bernier P, Kuuluvainen T, et al (2015a) Boreal forest health and global change. Science (80-) 349:819–822. doi: 10.1126/science.aaa9092

Gauthier S, Boucher D, Morissette J, De Grandpré L (2010) Fifty-seven years of composition change in the eastern boreal forest of Canada. J Veg Sci 21:772–785. doi: 10.1111/j.1654-1103.2010.01186.x

Gauthier S, Leduc A, Bergeron Y, Le Goff H (2008a) La fréquence des feux et l'aménagement forestier inspiré des perturbations naturelles. In: Gauthier S, Vaillancourt M-A, Leduc A, et al. (eds) Aménagement écosystémique en forêt boréale. Presses de l'Université du Québec, Québec, QC, Canada, pp 61–78

Gauthier S, Raulier F, Ouzennou H, Saucier J (2015b) Strategic analysis of forest vulnerability to risk related to fire: an example from the coniferous boreal forest of Quebec. Can J For Res 45:553–565. doi: 10.1139/cjfr-2014-0125

Gauthier S, Vaillancourt M-A, Leduc A, et al (2008b) Aménagement écosystémique en forêt boréale. Les Presses de l'Université du Québec, Québec, QC, Canada.

Girard F, De Grandpre L, Ruel JC (2014) Partial windthrow as a driving process of forest dynamics in old-growth boreal forests. Can J For Res 44:1165–1176. doi: 10.1139/cjfr-2013-0224

Girard F, Payette S, Gagnon R (2008) Rapid expansion of lichen woodlands within the closed-crown boreal forest zone over the last 50 years caused by stand disturbances in eastern Canada. J Biogeogr 35:529–537. doi: 10.1111/j.1365-

2699.2007.01816.x

Girard F, Payette S, Gagnon R (2009) Origin of the lichen-spruce woodland in the closed-crown forest zone of eastern Canada. Glob Ecol Biogeogr 18:291–303. doi: 10.1111/j.1466-8238.2009.00449.x

Girardin MP (2010) Wildfire risk inferred from tree rings in the Central Laurentians of boreal Quebec, Canada. Dendrochronologia 28:187–206. doi: 10.1016/j.dendro.2009.05.006

Girardin MP, Ali AA, Carcaillet C, et al (2009) Heterogeneous response of circumboreal wildfire risk to climate change since the early 1900s. Glob Chang Biol 15:2751–2769. doi: 10.1111/j.1365-2486.2009.01869.x

Girardin MP, Ali AA, Carcaillet C, et al (2013) Vegetation limits the impact of a warm climate on boreal wildfires. New Phytol 199:1001–1011. doi: 10.1111/nph.12322

Girardin MP, Mudelsee M (2008) Past and future changes in Canadian boreal wildfire activity. Ecol Appl 18:391–406. doi: 10.1890/07-0747.1

Girardin MP, Tardif J, Flannigan MD, et al (2004) Trends and periodicities in the Canadian Drought Code and their relationships with atmospheric circulation for the southern Canadian boreal forest. Can J For Res 34:103–119. doi: 10.1139/X03-195

Girardin MP, Wotton BM (2009) Summer moisture and wildfire risks across Canada. J Appl Meteorol Climatol 48:517–533. doi: 10.1175/2008JAMC1996.1

Greene DF, Macdonald SE, Haeussler S, et al (2007) The reduction of organic-layer depth by wildfire in the North American boreal forest and its effect on tree recruitment by seed. Can J For Res 37:1012–1023. doi: 10.1139/X06-245

Gunderson LH (2000) Ecological resilience - in theory and application. Annu Rev Ecol Syst 31:425–439.

Harper KA, Bergeron Y, Drapeau P, et al (2005) Structural development following fire in black spruce boreal forest. For Ecol Manage 206:293–306. doi: 10.1016/j.foreco.2004.11.008

Harper KA, Bergeron Y, Gauthier S, Drapeau P (2002) Post-fire development of canopy structure and composition in black spruce forests of Abitibi, Québec: a landscape scale study. Silva Fenn 36:249–263.

Hély C, Flannigan M, Bergeron Y, McRae D (2001) Role of vegetation and weather on fire behavior in the Canadian mixedwood boreal forest using two fire behavior prediction systems. Can J For Res 31:430–441. doi: 10.1139/cjfr-31-3-430

Héon J, Arseneault D, Parisien M-A (2014) Resistance of the boreal forest to high burn rates. Proc Natl Acad Sci 111:13888–13893. doi: 10.1073/pnas.1409316111

Hirsch K, Kafka V, Todd B (2004) Using forest management techniques to alter forest fuels and reduce wildfire size: an exploratory analysis. In: Engstrom RT, Galley KEM, De Groot WJ (eds) Proceedings of the 22nd Tall Timbers Fire Ecology Conference: Fire in Temperate, Boreal, and Montane Ecosystems, Tall Timbe. Tallahassee, FL, pp 175–184

Hu FS, Brubaker LB, Gavin DG, et al (2006) How climate and vegetation influence the fire regime of the Alaskan boreal biome: The Holocene perspective. Mitig Adapt Strateg Glob Chang 11:829–846. doi: 10.1007/s11027-005-9015-4

IPCC (2014) Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland

Jasinki JPP, Payette S (2005) The creation of alternative stable states in the southern boreal forest, Québec, Canada. Ecol Monogr 75:561–583.

Johnson EA (1992) Fire and Vegetation Dynamics - Studies from the North American Boreal Forest. Cambridge University Press, Cambridge, UK

Johnson EA, Gutsell SL (1994) Fire frequency models, methods and interpretations. Adv Ecol Res 25:239–287.

Johnston M, Williamson T, Price D, et al (2006) Adapting forest management to the impacts of climate change in Canada - Final report. Kingston, ON

Kasischke ES, Turetsky MR (2006) Recent changes in the fire regime across the North American boreal region-Spatial and temporal patterns of burning across Canada and Alaska. Geophys Res Lett 33:1–5. doi: 10.1029/2006GL025677

Kelly R, Chipman ML, Higuera PE, et al (2013) Recent burning of boreal forests exceeds fire regime limits of the past 10,000 years. PNAS 110:13055–13060. doi: 10.1073/pnas.1305069110

Kneeshaw D, Gauthier S (2003) Old growth in the boreal forest: A dynamic perspective at the stand and landscape level. Environ Rev 11:99–114. doi: 10.1139/A03-010

Krebs P, Pezzatti GB, Mazzoleni S, et al (2010) Fire regime: history and definition of a key concept in disturbance ecology. Theory Biosci 129:53–69. doi: 10.1007/s12064-010-0082-z

Kuuluvainen T (2002) Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. Silva Fenn 36:97–125.

Kuuluvainen T, Ankala T (2011) Natural forest dynamics in boreal in Fennoscandia: a review and classification. Silva Fenn 45:823–841. doi: 10.14214/sf.73

Landres PB, Morgan P, Swanson FJ (1999) Overview of the use of natural variability concepts in managing ecological systems. Ecol Appl 9:1179–1188.

Le Goff H, Sirois L (2004) Black spruce and jack pine dynamics simulated under varying fire cycles in the northern boreal forest of Quebec, Canada. Can J For Res 34:2399–2409. doi: 10.1139/X04-121

Liu Z, Yang J, Chang Y, et al (2012) Spatial patterns and drivers of fire occurrence and its future trend under climate change in a boreal forest of Northeast China. Glob Chang Biol 18:2041–2056. doi: 10.1111/j.1365-2486.2012.02649.x

Lotan JE (1976) Cone Serotiny - Fire Relationships in Lodgepole Pine. In: Tall timbers fire ecology conference proceedings 14, Tall Timbers Research Center. Tallahassee, FL, pp 267–278

Luyssaert S, Schulze E-D, Börner A, et al (2008) Old-growth forests as global carbon sinks. Nature 455:213–215. doi: 10.1038/nature07276

Macias Fauria M, Johnson E. (2008) Climate and wildfires in the North American boreal forest. Philos Trans R Soc B Biol Sci 363:2317–2329. doi: 10.1098/rstb.2007.2202

Macias Fauria M, Johnson EA (2006) Large-scale climatic patterns control large lightning fire occurrence in Canada and Alaska forest regions. J Geophys Res 111:1–17. doi: 10.1029/2006JG000181

Mansuy N, Boulanger Y, Terrier A, et al (2014) Spatial attributes of fire regime in eastern Canada: influences of regional landscape physiography and climate. Landsc Ecol 29:1157–1170. doi: 10.1007/s10980-014-0049-4

Mansuy N, Gauthier S, Bergeron Y (2013) Afforestation opportunities when stand productivity is driven by a high risk of natural disturbance: a review of the open lichen woodland in the eastern boreal forest of Canada. Mitig Adapt Strateg Glob Chang 18:245–264. doi: 10.1007/s11027-012-9362-x

Mansuy N, Gauthier S, Robitaille A, Bergeron Y (2010) The effects of surficial deposit-drainage combinations on spatial variations of fire cycles in the boreal forest of eastern Canada. Int J Wildl Fire 19:1083–1098. doi: 10.1071/WF09144

McCarthy J (2001) Gap dynamics of forest trees: A review with particular attention to boreal forests. Environ Rev 9:1–59. doi: 10.1139/a00-012

MFFPQ (2013) Rapport du Comité scientifique chargé d'examiner la limite nordique des forêts attribuables. Québec, QC, Canada

Moss M, Hermanutz L (2009) Postfire seedling recruitment at the southern limit of lichen woodland. Can J For Res 39:2299–2306. doi: 10.1139/X09-150

Oris F, Asselin H, Finsinger W, et al (2014) Long-term fire history in northern Quebec: Implications for the northern limit of commercial forests. J Appl Ecol 51:675–683. doi: 10.1111/1365-2664.12240

Parisien M-A, Parks SA, Krawchuk MA, et al (2014) An analysis of controls on fire activity in boreal Canada: Comparing models built with different temporal resolutions. Ecol Appl 24:1341–1356. doi: 10.1890/13-1477.1

Payette S, Bhiry N, Delwaide A, Simard M (2000) Origin of the lichen woodland at its southern range limit in eastern Canada: the catastrophic impact of insect defoliators and fire on the spruce-moss forest. Can J For Res 30:288–305.

Pham AT, De Grandpré L, Gauthier S, Bergeron Y (2004) Gap dynamics and replacement patterns in gaps of the northeastern boreal forest of Quebec. Can J For Res 34:353–364. doi: 10.1139/x03-265

Podur J, Wotton M (2010) Will climate change overwhelm fire management capacity? Ecol Modell 221:1301–1309. doi: 10.1016/j.ecolmodel.2010.01.013

Rogeau M-P, Armstrong GW (2017) Quantifying the effect of elevation and aspect on fire return intervals in the Canadian Rocky Mountains. For Ecol Manage 384:248–261. doi: 10.1016/j.foreco.2016.10.035

Rogers BM, Soja AJ, Goulden ML, Randerson JT (2015) Influence of tree species on continental differences in boreal fires and climate feedbacks. Nat Geosci 8:228–234. doi: 10.1038/NGEO2352

Ryan KC (2002) Dynamic interactions between forest structure and fire behavior in boreal ecosystems. Silva Fenn 36:13–39.

Saint-Germain M, Drapeau P, Buddle CM (2007) Host-use patterns of saproxylic phloeophagous and xylophagous Coleoptera adults and larvae along the decay gradient in standing dead black spruce and aspen. Ecography (Cop) 30:737–748. doi: 10.1111/j.2007.0906-7590.05080.x

Schmiegelow F, Mönkkönen M (2002) Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. Ecol Appl 12:375–389.

Seymour RS, Hunter Jr ML (1999) Principles of ecological forestry. In: Hunter Jr ML (ed) Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press, Cambridge, UK, pp 22–61

Shorohova E, Kneeshaw D, Kuuluvainen T, Gauthier S (2011) Variability and dynamics of old-growth forests in the circumboreal zone: implications for conservation, restoration and management. Silva Fenn 45:785–806.

Shvidenko AZ, Nilsson S (2000) Extent, distribution, and ecological role of fire in Russian forests. In: Kasischke ES, Stocks BJ (eds) Fire, Climate Change, and

Carbon Cycling in the Boreal Forest. Ecol. Stud. Ser, New York, New York, USA, pp 132–150

Simard M, Bernier PY, Bergeron Y, et al (2009) Paludification dynamics in the boreal forest of the James Bay Lowlands: effect of time since fire and topography. Can J For Res 39:546–552. doi: 10.1139/X08-195

Sirois L (2000) Spatiotemporal variation in black spruce cone and seed crops along a boreal forest - tree line transect. Can J Bot 30:900–909.

Soja AJ, Tchebakova NM, French NHF, et al (2007) Climate-induced boreal forest change: Predictions versus current observations. Glob Planet Change 56:274–296. doi: 10.1016/j.gloplacha.2006.07.028

Stocks B, Fosberg M, Lynham T, et al (1998) Climate change and forest fire potential in Russian and Canadian boreal forests. Clim Change 38:1–13.

Stocks BJ, Mason JA, Todd JB, et al (2003) Large forest fires in Canada, 1959–1997. J Geophys Res. doi: 10.1029/2001JD000484

Terrier A, Girardin MP, Périé C, et al (2013) Potential changes in forest composition could reduce impacts of climate change on boreal wildfires. Ecol Appl 23:21–35. doi: 10.1890/12-0425.1

Terrier A, Paquette M, Gauthier S, et al (2016) Influence of fuel load dynamics on carbon emission by wildfires in the Clay Belt boreal landscape. Forests 8:1–20. doi: 10.3390/F8010009

Van Wagner CE (1978) Age-class distribution and the forest fire cycle. Can J For Res 8:220–227.

Volney WJA, Fleming RA (2000) Climate change and impacts of boreal forest insects.

Agric Ecosyst Environ 82:283–294. doi: 10.1016/S0167-8809(00)00232-2

Waldron K, Ruel J-C, Gauthier S (2013) Forest structural attributes after windthrow and consequences of salvage logging. For Ecol Manage 289:28–37. doi: 10.1016/j.foreco.2012.10.006

Wang X, Thompson DK, Marshall GA, et al (2015) Increasing frequency of extreme fire weather in Canada with climate change. Clim Change 130:573–586. doi: 10.1007/s10584-015-1375-5

Weber MG, Flannigan MD (1997) Canadian boreal forest ecosystem structure and function in a changing climate: impact on fire regimes. Environ Rev 5:145–166. doi: 10.1139/a97-008

Weber MG, Stocks BJ (1998) Forest fires and sustainability in the boreal forests of Canada. Ambio 27:545–550.

Wein RW, MacLean DA (1983) The role of fire in northern circumpolar ecosystems, John Wiley. Toronto

Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW (2006) Warming and earlier spring increase western U.S. forest wildfire activity. Science (80-) 313:940–943. doi: 10.1126/science.1128834

Wotton B, Flannigan M (1993) Length of the fire season in a changing climate. For Chron 69:187–192.

Zhang Q, Chen W (2007) Fire cycle of the Canada's boreal region and its potential response to global change. J For Res 18:55–61. doi: 10.1007/s11676-007-0010-3

Zhang X, Vincent L, Hogg W, Niitsoo A (2000) Temperature and precipitation trends in Canada during the 20th century. Atmosphere-Ocean 38:395–429.