UNIVERSITÉ DU QUÉBEC À MONTRÉAL

DYNAMIQUE DE BOIS MORT EN RÉTENTION FORESTIÈRE LINÉAIRE DE LA FORÊT BORÉALE AMÉNAGÉE DU NORD-OUEST DU QUÉBEC

MÉMOIRE

PRÉSENTÉ

COMME EXIGENCE PARTIELLE

DE LA MAÎTRISE EN BIOLOGIE

PAR

CARINE CÔTÉ-GERMAIN

MARS 2018

REMERCIEMENTS

Mon parcours de maîtrise a été parsemé de défis et de surprises, autant au niveau académique que dans ma vie personnelle. Trois personnes ont joué un rôle essentiel dans l'aboutissement de ce projet à des niveaux complètement différents. L'arrivée de ma fille a causé de grands remous émotionnels et un certain ralentissement académique, mais m'a aussi fait énormément grandir. Elle m'a pourvu d'une meilleure confiance et d'une meilleure organisation, qualités essentielles pour l'aboutissement de ce projet de recherche. Merci Aria d'être arrivée dans ma vie à ce moment précis, malgré les apparences, tu as assurément choisi le meilleur temps. Merci aussi à mon complice de vie, Gabriel, qui a été un inébranlable support au travers les hauts et les bas de ces dernières années transformatrices. Merci pour tous ces repas cuisinés avec amour lors de mes semaines chargées, pour ton aide, tes conseils, et surtout, tes encouragements. Tu as été un allié indispensable. Finalement, un grand merci à mon directeur, Pierre, pour ton côté humain et hautement compréhensif. Malgré deux importants « changements de plans » (la maternité et le déménagement à l'autre bout du pays), tu es demeuré accommodant et je t'en suis très reconnaissante. Merci pour ta confiance en moi, ton support et ta vision scientifique perspicace. J'ai adoré ta façon de travailler, ton laisser-aller un peu déstabilisant au départ nous permet de nous dépasser et de gagner une expérience plus riche de nos projets de recherche.

Plusieurs autres personnes ont participé de façon importante à l'aboutissement de ce document par leurs précieuses connaissances et leurs judicieux conseils. D'abord mon co-directeur, Brian Harvey qui a grandement nourri mes réflexions lors de l'analyse

de mes données. Merci à Alain Leduc pour ton temps et ta grande perspicacité. Merci aux experts de la dendrochronologie, Igor Drobyshev pour la rapidité de tes réponses à mes nombreux courriels, tes conseils et ton expertise; et Virginie-Arielle Angers pour tes idées, tes conseils et ton expérience. J'avais une vague impression de marcher dans tes pas… Merci aussi à Daniel Kneeshaw qui a révisé ma proposition de recherche et qui, fidèle à lui-même, a bousculé mes réflexions et apporté une nouvelle perspective. Merci aussi à tous les professionnels de recherche du CEF qui ont apporté leur précieuse aide à mon projet : Daniel Lesieur, Mélanie Desrochers, Luc Lauzon et François Rousseu.

Finalement, un énorme merci aux aides de terrains et de laboratoire. D'abord Suzie Dubuc, merci pour ton souci du détail, ton dévouement et d'avoir été ma correspondante à distance à l'étape des travaux de laboratoire en dendrochronologie. Ton aide a grandement facilité mon travail alors que j'étais dans les comtés nordiques ! Merci aussi à Anne-Marie Béland, ton sourire et ton humour inébranlable tapissent mes souvenirs de terrain, à Réjean Deschênes, ton expertise et tes histoires auront profondément changé ma façon de faire du terrain, merci aussi pour tes nombreuses attentions. Merci à Audrey Sigouin, Louis-Joseph Drapeau, Frédéric Charron et Thomas Charron.

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RÉSUMÉ

Au cours des trois dernières décennies, l'étude du bois mort dans les forêts du monde a retenu l'attention de la communauté scientifique. En effet, son importance pour la biodiversité est largement documentée, ce qui motive l'industrie forestière et les gouvernements à modifier les pratiques sylvicoles pour conserver une structure de bois mort adéquate au maintien de la faune et de la flore qui y sont associées. Pour ce faire, la forêt boréale du Québec est généralement aménagée par des coupes équiennes avec une rétention d'habitats résiduels entre les aires de récoltes principalement de forme linéaire (séparateurs de coupe et bandes riveraines). L'objet de cette étude est donc d'évaluer la dynamique de bois mort dans ces forêts résiduelles dans le but de (i) caractériser le recrutement de bois et ses facteurs explicatifs sous-jacents au cours de son évolution depuis la coupe (jusqu'à 30 ans), (ii) évaluer la durabilité des habitats linéaires et le potentiel de recrutement de bois mort à long terme et (iii) d'évaluer les patrons de dégradation pour deux espèces d'arbre dominantes dans leurs écosystèmes respectifs (peuplier faux-tremble et épinette noire). L'étude a été réalisée en forêt boréale au nord de l'Abitibi-Témiscamingue. On y a mesuré la structure verticale et horizontale dans 26 séparateurs de coupe et 29 bandes riveraines répartis sur deux sous-domaines bioclimatiques (Sapinière à bouleau blanc et Pessière à mousses de l'Ouest) et couvrant une chronoséquence de temps depuis la coupe de 3 à 30 ans. De plus, des galettes de chicots et de billes au sol de peupliers faux-tremble (PET) et d'épinette noire (EPN) ont été prélevées. La dernière année de croissance de ces galettes a été déterminée par une analyse dendrochronologique. Les résultats montrent que les arbres en bordures de coupe (<6 mètres) sont grandement perturbés par l'ouverture, tandis qu'une largeur minimale de 100 mètres pour les séparateurs de coupe assure une forêt d'intérieur de qualité apte à soutenir un apport continu de bois mort semblable à celui des forêts matures qui forment des massifs. En général, les rétentions étudiées n'étaient pas dans un état de détérioration (disponibilité d'arbres morts sur pied) et démontraient une certaine durabilité à long terme en matière de recrutement de bois mort sur pied. Les patrons de dégradation du peuplier faux-tremble et de l'épinette noire ont montré une certaine vulnérabilité à la coupe forestière, mais la longévité de chicots est similaire aux données reportées dans les études en forêt naturelle pour la même région. Dans l'ensemble, nos résultats indiquent que les aménagements forestiers auraient avantage à élargir les habitats résiduels pour répondre efficacement aux objectifs de conservation de la biodiversité, notamment celle associée au bois mort.

Mots-Clés : Recrutement d'arbres morts sur pied, trajectoires de dégradation du bois, peuplier faux-tremble, épinette noire, rétention forestière linéaire, forêt boréale mixte, forêt boréale résineuse, aménagement durable des forêts, structure de la végétation, conservation de la biodiversité.

SUMMARY

The importance of deadwood for the maintenance of biodiversity and ecosystem functions in forest ecosystems is now widely recognized. Multiple species of fungus, microorganisms, invertebrates, and vertebrates depend on this key structural attribute for their life cycle. This central ecological role is an incentive for forest managers to leave linear retention forests and riparian strips between large cutblocks to mitigate impacts of timber harvesting on biodiversity. Our objective was to assess deadwood dynamics in these linear retention forests by (i) characterizing deadwood recruitment and underlying factors across stand evolution after harvest (up to 30 years), (ii) evaluate the sustainability of these linear retention habitats and their potential for deadwood recruitment in the long-term, and (iii) determine degradation pathways of two dominant tree species (trembling aspen and black spruce). The study was undertaken in the boreal forest of eastern Canada (Abitibi region, Québec). We measured the vertical and horizontal forest structure in 26 cutblock separators and 29 riparian strips in two bioclimatic domains (the black spruce-feathermoss forest and the balsam fir-white birch mixedwood forest) in a post-harvest chronosequence (3 to 30 years). In addition, we collected cross-sections from snags and logs on trembling aspen and black spruce to determine the last year of growth by dendrochronological analysis. Results show that trees close to harvest edges (< 6 meters) are strongly disturbed by the opening; however, habitat quality (standing deadwood availability) and sustainability (standing deadwood recruitment) in 100 meter-wide cutblock separators are in line with interior forest conditions. A key finding of this study is that linear retention habitats maintained structural attributes 30 years after harvesting, thus providing important biological legacy habitats to regenerating forest landscapes where deadwood recruitment was persistent. For both tree species, degradation patterns of standing dead stems were slightly more vulnerable in linear retention habitats than in continuous unharvested forests. However, the longevity of snags was similar to those in natural unmanaged forests. Overall, we conclude that forest management should increase linear retention width in order to increase the efficiency of biodiversity conservation measures in managed forest landscapes.

Keywords: Standing deadwood recruitment, deadwood degradation pathways, boreal mixedwoods, black spruce forest, trembling aspen, sustainable forest management, linear retention habitats, forest structure, biodiversity conservation.

INTRODUCTION GÉNÉRALE

L’importance du bois sénescent et mort pour la qualité des écosystèmes forestiers n’est plus à prouver, puisqu’au cours des trois dernières décennies les recherches sur ses fonctions écologiques se sont multipliées (Harmon et al. 1986, Franklin et al. 1987, Stokland 2001, Boucher et al. 2006, Drapeau et al. 2009b, Nappi and Drapeau 2009, Lassauce et al. 2011). L’apport structurel et alimentaire du bois mort ainsi que son rôle dans plusieurs processus biogéophysiques sont maintenant fortement documentés (Harmon et al. 1986). Une panoplie d’organismes forestiers s’installent et se succèdent à différentes étapes de la décomposition de l’arbre (Franklin et al. 1987). Les champignons sont parmi les premiers colonisateurs avec une proportion de cellules fongiques pouvant atteindre 35% de la biomasse d’un tronc mort (Swift 1973). Les insectes saproxyliques arrivent aussi très tôt dans la décomposition de l’arbre. Ils se définissent comme organisme dépendant, pour une partie ou la totalité de son cycle de vie, du bois mort ou sénescent ou encore d’un autre organisme qui en dépend (Speight 1989), et représentent 20 à 25% des espèces forestières (Elton 1966, Siitonen 2001). Les vertébrés sont aussi de grands utilisateurs de bois mort et sénescent. C’est le cas notamment des oiseaux cavicoles qui représentent une large proportion de la faune aviaire et qui ont fait l’objet de nombreuses études (Villard 1994, Eberhardt 1999, Martin and Eadie 1999, Imbeau and Desrochers 2002, Drapeau et al. 2009b, Nappi and Drapeau 2009, Ouellet-Lapointe et al. 2012, Cadieux and Drapeau 2017). Parmi eux, les pics sont reconnus à la fois comme des espèces clés et parapluies (Roberge et al. 2008) car ils créent des gites pour de nombreux utilisateurs de cavités : canards nicheurs, passereaux, oiseaux de proies et mammifères (Martin and Eadie 1999). Leur maintien dépend fortement de la disponibilité de bois sénescent et mort sur pied à différents stades de dégradation essentiels à l’ensemble de leurs activités vitales comprenant leur alimentation, leur habitat et le tambourinement (Eberhardt 1999, Imbeau and Desrochers 2002, Drapeau et al.

2009b, Nappi and Drapeau 2009). Le bois mort au sol, quant à lui représente une structure importante pour plusieurs petits mammifères et amphibiens et reptiles en tant que corridors de déplacement et de connectivité des habitats (Kimmins 2001). Certains végétaux comptent aussi parmi les utilisateurs de bois mort et sénescent, les troncs morts (au sol ou debout) représentent l'élément structurel le plus important pour les cryptogames menacés en milieu forestier (Berg et al. 1994). Une centaine d'espèces de mousses, hépatiques et lichens ont été identifié seulement sur l'épicéa commun en Suède (Kruys et al. 1999). Certaines espèces de plantes vasculaires, comme le bouleau jaune et le thuya occidental ont une plus grande facilité à germer et à croître sur les troncs et souches en décomposition qui deviennent une source de nutriments (Harmon et al. 1986, Franklin et al. 1987, Houle and Payette 1990; Robert et al. 2012). La disponibilité en bois sénescent et mort concerne donc l'ensemble des groupes d'organismes retrouvés en milieux forestiers. En plus de la quantité, la qualité de cette ressource doit être considérée dans les stratégies d'aménagement afin de maintenir l'ensemble des organismes associés au bois mort.

La production de bois mort est intimement liée à la dynamique de mortalité des arbres ce qui est liée au régime de perturbation spécifique à une région donnée. Certaines perturbations comme les feux ou les épidémies d'insectes peuvent générer une abondance de bois mort sur un très vaste territoire (Blais 1983, Morin et al. 1993, Bergeron et al. 2001, Perron 2003). En contrepartie, si les intervalles entre ces perturbations sont plus longs que la longévité des arbres, ces peuplements sont soumis à des perturbations secondaires comme le vent, la suppression, les insectes ou la sénescence naturelle. Ces perturbations sont plus petites et plus locales. Elles génèrent une dynamique de trouées liée à l'ouverture du couvert forestier par pied d'arbre (Kneeshaw and Bergeron 1998, McCarthy 2001, Pham et al. 2004). Ces dynamiques ont une influence dans l'espace déterminant une distribution spatialement agrégée ou dispersée du bois mort, mais aussi dans le temps puisque la cause de mortalité est un facteur déterminant dans la longévité des chicots (Taylor and MacLean 2007, Parish et al. 2010). Les principaux facteurs influençant la mortalité des arbres sont l'âge du peuplement et des arbres individuels, la densité et la productivité du site, les espèces présentes et leur taille (Bull et al. 1980, Franklin et al. 1987, Sturtevant et al. 1997, Hély et al. 2000, Stokland 2001, Ferguson and Archibald 2002, Parish et al. 2010). Les arbres d'une forêt jeune et équienne peuvent mourir par suppression qui résulte de la compétition entre les tiges pour les ressources et crée généralement une grande densité de chicots de petits diamètres (Hély et al. 2000, Parish et al. 2010). Au fur et à mesure que la forêt vieillit, les taux de mortalité diminuent et les causes se complexifient (Franklin et al. 1987). En général, la densité d'arbres morts sur pied diminue avec le temps, mais la proportion de gros chicots augmente (Cline et al. 1980). Ainsi, au cours des successions végétales, la structure de la forêt se diversifie par la création d'une canopée à plusieurs étages et la disponibilité de bois mort sous diverses formes (Cline et al. 1980, Harper and Macdonald 2002, Pham et al. 2004). De la sorte, les vieilles forêts fournissent des habitats uniques car elles sont fortement associées aux arbres et chicots à grand diamètre dont plusieurs animaux cavicoles dépendent (Cline et al. 1980, Harmon et al. 1986, Sturtevant et al. 1997, Clark et al. 1998, Lee 1998, Siitonen et al. 2000, Ferguson and Archibald 2002). De plus, les forêts inéquiennes ont généralement l'avantage de produire du bois mort de façon constante dans toutes les classes de diamètre et de dégradation (Lee 1998, Stokland 2001).

En Amérique du Nord, l'aménagement écosystémique, un concept visant à s'inspirer des perturbations naturelles afin de réduire les écarts entre la forêt aménagée et la forêt naturelle, est de plus en plus préconisé (Gauthier et al. 2008). Toutefois, la mise en œuvre de cette approche dans la planification forestière n'en est qu'à ses débuts et ce, même si plusieurs études ont démontré des différences majeures entre les forêts sous l'influence de perturbations naturelles et les forêts aménagées (Franklin et al. 2000, Bergeron et al. 2007, Cyr et al. 2009, Dragotescu and Kneeshaw 2012), notamment dans la proportion de forêts âgées. Des études en forêt naturelle de l'est du Canada ont montré que les cycles de feux sont en moyenne plus long que 100 ans et que la structure d'âge des forêts est constituée de plus de 50% de peuplements centenaires et plus de 15% sont bicentenaires (Bergeron et al. 2001). L'aménagement équiens en forêt boréale québécoise, quant à lui, prévoit une révolution forestière de 100 ans ou moins. L'objectif sylvicole consiste à réduire la structure d'âge des peuplements à des forêts qui ne dépassent pas l'âge de maturité commerciale (100 ans) pour être récoltés. Cette approche d'aménagement, fondée sur une normalisation de la structure d'âge des forêts, entraine une diminution considérable de la proportion de peuplements matures et surannés dans les paysages aménagés (Bergeron et al. 2002, Cyr et al. 2009). Or, comme déjà mentionné, les vieilles forêts sont fortement associées à la disponibilité d'arbres et chicots à grand diamètre essentiels à plusieurs organismes forestiers (Cline et al. 1980, Harmon et al. 1986, Sturtevant et al. 1997, Clark et al. 1998, Lee 1998, Siitonen et al. 2000). Ce rajeunissement du paysage menace donc les organismes associés au bois mort via la perte de diversité dans la structure verticale et horizontale (Boucher et al. 2006, Drapeau et al. 2009b).

Le gouvernement du Québec oblige les compagnies forestières à laisser des lisières boisées d'un minimum de 20 mètres de largeur en bordure de lacs et rivières (bandes riveraines) et de 60 à 100 mètres de largeur entre les aires de coupe (séparateurs) (Quebec government, 2015). Ces rétentions linéaires servent d'habitats refuges pour les organismes dépendants des forêts âgées car ils peuvent représenter les seuls habitats de ce type de couvert forestier sur plusieurs centaines de km^2 (Franklin 1993, Franklin et al. 2000). L'importance écologique de ces peuplements résiduels nécessite qu'on leur accorde une attention particulière afin de s'assurer que les éléments structurels retrouvés en forêt naturelle soient bien représentés dans les forêts aménagées pour permettre le rétablissement de l'écosystème. Or, les ouvertures créées par la coupe forestière engendrent un effet de bordure sur les peuplements en périphérie. Bien que les rétentions linéaires peuvent faciliter la connectivité des habitats servant à la dispersion des espèces dans les paysages fragmentés par la coupe

(Andren 1994, Franklin et al. 2000, Debinski and Holt 2000, Bennett 2003), la quantité de forêt d’intérieur y est réduite en raison du ratio élevé périmètre/superficie (Mascarúa López et al. 2006, Harper et al. 2016). L’un des impacts majeurs de l’effet de bordure consiste en une augmentation du taux de mortalité des arbres dans les forêts résiduelles, celui-ci peut être multiplié par un facteur de 2 à 4 selon les espèces, au cours des années suivant la récolte (Darveau et al. 1994, Esseen 1994, Bladon et al. 2008).

La dynamique du bois mort, sujet d’actualité dans le domaine de la biologie de la conservation, permet de comprendre la complexité de cet élément à diverses échelles spatiales et temporelles. Cette compréhension est essentielle, d’abord parce qu’elle permet une meilleure évaluation de la biodiversité potentiellement présente en paysage aménagé, mais aussi pour aider les forestiers et gestionnaires gouvernementaux responsables de la planification forestière qui s’inquiètent de plus en plus de la disponibilité du bois mort sur leur territoire d’affectation (Drapeau et al. 2002, MFFP 2005, Angers 2009).

À l’échelle du peuplement, l’étude de la dynamique du bois sénescent et mort consiste à mesurer, quantifier et caractériser l’apport en bois mort, sa répartition structurelle, sa diversité en stade de décomposition et le potentiel de recrutement, ainsi que les facteurs influençant ces processus. Elle permet d’évaluer la structure horizontale et verticale d’un peuplement sur une échelle spatiale ainsi que d’émettre des prévisions à plus ou moins long terme sur son évolution. À l’échelle de l’arbre, les patrons de mortalité et de dégradation des arbres sont propres à chaque espèce et permettent une évaluation plus fine de la dynamique opérée dans les écosystèmes (Alban and Pastor 1993, Garber et al. 2005, Brais et al. 2006, Aakala et al. 2008, Angers 2011). Ces patrons de dégradation se dessinent par la cause de mortalité préférentielle, la longévité des chicots, le taux de décomposition du bois et le parcours des tiges au travers des classes de dégradation. La longévité des chicots traduit le temps de rétention de cette structure éphémère et influence la densité retrouvée dans les peuplements (Keen 1929, 1955, Cline et al. 1980, Lee 1998, Everett et al. 1999, Storaunet and Rolstad 2002, Garber et al. 2005, Angers et al. 2010). La décomposition des tiges est un processus lent et difficile à mesurer car elle dépend de plusieurs facteurs biotiques et abiotiques (Erickson et al. 1985, Harmon et al. 1986, Alban and Pastor 1993). Calculer la perte de densité du bois mort permet une certaine évaluation de son temps de rétention dans l'écosystème (Johnson and Greene 1991, Alban and Pastor 1993, Krankina and Harmon 1995, Harmon et al. 2000, Brais et al. 2006). Ces processus sont fortement influencés par la cause de mortalité et leur position dans l'écosystème (Johnson and Greene 1991, Storaunet and Rolstad 2002, Garber et al. 2005).

Les études de la dynamique du bois mort en forêt naturelle de l'Ouest du Canada sont nombreuses (Spies et al. 1988, Johnson and Greene 1991, Clark et al. 1998, Lee 1998, Huggard 1999). Il en est de même pour la forêt boréale de l'Est non aménagée (Paré and Bergeron 1995, Hély et al. 2000, Brais et al. 2005, Boulanger and Sirois 2006, Aakala et al. 2007, 2008, Angers et al. 2010). Quelques études ont été effectuées en forêt aménagée (Cline et al. 1980, Garber et al. 2005, Parish et al. 2010), mais très peu en forêt boréale aménagée de l'Est du Canada (Ferguson and Archibald 2002, Mascarúa López et al. 2006, Moussaoui et al. 2016).

La forêt boréale du Québec est aménagée depuis plus de trente ans au moyen de grandes agglomérations de coupes équiennes séparées par des habitats linéaires de forêts résiduelles. La présente étude vise à évaluer la dynamique du bois mort dans ces habitats résiduels linéaires dans les domaines bioclimatiques de la forêt mixte de sapinière à bouleau blanc et de la forêt coniférienne de la pessière à mousses de l'Ouest du Québec.

Cette étude vise à approfondir nos connaissances sur la qualité, la quantité et la diversité du bois mort dans les séparateurs de coupe et les bandes riveraines au sein des agglomérations de coupes. De plus, une approche de chronoséquence permet d'évaluer la dynamique temporelle du bois mort dans les habitats linéaires en substituant le temps par l'espace et en échantillonnant des rétentions créées le long d'un gradient qui va de 3 à 30 ans après la coupe. Notre analyse s'effectue donc à deux échelles, il y a d'abord une caractérisation à l'échelle des peuplements de la structure du couvert forestier dans les habitats résiduels. Nous analysons ensuite à l'échelle de l'arbre, la dynamique du bois mort au moyen d'une approche dendrochronologique par le prélèvement de galettes d'arbres sur les chicots et les billes au sol. Ce mémoire est divisé en deux chapitres ; nos objectifs pour le premier chapitre sont : (1) de caractériser le recrutement de bois dans les peuplements résiduels en termes de qualité et quantité au cours de son évolution post-coupe, en démontrant les principaux facteurs en jeux, et (2) d'évaluer la durabilité des habitats linéaires en ce qui concerne la structure du couvert forestier et le potentiel recrutement de bois mort. Dans le deuxième chapitre, nous évaluons la dynamique du bois mort pour deux espèces d'arbre dominant dans leur domaine bioclimatique respectif (peuplier faux-tremble en forêt boréale mixte et épinette noire en pessière à moussses).

CHAPTER I

DEADWOOD DYNAMICS IN LINEAR RETENTION IN MANAGED BOREAL FORESTS IN NORTHWESTERN QUEBEC

1.1 INTRODUCTION

Most of the commercial boreal forest in Canada is under an even-aged harvesting regime with a dispersed forest retention (Bergeron and Harvey 1997, Drapeau et al. 2009a, Gauthier et al. 2009, 2015a). This management regime leads to landscape rejuvenation with the overrepresentation of regenerating stands and the concurrent reduction of mature and old-growth forests (Drapeau et al. 2000, 2016, Bergeron et al. 2002, Gauthier et al. 2009) in comparison with the natural disturbance regime under which the boreal forest has evolved (Johnson and Van Wagner 1985, Delong and Tanner 1996, Bergeron et al. 2001, 2002, 2004a, 2017). The reduction of old forests and the concomitant simplification of stand structure in managed forests (less heterogeneity in the vertical and horizontal structure, fewer large old trees, decaying trees and deadwood) are among the persistant concerns with regard to biodiversity conservation (Franklin et al. 2002, Boucher et al. 2006, Drapeau et al. 2009a, Stokland et al. 2012, Kuuluvainen et al. 2015). Coarse woody debris, including large standing or downed dead trees, are key attributes found in old-growth forests, critical for numerous organisms (Cline et al. 1980, Harmon et al. 1986, Berg et al. 1994, Sturtevant et al. 1997, Lee 1998, Siitonen 2001, Imbeau and Desrochers 2002, Ferguson and Archibald 2002, Drapeau et al. 2009b, Stokland et al. 2012).

In managed boreal forest landscapes, habitat retention can serve as a lifeboat for organisms associated with old forests. That may represent the last remaining fragment of old stands across several hundreds of square kilometers (Franklin 1993, Franklin et al. 2000). This retention may take the form of islands and patches in the middle of a large aggregated clearcuts or be organized in linear retention strips (riparian buffers along watersways and cutblock separators of different widths between clearcut areas). In Québec, linear retention has become the most prevalent mode of forest retention in managed forest landscapes since the 1980's (Quebec government, 2015). Linear retention provides a level of connectivity (travel corridors) between unharvested habitats, thus assisting dispersal for some species throughout fragmented landscapes (Andren 1994, Franklin et al. 2000, Debinski and Holt 2000, Bennett 2003). Conversely, linear retention is likely to be more vulnerable to edge effects due to their high perimeter-area ratio and general absence of core habitat (Mascarúa López et al. 2006, Harper et al. 2016). The extent of edge influence is significant in linear habitats in the eastern black spruce forest in that it can affect the entire habitat when the residual forest is too narrow (Mascarúa López et al. 2006).

Edge-effects in linear retention could thus alter the long-term capacity of these habitats for biodiversity throughout the reconstruction phase of forest cover in cutover areas. Tree dynamics may be altered first by strongly increasing the mortality rate of stems in the initial years after harvest (Darveau et al. 1994, Esseen 1994, Harper et al. 2005, Bebber et al. 2005, Bladon et al. 2008, Lavoie et al. 2012) and second, by modifying the factors driving tree mortality and degradation, such as humidity, wind exposition, temperature variations, and soil disturbance (Erickson et al. 1985, Chen et al. 1995, Harper and Macdonald 2002). Other factors that influence tree mortality are stand age, tree density, tree species and size (Bull et al. 1980, Franklin et al. 1987, Sturtevant et al. 1997, Hély et al. 2000, Stokland 2001, Ferguson and Archibald 2002, Parish et al. 2010). Along riparian forests in boreal mixedwood forests, beaver activity can strongly affect deciduous tree survival. Tree mortality degradation processes can be altered by felling or flooding of live trees that do not show any sign of senescence (Naiman et al. 1986, Nummi and Kuuluvainen 2013). Linear retention strips are generally vulnerable to uprooting due to increased wind exposure. Levels of downed woody debris tend to be greater at the edges of linear habitats compromising standing dead wood recruitment (Ruel et al. 2001, Lavoie et al. 2012). Furthermore, uneven-aged forest tends to produce deadwood continually across diameter and degradation classes (Lee 1998, Stokland 2001). Deadwood dynamics in a territory with even-aged management is not likely to follow such a pattern; thus, sustainability of deadwood recruitment is not ensured. Persistence of vertical and horizontal structure in linear retention may be jeopardized. In addition to directly affecting existing stand structure of living trees, a pulse in deadwood recruitment following the creation of linear retention may reduce future recruitment. Several studies have examined deadwood in dispersed and grouped forest retention in clearcut landscapes (Cline et al. 1980, Bebber et al. 2005, Bladon et al. 2008, Lavoie et al. 2012, Urgenson et al. 2013), and in linear retention (Mascarúa López et al. 2006, Braithwaite and Mallik 2012). A better understanding of live and dead tree dynamics, key drivers of vertical and horizontal heterogeneity of forests in linear retention, is critical for evaluating whether these habitats can provide old forest conditions with regards to standing decaying and dead wood over the long-term for organisms that are dependent on tree decay processes (Thorpe and Thomas 2007, Moussaoui et al. 2016). To do so we will evaluate how deadwood recruitment in linear retention changes over time after harvesting.

We use a chronosequence approach to measure changes in stand structure and deadwood recruitment in linear retention (cutblock separators and riparian buffers) created over a period of 35 years. These habitats are situated in managed boreal mixedwood and coniferous forest landscapes in northwestern Quebec characterised by aggregated clearcuts. More specifically we (1) measure the main factors driving deadwood recruitment, (2) document the vertical and horizontal structure of deadwood components in these linear retention strips, and (3) evaluate the sustainability of these habitats for long-term recruitment of standing deadwood of quality (dbh and decay classes) for biodiversity. We hypothesize that tree mortality will be higher near the edges of linear retention, and that the orientation of retention strips will influence tree mortality. We predict that riparian buffers will be more resistant to edge effects particularly with regards to uprooting, and that the complexity of the vertical structure and long-term ability of these habitats to maintain old forests attributes will be higher than in cutblock separators.

1.2 METHODS

1.2.1 Study Area

The study was conducted over a vast territory of the managed boreal forest in northwestern Quebec in Abitibi and south of Nord-du-Quebec (78°30’ – 79°30’ W, 48° 00’ – 50°00’N) (Figure 1.1) where two sub-bioclimatic domains meet: a mixedwood ecosystem in the south, the balsam fir-white birch forest, and a predominantly coniferous ecosystem in the north, the black spruce-feathermoss forest (Saucier et al. 2003). The study region is located in the Northern Clay Belt, a major physiographic region created by proglacial lake depositions of lakes Ojibway and Barlow during the last glacial period (Vincent and Hardy 1977, Harvey and Leduc 1999). The region is characterized by a relatively flat topography; mean temperature varies between 0°C and 2.5°C, annual precipitations between 800 and 900 mm and the growing season lasts from 150 to 160 days (Harvey and Leduc 1999).

Following a major disturbance such as fire, the balsam fir-white birch forest is initially dominated by shade-intolerant deciduous species such as trembling aspen (*Populus tremuloides*) and white birch *(Betula papyrifera*) on mesic sites. Coniferous species, balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), black spruce (*Picea mariana*) and northern-white cedar (*Thuja occidentalis*) gradually recruit into the canopy as stands age (Bergeron and Dubuc 1989, Harvey et al. 2002). Natural disturbances include fire (Bergeron et al. 2004a), and insect outbreaks such as spruce budworm and tent caterpillar (Morin et al. 1993, Cooke and Lorenzetti 2006). The fire cycle in the mixedwood part of the study area vary from 100 to more than 1000 years (Bergeron et al. 2001, Gauthier et al. 2015b); last major fires occurred in 1760 and 1923 (Bergeron 1991, Dansereau and Bergeron 1993). Spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks are not as harmful as in the east of the province but are still a threat to balsam fir and, to some extent, black and white spruce (Bouchard et al. 2005). The last outbreak in this region occurred between 1972 and 1996 (Bouchard et al. 2005; Morin et al 1993). The forest tent caterpillar (*Malacosoma disstria* (Hbn.)) affects growth and survival of trembling aspen and other deciduous species. Outbreaks occur approximately every 10 years in this region, with the last major epidemic taking place in the late 1990's – early 2000's (Cooke and Lorenzetti 2006). Signs of an outbreak started to appear towards the end of our sampling season.

The black spruce-feathermoss forest is dominated by black spruce and jack pine (*Pinus banksiana*) with a lower occurrence of balsam fir and intolerant deciduous species (Gauthier et al. 2000). Fire cycle in this region vary from 600 to 800 years (Gauthier et al. 2015b), and mean area burnt is larger in the coniferous forest than the mixedwood forest (Bergeron et al. 2004b). After fire, when present in the buried forest, jack pine dominates the regenerating stand in association with black spruce (Harper et al. 2003). As stands age, paludification occurs on lowlands and flat sites. The process is an accumulation of organic matter associated with slow drainage, and resulting in limited access to nutrients in the mineral soil (Simard et al. 2007). These conditions provide competitive advantages black spruce that dominates stands (Gauthier et al. 2000). The relatively low presence of balsam fir diminishes the importance of spruce budworm in the black spruce forest, and hence, in the absence of fire, secondary disturbances such as wind-related death, diseases and senescence tend to influence stand dynamics and structure (Kneeshaw and Bergeron 1996, Gauthier et al. 2000, Harper et al. 2002).

The boreal forest is generally managed in an even-aged regime in which retention habitats such as island patches, riparian strips, and cutblock separators are left in or around large harvest blocks. Our study concentrates on these last two types of retention. According to Québec forest regulations, riparian strips must be at least 20 meters wide whereas cutblock separators can vary between 60 to 100 meters wide, depending on the size of neighbouring even-aged cut areas (Quebec governement, 2015). The oldest cutover areas found with linear retention in our study region were between 30 and 40 years old in the mixed and coniferous forests, respectively (Figure 1.2).

1.2.2 Data Collection

Sites were selected a priori using ArcGIS software and digital forest inventory provided by the government of Quebec (1:20 000). Site selection was based on tree species composition (trembling aspen as dominant in the mixedwood forest; black spruce as dominant species in the coniferous forest), soil type, drainage, canopy cover (≥60%) and stand age (≥80 years old). Further selection criteria were retention type (riparian strip or cutblock separator) and time of harvest of adjacent cuts. In the balsam fir-white birch mixedwood bioclimatic zone, we sampled 14 cutblock separators and 14 riparian strips, while 12 cutblock separators and 15 riparian strips were sampled in the black spruce-feathermoss zone. Sites were also selected to encompass the entire period in which aggregated clearcuts and linear retention were part of Quebec's management regime (Figure 1.2) (Quebec government, 2015). Each site was sampled using three or four rectangular plots of 6 m X 70 m aligned parallel to the linear retention, one along each edge and one or two in the middle of the strip depending on the width of the retention. Each plot was separated by 30 meters to ensure plot independence. Typically, riparian strips had one plot in the middle, one plot along the harvest edge and one plot along the stream side edge, whereas the cutblock separators had two plots in the middle and one plot on each edge side of clearcuts.

Data collection on trees was conducted in the summer of 2015 and consisted of characterizing the structure of live trees, standing dead trees and downed coarse woody debris (CWD). For each standing stem (alive or dead) with a diameter at breast height greater than 9 centimeters (merchantable size), we noted tree species, diameter at breast height (dbh) and degradation stage based on Imbeau and Desrochers' (2002) classification system for conifers and an adapted version for deciduous trees. In addition, for standing dead trees, we noted height with a clinometer, stem state (whole or broken), abundance of branches and twigs and bark cover by visual inspection and wood penetrability by inserting a knife into the wood in several locations around the bole between 1 and 1.3 m using the approach proposed by Angers et al. (2012a).

Downed coarse woody debris data was collected the same summer following to the line-intercept method (Harmon and Sexton 1996). Line intercepts ran the full length of sample plots and were positioned parallel to the retention strip on the inner side of edge plots or in the middle of center plots. The total length per site of line intercepts was 210 meters in riparian strips and 280 meters in cutblock separators. All downed deadwood $\geq$9 cm crossing the intercept was measured. Downed tree characteristics measured were: diameter at intercept (used for volume calculation), tree species, decay class using Desponts et al. (2002) classification system, length, state (uprooted, broken or beaver-related death), azimuth, wood penetrability, % bark cover and abundance of branches and twigs. Leaning dead trees were considered as downed deadwood if they formed an angle lower than 45^{o} with the ground (Harmon and Sexton, 1996). Beaver marks on dead trees were also noted.

To determine the exact stand age, we sampled cores below one meter in 5 dominant trees per site in coniferous study sites and of 10 dominant trees per site in mixedwood sites. We also measured the organic layer thickness (cm) and the width of linear retention in the middle of every plot (m) (Table 1.1).

1.2.3 Volume calculation

Live stand volume was calculated using Fortin et al. (2007) model. To do so, we used Poulin and Messier (2006) equation for a dbh–height relationship because only dbh was measured in the field. Parameters for most species were established by previous studies (Poulin and Messier 2006, Fortin et al. 2007, Ste-Marie 2009). However, some less common species have never been subject to allometric studies, and in those cases, we used the parameters of the most similar species (for instance, trembling aspen's parameters were used for balsam aspen). Standing deadwood volume was calculated depending on tree degradation class. Less degraded trees (classes 4 and 5) generally retain their branches and full height, therefore volume was calculated as for living trees (Fortin et al. 2007). For the more degraded dead trees (classes 6, 7 and 8), the volume was calculated using a cylinder volume equation. Volume of downed deadwood was calculated following the equation from Harmon and Sexton (1996):

$$\mathrm{V} = 9.869\,\frac{(\text{Diameter at intercept})^2}{8\cdot(\text{Length of line sampled})}$$

1.2.4 Statistical analyses

Separate analyses were conducted on data from each bioclimatic zone. Recent deadwood recruitment was characterized by summing early decay classes, of standing (4 and 5) and downed wood (9 and 10) (Table 1.1). Angers et al. (2012a) showed that decay class was a fairly good indication of time since death for the studied species. Because initial stand volume (ISV) represents living tree volume at the time of creation of the linear retention, it is calculated by summing current living volume and recent recruitment deadwood volume. All statistical analyses were performed using R software (R core Team 2014).

1.2.4.1 Recent deadwood recruitment drivers

Model selection based on Akaike's information criterion was conducted to determine the factors associated with deadwood recruitment (Burnham and Anderson 2002). Stand age, initial stand volume (ISV) and the presence of beaver activity are important factors driving tree mortality (Sturtevant et al. 1997, Hély et al. 2000, Ferguson and Archibald 2002, Nummi and Kuuluvainen 2013, Moussaoui et al. 2016); therefore, these factors were part of our basic model, a linear mixed effect model fit by maximum likelihood (Aitchison and Silvey 1957, Pinheiro et al. 2008). Sites were included as random effects due to our nested sampling design. Assumptions of normality and homoscedasticity were verified graphically; normality of random effects was also verified with a Shapiro test on intercepts. An extreme value (one plot) was identified in the mixed wood forest dataset and was thus removed with respect to these statistical assumptions. Square-root transformation was performed on the response variable to improve the residuals distribution. The additional factors tested in model selection were retention type, time since harvest (TSH), site width (SW), orientation (OR), plot location (PL: harvest edge, center, or stream side edge) and organic layer thickness (OL). Assumptions were again verified graphically to ensure the validity of every mixed effect linear model used in this analysis. The independence of the explanatory variables was verified using Pearson correlation. We built the best model by stepwise model selection, and model comparisons were made using the second-order Akaike information criterion (AICc) (Burnham and Anderson 2002). At first, we added every additional factor to our basic model separately, making six new models. If one factor improved the basic model (lower AICc), we made a second model selection with that new model and added a second additional factor. We repeated these steps until adding a factor or interaction did not improve the model. A model was considered to improve the basic model if it diminished the AICc by 2 or more. The best model for each forest type was then examined to assess the effect of each variable on deadwood recruitment with unconditional 95% confidence intervals and P-value.

1.2.4.2 Effects of retention width

While tree mortality along *edges* of linear retention habitats has been documented (Mascarúa López et al. 2006), and is unlikely to differ with width of linear retention, this may not be the case for deadwood recruitment at the *center* of linear retention strips. A linear mixed effect model (Pinheiro et al. 2008) was used with the data subset containing only the middle plots to evaluate the influence of retention width influence on deadwood recruitment in the middle of our linear retention strips. Site was included as a random effect since two plots were sampled in the middle of each cutblock separator. Assumptions of normality and homoscedasticity were verified graphically, the normality of random effects was also verified with a Shapiro test on intercepts. A log transformation on recent deadwood volume, the response variable, was performed to improve the residuals distribution (log (1+y)).

1.2.4.3 Spatial distribution of standing and downed deadwoods

Vertical and horizontal deadwood structure was assessed using the recent snag volume as a proportion of recent deadwood volume. Differences in the spatial distribution of snags were assessed by comparing the proportion measured in the middle and at the edges using ANOVA. Harvest edges were compared with the center of cutblock separators, whereas comparisons were made among stream side edge, harvest edge and center of riparian buffer strips.

1.2.4.4 Long-term sustainability for deadwood recruitment

To evaluate the sustainability of standing deadwood recruitment in linear retention strips, we used Moussaoui et al (2016) graphic approach of dead versus live volume in order to compare our sites with threshold values found in nearby natural forests.

1.2.4.5 Poplar in southern boreal mixedwood forests

Assessment of the sustainability of standing dead tree recruitment in the mixedwood forest focused on poplar species (primarily trembling aspen, but including some balsam poplar) in the form of standing dead trees with a large dbh (≥20 cm), since those are a deadwood component of primary importance for the cavity-using community (Cadieux 2011, Ouellet-Lapointe et al. 2012, Nappi et al. 2015). A descriptive graphic analysis was performed using proportion of standing dead poplar trees ≥ 20cm dbh over the total number of poplar trees with dbh ≥ 20cm. We eliminated sites containing less than five large aspen stems to evaluate tree dynamics in aspen-dominated stands specifically. Rather than applying a threshold, we used range values (mean ± standard deviation) found in natural forests in the same study area (Y. Bergeron's permanent plot data base in Lake Duparquet Forest). Mean (and sd values) proportion of standing dead poplar in natural forest stands was calculated from this database using aspen-dominated sites where stand age varied between 71 and 145 years old. This range was used as our "natural variability" and was plotted on the descriptive graphic with our sample sites for comparison. Those that were found outside of this natural variability showing an overproduction of deadwood could be an indication of the next cohort taking over the stands (Bergeron and Dubuc 1989), whereas sites below this natural variability would be deprived of this important deadwood component, which is large standing dead trees. Investigation of the diametrical distribution was also completed to better understand the stand stage and project future deadwood recruitment.

Live tree volume was plotted on the y-axis with a lower threshold of 100 m^3/ha under which the mixedwood forest canopy is considered open and unproductive. Any site below that threshold would not likely provide much deadwood in the long-term.

1.2.4.6 Black spruce in northern coniferous forests

The proportion of recent deadwood (recent deadwood volume relative to initial stand volume) expected in the natural forest was calculated by incorporating black spruce mortality rate and deadwood retention time of black spruce trees in the first degradation stages for the coniferous forest. Black spruce has a relatively constant mortality rate of 1-2 % per year (Lussier et al. 2002, Bouchard et al. 2005, Aakala et al. 2007) and a persistence time in the first degradation stages ranging between 5 and 15 years (Angers et al. 2012a). A proportion of recent deadwood volume exceeding a maximum threshold of 30% would thus indicate long-term recruitment of dead trees in linear retention strips is not sustainable (Moussaoui et al. 2016). Moreover, recent deadwood volume proportions exceeding this threshold value could potentially indicate a collapse of the linear retention towards an open canopy. Live volume threshold for the coniferous forest was set to 60 m^3/ha (Moussaoui et al. 2016). Mature stands dominated by black spruce with lower timber volumes generally have open canopies and low productivity.

1.3 RESULTS

1.3.1 Recent deadwood recruitment drivers

Parameters included in the model selection analyses involved continuous (Table 1.1) and discrete (Table 1.2) variables. Stand age varied from 67 to 124 years old in the mixedwood forest and from 89 to 176 years old in the coniferous forest. Initial stand volume and recent deadwood volume were higher in riparian buffer strips than in cutblock separators for both bioclimatic domains (Table 1.1). Organic layer thickness was mainly below 10 cm in the mixedwood forest, and between 10 and 20 cm in the coniferous forest. Beaver occurrence was only observed in mixedwood riparian strips (Table 1.2). Retention type, orientation, and organic layer thickness did not have a significant influence on deadwood recruitment.

In mixedwood linear retention sites, PL and TSH significantly improved our basic model (Table 1.3). Recent deadwood volume was significantly lower in the center (-2.55 ± 1.64) and along stream side edges (-2.04 ± 1.08) than along harvested edges. Deadwood recruitment increased significantly with time since harvest (0.10 ± 0.08) although high variability was observed in the first 20 years following harvesting (Figure 1.3). Linear regression slope was strongly influenced during the first two decades whereas older sites did not appear to follow the same trend; i.e. lower deadwood recruitment in third decade. Beaver occurrence and initial stand volume also significantly increased recent deadwood volume as expected. In contrast, stand age within the range covered in this study did not show a significant effect, indicating that our preliminary site selection design controlled well for stand age differences (Table 1.1).

In the coniferous forest, beaver occurrence was not included in the base model due to a weak occurrence while the other two base model parameters (stand age and initial stand volume) both increased significantly recent deadwood volume while. The best model in the coniferous forest included plot location as the only additional factor with a significant effect (Table 1.3). The center of linear retention habitats had lower recent deadwood volume than harvest edge (18.96 ± 9.70) for both retention types, and than stream side edge (8.69 ±5.76) for riparian strips. An interaction between plot location and initial stand volume (ISV) showed a significant decrease in ISV variable effect on deadwood recruitment along stream side edge (ISVstream side edge = -0.03 ± 0.02) of riparian strips. Time since harvest was not a significant parameter for deadwood recruitment, although a highly variable distribution pattern in the first two decades similar to that in the mixedwood forest was evident (Figure 1.3).

1.3.2 Effects of retention width

Plots in the center of retention strips were at various distances from the edge, depending on site width. Riparian buffer strips were generally narrower with the center plot around 10 m from the cut; centers of cutblock separators ranged between 30 and 70 m from harvested edges. Site width had a significant effect on deadwood recruitment in the center of linear retention strips in mixedwood forests (P-value < 0.0001). Cutblock separators wider than 100 m showed a reduced recent deadwood volume at their center, whereas narrower sites (<50m) had about twice as much the recent deadwood volume in their center (Figure 1.4). In the coniferous forest, the range of site width was lower with the maximum around 100 m (Table 1.1). The effect of retention width was marginal (P-value = 0.0634), but the trend was similar to that of mixedwood but with a softer slope. Recent deadwood volume was in general lower in coniferous forest (Figure 1.4).

1.3.3 Spatial distribution of standing and downed deadwood

In mixedwood retentions, cutblock separators showed a significantly higher proportion of snags in the center (mean = 0.43) than along harvested edges (mean = 0.13) (P-value = 0.00278) (Figure 1.5). However, variability was greater in the center of cutblock separators. Conversely, no significant difference in the spatial distribution of standing and downed deadwood was apparent across riparian buffer strips in mixedwood forests (Figure 1.5). Although mean recent deadwood volume was slightly higher in this retention type compared to cutblock separators (Table 1.1), snag proportion was low on both edges (harvest, 0.079 and stream side, 0.16) and in the center (0.091), indicating a greater abundance of downed deadwood.

In coniferous forests, both retention types showed a significantly higher contribution of snags to recent deadwood volume in the center than along the harvest edges (Figure 1.5). However, the difference was stronger in cutblock separators than in riparian strips (P-value = 00029, and P-value = 0.0426 respectively). The proportion of snags in stream side edges was similar to what is found in the center of riparian strips. The contribution of snags to overall deadwood recruitment was highest in the center of cutblock separators (snag mean proportion of 0.61); followed by the center of riparian strips (0.28), cutblock separator harvest edges (0.25), riparian edges (0.25), and harvest edges of riparian strips (0.12).

1.3.4 Long-term sustainability for deadwood recruitment

1.3.4.1 Poplar in southern boreal mixedwood forests

Sites in the mixedwood forest presumably had enough living tree volume to ensure the maintenance of closed canopy conditions since standing live tree volumes were above the threshold of 100 m^3/ha (Figure 1.6). Indeed, most sites contained high living tree volumes with values over the 200 m^3/ha. Many sites were within the range of natural variability of large standing dead poplar tree proportions (trembling aspen and balsam poplar). Few sites were above this natural variability (MS04, MS06, MS10 and MS11). Their tree diametrical distribution showed living poplars were still present and mainly in larger diameter classes whereas small diameter classes were essentially represented by coniferous species (Figure 1.7). MS04 and MS11 also showed a limited amount of small diameter trees whereas MS10 and MS06 had a good understory of conifer established in the stand. Six sample sites were removed from this analysis because they had less than 5 dominant aspen trees.

Several sites could, however, be considered outside of the natural variability range for the proportion of large standing dead poplar trees (MB02, MB06, MB08, MS01 and

MS07, Figure 1.6). All showed a tree diametrical distribution in which poplars were present in every diameter class (Figure 1.7). MS07 was composed essentially of the initial cohort of poplars in every class, whereas other sites had a certain amount of coniferous stems in smaller diameter classes which would indicate a transition phase towards eventual conifer canopy dominance. MB02, MS01 and MS07 had several aspen stems in the larger diameter classes. Younger stands with low values of large deadwood stems certainly show a long-term potential for both closed canopy and future deadwood recruitment.

1.3.4.2 Black spruce in northern coniferous forests

All sites showed standing live tree volumes above the threshold of 60 m^3/ha indicating they all have a fairly closed canopy. Regardless of time since harvest, canopy closure in these linear retention habitats was not altered when compared to natural forests. The majority of sites were also under the threshold value of 30% for the proportion of recent deadwood for a stand to maintain its recruitment in the future (Figure 1.8). Tree mortality due to the edge creation was not excessive in linear retention compared with continuous natural forest stands.

Among sites with a recent deadwood proportion over the 30% threshold, most were close to the line (PB11, PS07, PB09 and PB08, Figure 1.8) and their sustainability for deadwood production could be of concern. Tree diametrical distribution showed a truncated normal distribution in most of the sites, thus, ostensibly, ensuring tree recruitment in a longer term (Figure 1.9). However, sites with higher proportions of deadwood showed low tree recruitment. PB08 and PB09 were the most threatened riparian strips in terms of continuous deadwood recruitment with the lowest living tree volume and a low number of stems in every diameter class (Figures 1.8 and 1.9).

1.4 DISCUSSION

Our first objective intended to determine the main factors influencing tree mortality in Québec's forest retention system of linear habitats in aggregated even-aged harvested landscapes. Besides our base model parameters (stand age, initial stand volume, and the presence of beaver activity), the spatial location within linear habitats and time since harvest influenced significantly deadwood volume in the mixedwood ecosystem. Contrary to other studies, we did not find any influence of orientation of the linear retention in the landscape (DeWalle 1983, Ruel 1995). Linear retention strips encountered important tree mortality after their creation by even-aged harvests, regardless of wind direction. Contrarily to our prediction, we did not find significant differences in deadwood volume between cutblock separators or riparian buffers suggesting that both habitats maintained old forest decaying and deadwood attributes through time. One difference observed between retention types was the absence of influence of initial condition in riparian buffers. In fact, initial stand conditions are reported as being a major factor driving deadwood volume after harvest (Riopel et al. 2010, Moussaoui et al. 2016), but they did not have an important influence on mortality in stream side edges of riparian strips in the coniferous forest. Recent deadwood volume did not vary with live tree density indicating that trees in this situation were not vulnerable to greater opening.

In contrast to mixedwood forests, stand age in coniferous forests covered a range wide enough to detect an age effect. *A priori* determination of stand age in coniferous forest is less precise than in the mixedwood forest, mainly due to less sharp transition between successional stages (Bergeron and Dubuc 1989, Gauthier et al. 2000, Pothier et al. 2004).

1.4.1 Spatial distribution and vertical structure

Wind damage of trees was gradually reduced with distance from clearcut edge. Higher recent deadwood volume measured in harvest side forest edges corroborated other edge effect studies (Burton 2002, Harper et al. 2002, 2004, Mascarúa López et al. 2006, Braithwaite and Mallik 2012, Dupuch and Fortin 2013). Such mortality can be caused by a drastic change in abiotic factors, particularly wind exposure, decreased humidity combined with greater evapotranspiration and increased light penetration (Ranney et al. 1981, Kapos 1989, Chen et al. 1992, Esseen 1994, Murcia 1995, Laurance et al. 1998). We also observed low recruitment of unbroken standing dead trees along clearcut edges. Mortality mostly occurred by uprooting or stem breakage, providing an over-representation of downed deadwood. Wind damage was less evident in the center of linear retention strips, especially in cutblock separators with larger retention widths (60 - 100 m), thus allowing for a longer retention of standing deadwood. Low occurrence of snags across riparian buffers reported by Harper (1999), Harper and Macdonald (2001), and Mascarúa López et al. (2006) has been attributed to the adapation of stands to openings created by local natural disturbances occurring in riparian ecotones. However, results from our study differ in that riparian buffers had a slightly higher amount of deadwood volume than cutblock separators (Table 1.1). However, centers of riparian strips in the mixedwood ecosystem did not show a higher proportion of snags suggesting a relatively homogeneous effect of wind exposure throughout the retention strips.

The coniferous forest seemed to be better adapted to openings since snags proportion was generally greater in strip centers than edges for both retention types. This could be due to the biology of the dominant tree species: according to Angers et al, (2010), trembling aspen and balsam fir are more susceptible to stem breakage when exposed to strong winds, whereas black spruce and jack pine snags tend to stay intact for a longer period. Susceptibility to pathogens can also explain the greater occurrence of downed dead wood in mixedwood forests. For instance, balsam fir is vulnerable to but and root rots (Whitney, 1989), thus more susceptible to uprooting (Lavoie et al. 2012). Whereas trembling aspen is susceptible to hearth rot, which promotes stem breakages (Hale and Pastor 1998, Siitonen 2001) Therefore, such vertical deadwood structure is more fragile in the mixedwood forest ecosystem. We did not include standing broken stems in this analysis as they are classified in advanced degradation stages and could have been present before the cut. However, this type of deadwood can contribute to vertical structure, and therefore increase the availability of standing dead trees in the mixedwood ecosystem.

1.4.2 Retention width and core mortality

The center of wider linear retention habitats (cutblock separators) had less recent deadwood volume. This relationship was significant in the mixedwood forest where the range of widths was larger than in the coniferous forest. There was a reduction in mortality until width was at least 100 meters (see Figure 1.4), which means a minimum distance of 50 meters from the harvest area. This corroborates Harper and Macdonald (2002) findings for the aspen-dominated boreal forest where higher deadwood volume was observed within 5 to 40 meters from harvest edges, and Burton’s (2002) study in the sub-boreal forest of western Canada, where edge effect on tree mortality reaches 55 to 60 meters. The convergence of results among regions suggests that linear retention in the Canadian mixedwood boreal forest should be at least 100 meters wide to ensure a core area with structural features of interior forests.

In the coniferous forest, these trends were similar although not significant. This could be caused by the absence of very large cutblock separators, our largest sample sites were about 100 meters wide. However, tree mortality and accumulation of deadwood as a result of edge creation have been reported to extend to a shorter distance of 5 to 30 meters in this ecosystem (Harper and Macdonald 2002, Mascarúa López et al.

2006). These studies were conducted between 5 to 10 years after harvest and it is possible that structural damage could continue to occur after this time period. The lower stand productivity in the black spruce forest of the Claybelt lowlands (Lecomte et al. 2006, Simard et al. 2007, Fenton and Bergeron 2008) would also explain lower recent deadwood volumes in these forests compared to the mixedwood forest. Therefore, the range of recent deadwood recruitment is lower and is less likely to present significant differences. Mascarúa López et al. (2006) considered that cutblock separators under 60 meters wide do not contain proper interior forest, although they did not sample wider linear retention strips. Our results show that there is still a slight reduction of deadwood recruitment in the center of linear retention strips up to 100 meters wide. It would be interesting to assess if deadwood recruitment is affected by edge effects in linear retention strips wider than 100 meters. This could provide evidence for justifying wider cutblock separators in management planning. Our results reiterate the importance of ensuring that the structural features of the interior forest which are essential for the conservation of many species are maintained through conservation planning of larger linear retention habitats (Hannon et al. 2002, Potvin and Bertrand 2004, Mascarúa López et al. 2006).

1.4.3 Temporal evolution

For both sub-bioclimatic domains, the first two decades after harvest are characterized by variable but generally high mortality rates followed by a more stable state with lower mortality. This suggests a period of instability where linear retention stands cope with the new canopy opening. Several authors have also found highest mortality rates in early years after harvest (Darveau et al. 1994, Esseen 1994, Bladon et al. 2008, Lavoie et al. 2012, Urgenson et al. 2013). Few studies have documented a long-term post-harvest edge effects, but Moussaoui et al. (2016) found old cut separators (>20 years) to have less recent deadwood than younger retentions. As well, Dupuch and Fortin (2013) observed an accumulation of woody debris, from all decay classes, to persist for 40 years. Because tree bole degradation in the boreal forest can take 15-20 years (Angers et al. 2012b), this allows for 20 years of recruitment. Live trees remaining 20 years after harvest are generally physiologically adapted to post disturbance conditions. Trees adapt their root structures and wood density to wind exposition (Urban et al. 1994, Gardiner et al. 1997) and become less vulnerable to the opening. As well, the regeneration growth in the harvested area gradually "soften the edge" of abrupt retention borders (Harper et al. 2005, 2014). Old linear retention strips (> 20 years after harvest) were less common in the studied area, and thus less sampled. However, our results indicate that these sites were generally not in a state of deterioration in which tree fall leads to open linear habitat with few standing trees (dead or alive). After edge creation, the deadwood dynamics in retention stands is the result of two very different ecosystems evolving next to each other (Esseen, 1994). While regenerating areas gradually soften the edge, retention stands undergo natural aging and forest succession including tree mortality.

Overall, the linear retention habitats investigated in this study retained enough live trees and tree diameter profiles to ensure deadwood sustainability (long-term recruitment). The relatively high density of smaller diameter classes is particularly important in this respect. In the coniferous forest, few sites experienced excessive mortality leaving little live structures. These sites could be exposed to vulnerable topographic features, although this was not assessed in this study. Topography combined with wind direction can strongly influence tree mortality, especially in riparian strips (Ruel et al. 2001). In the mixedwood forest, most of the sites that were out of the natural range of large aspen snag proportion also had tree diameter distributions indicating that they were transitioning towards a second cohort with coniferous tree dominance. In natural boreal mixedwood forests, this transition occurs as the large deciduous trees die, and coniferous species slowly take over the canopy of the stand (Bergeron and Dubuc 1989, Harvey et al. 2002). Sites presenting higher proportions of large aspen snags could be a little ahead of the natural succession timeline, caused by the prompted mortality of dominant deciduous trees after harvest. Among sites below the natural variability of snag proportion, some could be transitioning to the second cohort structure without providing the vertical deadwood structure associated with standing mortality as a result of uprooting or stem breakage near the base of the tree. However, tree diameter profiles show the overall presence of live aspen that can provide future vertical deadwood features. None of the sites are susceptible to decline, in that these stands apparently provided adequate vertical live and dead structure that could support deadwood dependent biodiversity.

1.4.4 Conclusion and management implications

Our results show that linear retention strips investigated in this study in both boreal mixedwood and coniferous forests persist as forest stands over the 35-year period following logging. Even though retention edges are affected by environmental conditions, our results show that linear habitats are resilient with regards to the underlying processes (dead tree recruitment and deadwood decay) for sustaining over the long-term, legacies of structural habitat features of old forests. Indeed, few linear retention habitats, regardless of the type (cutblock separators or riparian buffers), are in the process of collapsing and transforming into open habitats. Moreover, our analysis of deadwood recruitment suggests that they provide live and dead structures comparable to unmanaged natural forests. This suggests that they are likely to evolve but persist with old forest legacies throughout the entire rotation time for the managed forest to develop into a mature forest landscape. That said, larger linear retention strips (>100 meters) in both forest cover types would improve biodiversity conservation of organisms associated with standing decaying and dead trees particularly where they are permanently maintained throughout the duration of the management rotation; that is until clearcut agglomerations become mature to old forests that can in turn provide live and dead structures features in proportions corresponding.

1.5 REFERENCES

Aakala, T., Kuuluvainen, T., De Grandpré, L., et Gauthier, S. 2007. Trees dying standing in the northeastern boreal old-growth forests of Quebec: spatial patterns, rates, and temporal variation. Can. J. For. Res. **37**: 50–61. doi:10.1139/x06-201.

Aitchison, J., et Silvey, S.D. 1957. The generalization of probit analysis to the case of multiple responses. Biometrika Trust **44**(1): 131–140.

Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat : a review. Oikos **71**(3): 355–366.

Angers, V.A., Bergeron, Y., et Drapeau, P. 2012a. Morphological attributes and snag classification of four North American boreal tree species: Relationships with time since death and wood density. For. Ecol. Manage. **263**: 138–147.

Angers, V.A., Drapeau, P., et Bergeron, Y. 2010. Snag degradation pathways of four North American boreal tree species. For. Ecol. Manage. **259**(3): 246–256. doi:10.1016/j.foreco.2009.09.026.

Angers, V.A., Drapeau, P., et Bergeron, Y. 2012b. Mineralization rates and factors influencing snag decay in four North American boreal tree species. Can. J. For. Res. **42**(1): 157–166. doi:10.1139/x11-167.

Bebber, D.P., Cole, W.G., Thomas, S.C., Balsillie, D., et Duinker, P. 2005. Effects of retention harvests on structure of old-growth Pinus strobus L. stands in Ontario. For. Ecol. Manage. **205**(1–3): 91–103. doi:10.1016/j.foreco.2004.10.048.

Bennett, A.F. 2003. Linkages in the landscape: The role of corridors and connectivity in wildlife conservation. *In* Iucn. doi:10.2305/IUCN.CH.2004.FR.1.en.

Berg, A., Ehnstrom, B., Gustafsson, L., Hallingback, T., Jonsell, M., et Weslien, J. 1994. Threatened plant, animal, and fungus species in swedish forests : distribution and habitat associations. Soc. Conserv. Biol. **8**(3): 718–731.

Bergeron, Y. 1991. The influence of island and mainland lakeshore landscapes on boreal forest fire regimes. Ecology **72**(6): 1980–1992.

Bergeron, Y., et Dubuc, M. 1989. Succession in the southern part of the Canadian boreal forest. Vegetatio **79**: 51–63.

Bergeron, Y., Flannigan, M., Gauthier, S., Leduc, A., et Lefort, P. 2004a. Past, current and future fire frequency in the Canadian Boreal Forest: Implications for sustainable forest management. AMBIO A J. Hum. Environ. **33**(6): 356. doi:10.1639/0044-7447(2004)033[0356:PCAFFF]2.0.CO;2.

Bergeron, Y., Gauthier, S., Flannigan, M., et Kafka, V. 2004b. Fire regimes at the transition between mixed wood and coniferous boreal forest in Northwestern Quebec. Ecology **85**(7): 1916–1932. doi:10.1890/02-0716.

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

Bergeron, Y., et Harvey, B.D. 1997. Basing silviculture on natural ecosystem dynamics: An approach applied to the southern boreal mixedwood forest of Quebec. For. Ecol. Manage. **92**(1–3): 235–242. doi:10.1016/S0378-1127(96)03924-2.

Bergeron, Y., Irulappa Pillai Vijayakumar, D., Ouzennou, H., Raulier, F., Leduc, A., et 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. For. An Int. J. For. Res. **90**(4): 485–495.

Bergeron, Y., Leduc, A., Harvey, B.D., et Gauthier, S. 2002. Natural fire regime : A guide for sustainable management of the canadian boreal forest. Silva Fenn. **36**(January): 81–95.

Bladon, K.D., Lieffers, V.J., Silins, U., Landhäusser, S.M., et Blenis, P. V. 2008. Elevated mortality of residual trees following structural retention harvesting in boreal mixedwoods. For. Chron. **84**(1): 70–75. doi:10.5558/tfc84070-1.

Bouchard, M., Kneeshaw, D.D., et Bergeron, Y. 2005. Mortality and stand renewal patterns following the last spruce budworm outbreak in mixed forests of western Quebec. For. Ecol. Manage. **204**(2–3): 297–313. doi:10.1016/j.foreco.2004.09.017.

Boucher, D., Gauthier, S., et 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**(2): 172–180. doi:10.2980/i1195-6860-13-2-172.1.

Braithwaite, N.T., et Mallik, A.U. 2012. Edge effects of wildfire and riparian buffers along boreal forest streams. J. Appl. Ecol. **49**(1): 192–201. doi:10.1111/j.1365-2664.2011.02076.x.

Bull, E.L., Twombly, A.D., et Quigley, T.M. 1980. Perpetuating snags in managed mixed conifer forests of Blue Montain, Oregon. USDA For. Serv. Gen. Tech. Rep.: 325–336.

Burnham, K.P., et Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach (2nd ed). *In* Ecological Modelling. Springler Verlag, New York, NY. doi:10.1016/j.ecolmodel.2003.11.004.

Burton, P.J. 2002. Effects of clearcut edges on trees in the sub-boreal spruce zone of Northwest-Central British Columbia. Silva Fenn. **36**(1): 329–352.

Cadieux, P. 2011. Dynamique de la faune cavicole le long d'un gradient d'âge en forêt boréale mixte de l'Est de l'Amérique du Nord Mémoire de maîtrise. Université du Québec à Montréal.

Chen, J., Franklin, J.F., et Lower, J.S. 1995. Comparison of abiotic and structurally defined patch patterns in a hypothetical forest landscape. Conserv. Biol. **10**(3): 854–862.

Chen, J., Franklin, J.F., et Spies, T.A. 1992. Vegetation responses to edge environments in old-growth douglas-fir forests. Ecol. Appl. **2**(4): 387–396.

Cline, S.P., Berg, A.B., et Wight, H.M. 1980. Snag characteristics and dynamics in Douglas-Fir forests, western Oregon. J. Wildl. Manage. **44**(4): 773–786.

Cooke, B.J., et Lorenzetti, F. 2006. The dynamics of forest tent caterpillar outbreaks in Québec, Canada. For. Ecol. Manage. **226**: 110–121. doi:10.1111/j.1600-0587.2011.07083.x.

Dansereau, P.-R., et Yves Bergeron. 1993. Fire history in the southern boreal forest of northwestern Quebec. Can. J. For. Res. **23**: 25–32.

Darveau, M., Bélanger, L., et Ruel, J.-C. 1994. Mid-term effects of windfall on bird use of riparian forest strips. Int. Congr. Game Biol. **21**(2): 104–109.

Debinski, D.M., et Holt, R.D. 2000. A Survey and overview of habitat fragmentation experiments. Conserv. Biol. **14**(2): 342–355. doi:10.1046/j.1523-1739.2000.98081.x.

Delong, S.C., et Tanner, D. 1996. Managing the pattern of forest harvest: lessons from wildfire. Biodivers. Conserv. **5**: 1191–1205.

Desponts, M., Desrochers, A., Bélanger, L., et Huot, J. 2002. Structure de sapinières aménagées et anciennes du massif des Laurentides (Québec) et diversité des plantes invasculaires. Can. J. For. Res. **32**(12): 2077–2093. doi:10.1139/x02-127.

DeWalle, D.R. 1983. Wind damage around clearcuts in the Ridge and Valley province of Pennsylvania. J. For. **81**(3): 158–172.

Drapeau, P., Leduc, A., et Bergeron, Y. 2009a. Bridging ecosystem and multiple species approaches for setting conservation targets in managed boreal landscapes. *In* Villard, M.A., Gunnar-Jonsson, B.G., (Eds), Setting conservation targets for managed forest landscapes. Cambridge University Press, Cambridge, UK, pp. 129-160, 426pages

Drapeau, P., Leduc, A., Giroux, J., Savard, J.L., et Vickery, W.L. 2000. Landscape-scale disturbances and changes in bird communities of boreal mixed-wood forests. Ecol. Monogr. **70**(3): 423–444.

Drapeau, P., Nappi, A., Imbeau, L., et Saint-Germain, M. 2009b. Standing deadwood for keystone bird species in the eastern boreal forest: Managing for snag dynamics. For. Chron. **85**(2): 227–234. doi:10.5558/tfc85227-2.

Drapeau, P., Villard, M.A., Leduc, A., et Hannon, S.J. 2016. Natural disturbance regimes as templates for the response of bird species assemblages to contemporary forest management. Divers. Distrib. **22**(4): 385–399. doi:10.1111/ddi.12407.

Dupuch, A., et Fortin, D. 2013. The extent of edge effects increases during post-harvesting forest succession. Biol. Conserv. **162**: 9–16. Elsevier Ltd. doi:10.1016/j.biocon.2013.03.023.

Erickson, H.E., Edmonds, R.L., et Peterson, C.E. 1985. Decomposition of logging residues in Douglas-fir, western hemlock, Pacific silver fir, and ponderosa pine ecosystems. Can. J. For. Res. (15): 914–921..

Esseen, P.-A. 1994. Tree mortality patterns after experimental fragmentation of an old-growth conifer forest. Biol. Conserv. **68**: 19–28.

Fenton, N.J., et Bergeron, Y. 2008. Does time or habitat make old-growth forests species rich? Bryophyte richness in boreal Picea mariana forests. Biol. Conserv. **141**(5): 1389–1399. doi:10.1016/j.biocon.2008.03.019.

Ferguson, S.H., et Archibald, D.J. 2002. The 3/4 power law in forest management: how to grow dead trees. For. Ecol. Manage. **169**(3): 283–292. doi:10.1016/S0378-1127(01)00766-6.

Fortin, M., DeBlois, J., Bernier, S., et Blais, G. 2007. Mise au point d’un tarif de cubage général pour les forêts québécoises: Une approche pour mieux évaluer l’incertitude associée aux prévisions. For. Chron. **83**(5): 754–765. doi:10.5558/tfc83754-5.

Franklin, J.F. 1993. Preserving Biodiversity : Species, ecosystems, or landscapes ? Ecol. Appl. **3**(2): 202–205.

Franklin, J.F., Lindenmayer, D.B., Macmahon, J.A., Mckee, A., Magnuson, J., Perry, D.A., Waide, R., et Foster, D.R. 2000. Threads of continuity. Conserv. Pract. 1:9-16.

Franklin, J.F., Shugart, H., et Harmon, M.E. 1987. Tree death as an ecological process. Bioscience **37**(8): 550–556.

Franklin, J.F., Spies, T.A., Pelt, R. Van, Carey, A.B., Thornburgh, D. a, Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., et Chen, J. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For. Ecol. Manage. **155**(1–3): 399–423. doi:10.1016/S0378-1127(01)00575-8.

Gardiner, B.A., Stacey, G.R., Belcher, R.E., et Wood, C.J. 1997. Field and wind tunnel assessments of the implications of respacing and thinning for tree stability. Forestry **70**(3): 233–252. doi:10.1093/forestry/70.3.233.

Gauthier, S., Bernier, P.Y., Boulanger, Y., Guo, J., Guindon, L., Beaudoin, A., et Boucher, D. 2015a. Vulnerability of timber supply to projected changes in fire regime in Canada's managed forests. Can. J. For. Res. **1447**: 1–33. doi:10.1139/cjfr-2015-0079.

Gauthier, S., Raulier, F., Ouzennou, H. et Saucier, J.-P. 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.

Gauthier, S., DeGrandpré, L., et Bergeron, Y. 2000. Differences in forest composition in two boreal forest ecoregions of Quebec. J. Veg. Sci. **11**(6): 781–790.

Gauthier, S., Vaillancourt, M.-A., Kneeshaw, D.D., Drapeau, P., DeGrandpré, L., Claveau, Y., et Pare, D. 2009. Forest Ecosystem Management: Origins and Foundations. *In* Ecosystem management in the boreal forest. Presses de l'Université du Québec, Québec, Qc. pp. 13–38.

Hale, C.M., et Pastor, J. 1998. Nitrogen content, decay rates, and decompositional dynamics of hollow versus solid hardwood logs in hardwood forests of Minnesota, U.S.A. Can. J. For. Res. **28**(9): 1276–1285. doi:10.1139/x98-097.

Hannon, S.J., Paszkowski, C.A., Boutin, S., DeGroot, J., Macdonald, S.E., Wheatley, M., et Eaton, B.R. 2002. Abundance and species composition of amphibians, small mammals, and songbirds in riparian forest buffer strips of varying widths in the boreal mixedwood of Alberta. Can. J. For. Res. **32**(10): 1784–1800. doi:10.1139/x02-092.

Harmon, M.E., Franklin, J.F., Swanson, F., Sollins, P., Gregory, S. V., Lattin, J.D., Anderson, N.., Cline, S.P., Aumen, N.., Sedell, J.., Lienkaemper, G.., Cromack Jr, K., et Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. (15): 133–302.

Harmon, M.E., et Sexton, J. 1996. Guidelines for measurements of woody detritus in forest ecosystems.

Harper, K.A. 1999. Variability in forest structure and composition along edge-to-interior gradients from lakeshore and clearcut edges and in riparian buffers in the aspen- dominated mixedwood boreal forest. Dissertation. University of Alberta. Edmonton, Alberta, Canada.

Harper, K.A., Bergeron, Y., Gauthier, S., et 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.

Harper, K.A., Boudreault, C., DeGrandpré, L., Drapeau, P., Gauthier, S., et Bergeron, Y. 2003. Structure, composition, and diversity of old-growth black spruce boreal forest of the Clay Belt region in Quebec and Ontario. Environ. Rev. **11**(S1): S79–S98. doi:10.1139/a03-013.

Harper, K.A., Drapeau, P., Lesieur, D., et Bergeron, Y. 2014. Forest structure and composition at fire edges of different ages: Evidence of persistent structural features on the landscape. For. Ecol. Manage. **314**: 131–140. Elsevier B.V. doi:10.1016/j.foreco.2013.12.009.

Harper, K.A., Drapeau, P., Lesieur, D., et Bergeron, Y. 2016. Negligible structural development and edge influence on the understorey at 16–17-yr-old clear-cut edges in black spruce forest. Appl. Veg. Sci. **19**(3): 462–473. doi:10.1111/avsc.12226.

Harper, K.A., Lesieur, D., Bergeron, Y., et Drapeau, P. 2004. Forest structure and composition at young fire and cut edges in black spruce boreal forest. Can. J. For. Res. **34**(2): 289–302. doi:10.1139/x03-279.

Harper, K.A., et Macdonald, S.E. 2001. Structure and composition of riparian boreal forest: New methods for analyzing edge influence. Ecology **82**(3): 649–659.

Harper, K.A., et Macdonald, S.E. 2002. Structure and composition of edges next to regenerating clear-cuts in mixed-wood boreal forest. J. Veg. Sci. **13**: 535–546.

Harper, K.A., Macdonald, S.E., Burton, P.J., Chen, J., Brosofske, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D., Jaiteh, M.S., et Esseen, P.-A. 2005. Edge influence on forest structure and composition in fragmented landscapes. Conserv. Biol. **19**(3): 768–782. doi:10.1111/j.1523-1739.2005.00045.x.

Harvey, B.D., et Leduc, A. 1999. Plan général d'aménagement - Forêt d'enseignement et de recherche du lac Duparquet (1998-2023). Université du Québec en Abitibi-Témiscamingue.153 pages

Harvey, B.D., Leduc, A., Gauthier, S., et Bergeron, Y. 2002. Stand-landscape integration in natural disturbance-based management of the southern boreal forest. For. Ecol. Manage. **155**(1–3): 369–385. doi:10.1016/S0378-1127(01)00573-4.

Hély, C., Bergeron, Y., et Flannigan, M.D. 2000. Coarse woody debris in the southeastern Canadian boreal forest: composition and load variations in relation to stand replacement. Can. J. For. Res. **30**(5): 674–687. doi:10.1139/x99-256.

Imbeau, L., et Desrochers, A. 2002. Foraging ecology and use of drumming trees by three-toed woodpeckers. J. Wildl. Manage. **66**(1): 222–231.

Johnson, E.A., et Van Wagner, C.E. 1985. The theory and use of two fire history models. Can. J. For. Res. **15**: 214–220.

Kapos, V. 1989. Effects of isolation on the water status of forest patches in the brazilian amazon. J. Trop. Ecol. **5**(2): 173–185.

Kneeshaw, D.D., et Bergeron, Y. 1996. Ecological factors affecting the abundance of advance regeneration in Quebec's southwestern boreal forest. Can. J. For. Res. **26**: 888–898.

Kuuluvainen, T., Bergeron, Y., et Coates, K.D. 2015. Restoration and ecosystem-based management in the circumboreal forest: background, challenges, and opportunities. *In* Restoration of Boreal and Temperate Forests, Second Edi. CRC Press. pp. 251–270.

Laurance, W.F., Ferreira, L. V., Rankin-de Merona, J.M., et Laurance, S.G. 1998. Rain forest fragmentation and the dynamics of Amazonian tree communities. Ecology **79**(6): 2032–2040. doi:10.2307/176707.

Lavoie, S., Ruel, J.-C., Bergeron, Y., et Harvey, B.D. 2012. Windthrow after group and dispersed tree retention in eastern Canada. For. Ecol. Manage. **269**: 158–167. doi:10.1016/j.foreco.2011.12.018.

Lecomte, N., Simard, M., Fenton, N., et Bergeron, Y. 2006. Fire severity and long-term ecosystem biomass dynamics in coniferous boreal forests of eastern Canada. Ecosystems **9**(8): 1215–1230. doi:10.1007/s10021-004-0168-x.

Lee, P. 1998. Dynamics of snags in aspen-dominated midboreal forests. For. Ecol. Manage. **105**(1–3): 263–272. doi:10.1016/S0378-1127(97)00286-7.

Lussier, J.-M., Morin, H., et Gagnon, R. 2002. Mortality in black spruce stands of fire or clear-cut origin. Can. J. For. Res. **32**(3): 539–547. doi:10.1139/x01-201.

Mascarúa López, L.E., Harper, K.A., et Drapeau, P. 2006. Edge influence on forest structure in large forest remnants, cutblock separators, and riparian buffers in managed black spruce forests. Ecoscience **13**(2): 226–233. doi:10.2980/i1195-6860-13-2-226.1.

Morin, H., Laprise, D., et Bergeron, Y. 1993. Chronology of spruce budworm outbreaks near Lake Duparquet, Abitibi region, Quebec. Can. J. For. Res. **23**: 1497–1506.

Moussaoui, L., Fenton, N.J., Leduc, A., et Bergeron, Y. 2016. Deadwood abundance in post-harvest and post-fire residual patches: An evaluation of patch temporal dynamics in black spruce boreal forest. For. Ecol. Manage. **368**: 17–27. Elsevier B.V. doi:10.1016/j.foreco.2016.03.012.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Tree **10**(2): 58–62.

Naiman, R.J., Melillo, J.M., et Hobbie, J.E. 1986. Ecosystem Alteration of Boreal Forest Streams by Beaver (Castor canadensis). Ecol. Soc. Am. **67**(5): 1254–1269.

Nappi, A., Drapeau, P., et Leduc, A. 2015. How important is dead wood for woodpeckers foraging in eastern North American boreal forests? For. Ecol. Manage. **346**: 10–21. Elsevier B.V. doi:10.1016/j.foreco.2015.02.028.

Nummi, P., et Kuuluvainen, T. 2013. Forest disturbance by an ecosystem engineer: beaver in boreal forest landscapes. Boreal Environ. Res. **18**: 13–24..

Ouellet-Lapointe, U., Drapeau, P., Cadieux, P., et Imbeau, L. 2012. Woodpecker excavations suitability for and occupancy by cavity users in the boreal mixedwood forest of Eastern Canada. Ecoscience **19**(4): 391–397. doi:10.2980/19-4-3582.

Parish, R., Antos, J. a., Ott, P.K., et Lucca, C.M. Di. 2010. Snag longevity of Douglas-fir, western hemlock, and western redcedar from permanent sample plots in coastal British Columbia. For. Ecol. Manage. **259**(3): 633–640. doi:10.1016/j.foreco.2009.11.022.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., et the R Development Core Team. 2008. The nlme package. Available at http://cran.stat.sfu.ca/.

Pothier, D., Raulier, F. et Riopel, M., 2004. Ageing and decline of trembling aspen stands in Quebec. Can. J. Forest Res. 34, 1251–1258. http://dx.doi.org/10.1139/x04-017.

Potvin, F., et Bertrand, N. 2004. Leaving forest strips in large clearcut landscapes of boreal forest: A management scenario suitable for wildlife? For. Chron. **80**(1): 44–53. doi:10.5558/tfc80044-1.

Poulin, J., et Messier, C. 2006. Rapport de paramétrisation du modèle de simulation de la dynamique forestière SORTIE-ND pour la forêt boréale et sub-boréale de l'ouest du Québec. [Rapport non publié] Montréal, QC

Gouvernement du Québec. 2015. Règlement sur les normes d'intervention forestières, chapter A-18.1, r. 7 (mise à jour le 1 June 2017).

R Core Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Ranney, J.W., Bruner, M.C., et Levenson, J. 1981. The importance of edge in the structure and dynamics of forest islands. pp. 67–69 *In* Forest islands in man dominated landscapes. *Edited by* R. Burgess and D. Sharp. Springler Verlag, New York, NY..

Riopel, M., Bégin, J., et Ruel, J.-C. 2010. Probabilités de pertes des tiges individuelles, cinq ans après des coupes avec protection des petites tiges marchandes, dans des forêts résineuses du Québec. Can. J. For. Res. **40**(7): 1458–1472. doi:10.1139/X10-059.

Ruel, J.-C. 1995. Understanding windthrow : Silvicultural implications. For. Chron. **71**(4): 434–445.

Ruel, J.-C., Pin, D., et Cooper, K. 2001. Windthrow in riparian buffer strips: effect of wind exposure, thinning and strip width. For. Ecol. Manage. **143**(1–3): 105–113. doi:10.1016/S0378-1127(00)00510-7.

Saucier, J.-P., Grondin, P., Robitaille, A., et Bergeron, J.-F. 2003. Zone de végétation et domaines bioclimatiques du Québec. Ressources naturelles, Faune et Parcs.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms : Fennoscandian Boreal Forests as an Example. Oikos (49): 11–41.

Simard, M., Lecomte, N., Bergeron, Y., Bernier, P.Y., et Paré, D. 2007. Forest productivity decline caused by successional paludification of boreal soils. Ecol. Appl. **17**(6): 1619–1637. doi:10.1890/06-1795.1.

Ste-Marie, G. 2009. Interactions entre le peuplier faux-tremble et l'épinette noire en forêt boréale de l'ouest du Québec. Mémoire de maîtrise, Université du Québec à Montréal. 91 pages

Stokland, J., Siitonen, J., et Jonsson, B.G. 2012. Biodiversity in dead wood. Cambridge University Press, Cambridge.

Stokland, J.N. 2001. The coarse woody debris profile : An archive of recent forest history and an important biodiversity indicator. Oikos (49): 71–83.

Sturtevant, B.R., Bissonette, J.A., Long, J.N., et Roberts, D.W. 1997. Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland Ecol. Appl. **7**(2): 702–712.

Thorpe, H.C., et Thomas, S.C. 2007. Partial harvesting in the Canadian boreal: Success will depend on stand dynamic responses. For. Chron. **83**(3): 319–325. doi:10.5558/tfc83319-3.

Urban, S.T., Lieffers, V.J., et Macdonald, S.E. 1994. Release in radial growth in the trunk and structural roots of white spruce as measured by dendrochronology. Can. J. For. Res. **24**: 1550–1556.

Urgenson, L.S., Halpern, C.B., et Anderson, P.D. 2013. Level and pattern of overstory retention influence rates and forms of tree mortality in mature, coniferous forests of the Pacific Northwest, USA. For. Ecol. Manage. **308**: 116–127. Elsevier B.V. doi:10.1016/j.foreco.2013.07.021.

Vincent, J.-S., et Hardy, L. 1977. L'évolution et l'extension des lacs glaciaires Barlow et Ojibway en territoire québécois. Géographie Phys. Quat. **31**(3–4): 357. doi:10.7202/1000283ar.

Whitney, R.D., 1989. Root-rot damage in naturally regenerated stands of spruce and balsam fir in Ontario. Can J. For. Res. 19, 295-308.

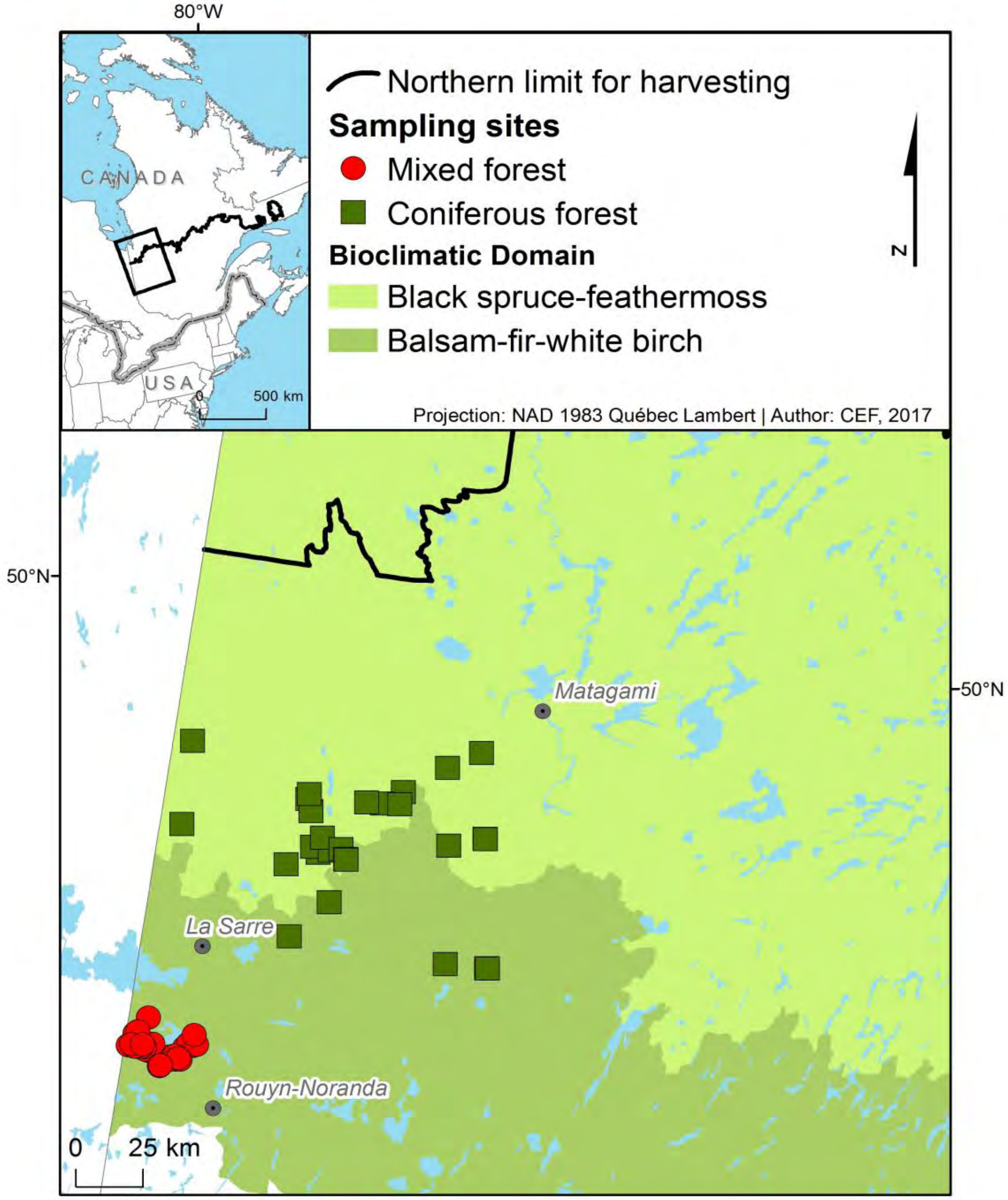

Figure 1.1 Location of study area and sample sites.

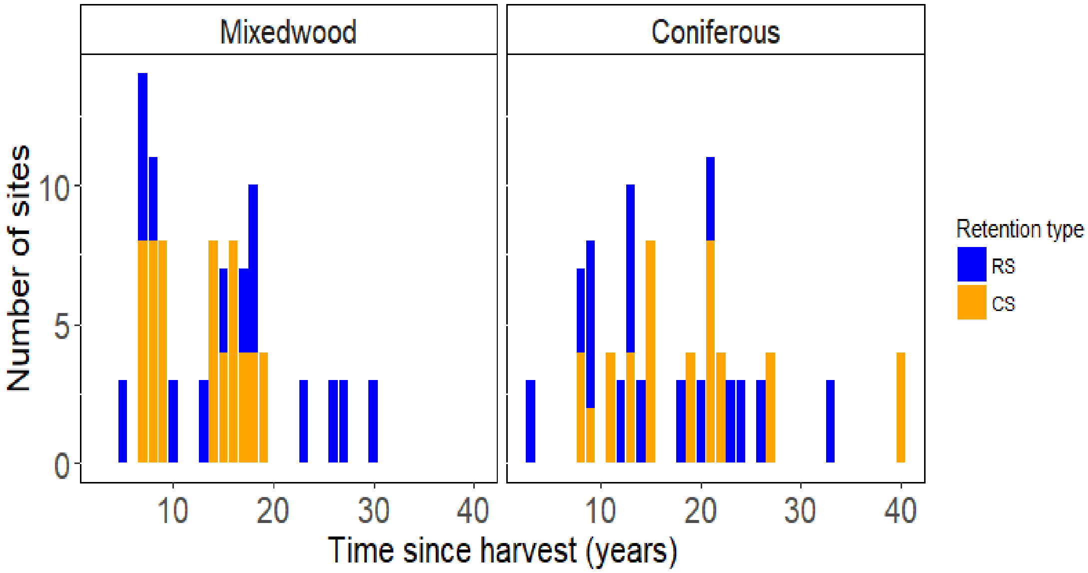

Figure 1.2 Distribution of sample sites with time since harvest (TSH) and retention type in both bioclimatic domains. RS: riparian strips, CS: cutblock separators.

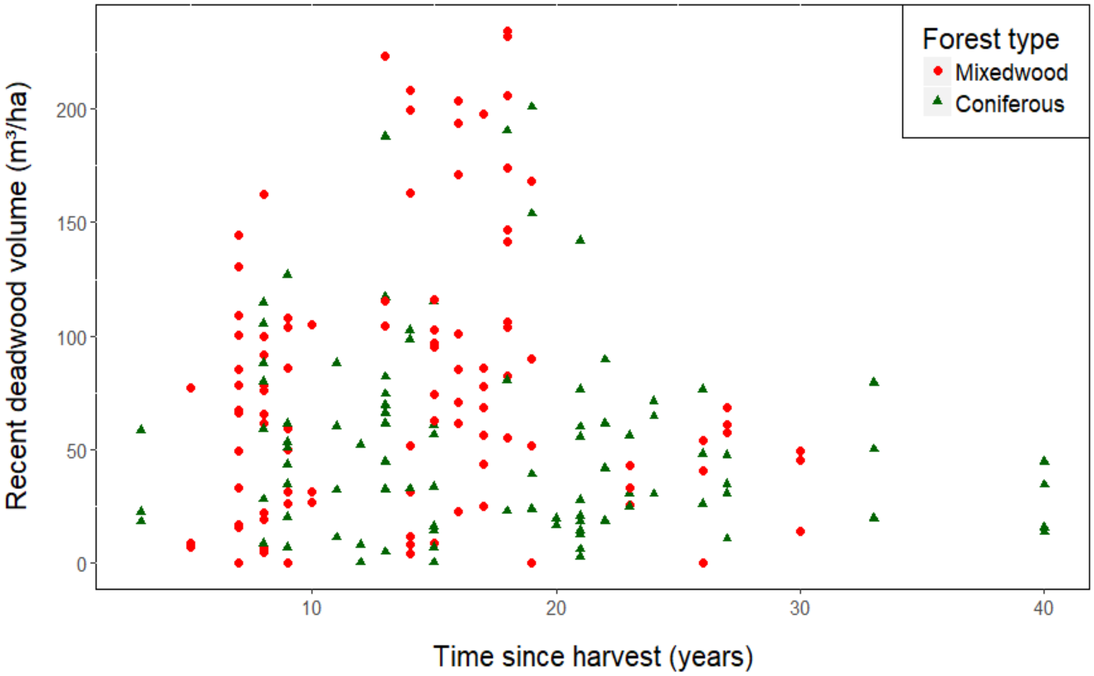

Figure 1.3 Deadwood recruitment vs time since harvest (TSH) in mixedwood and coniferous forests.

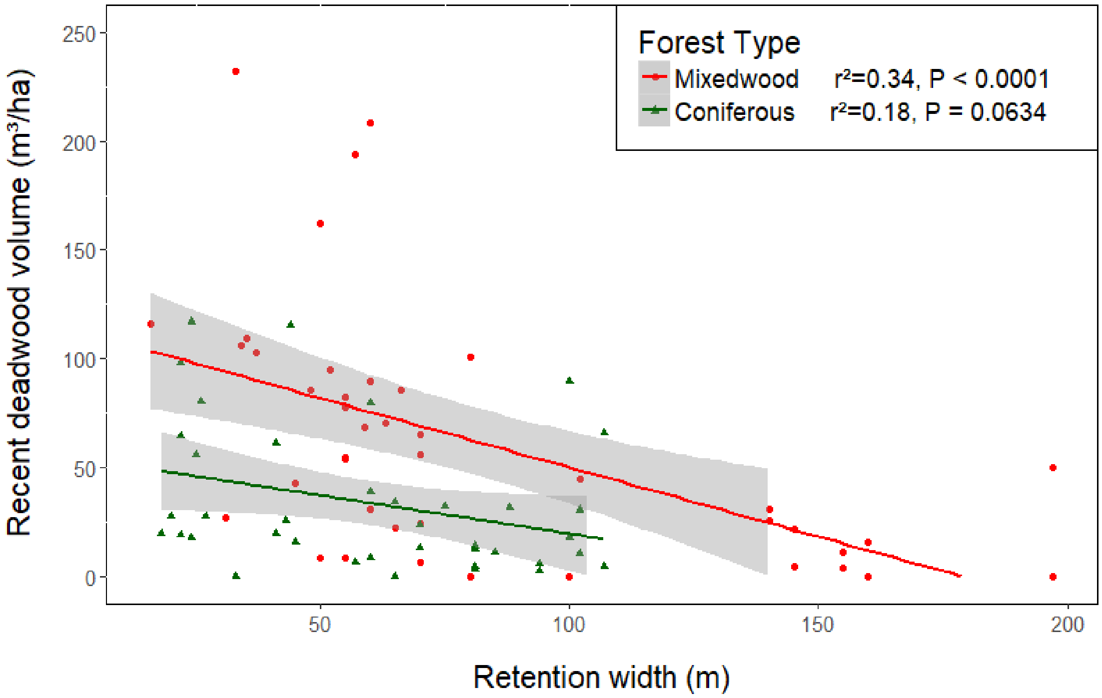

Figure 1.4 Effect of linear retention width on deadwood recruitment in the center plot of retention stands for both bioclimatic domains. A linear model was performed on both sub-sets of data, r-square and p-value are indicated in the legend.

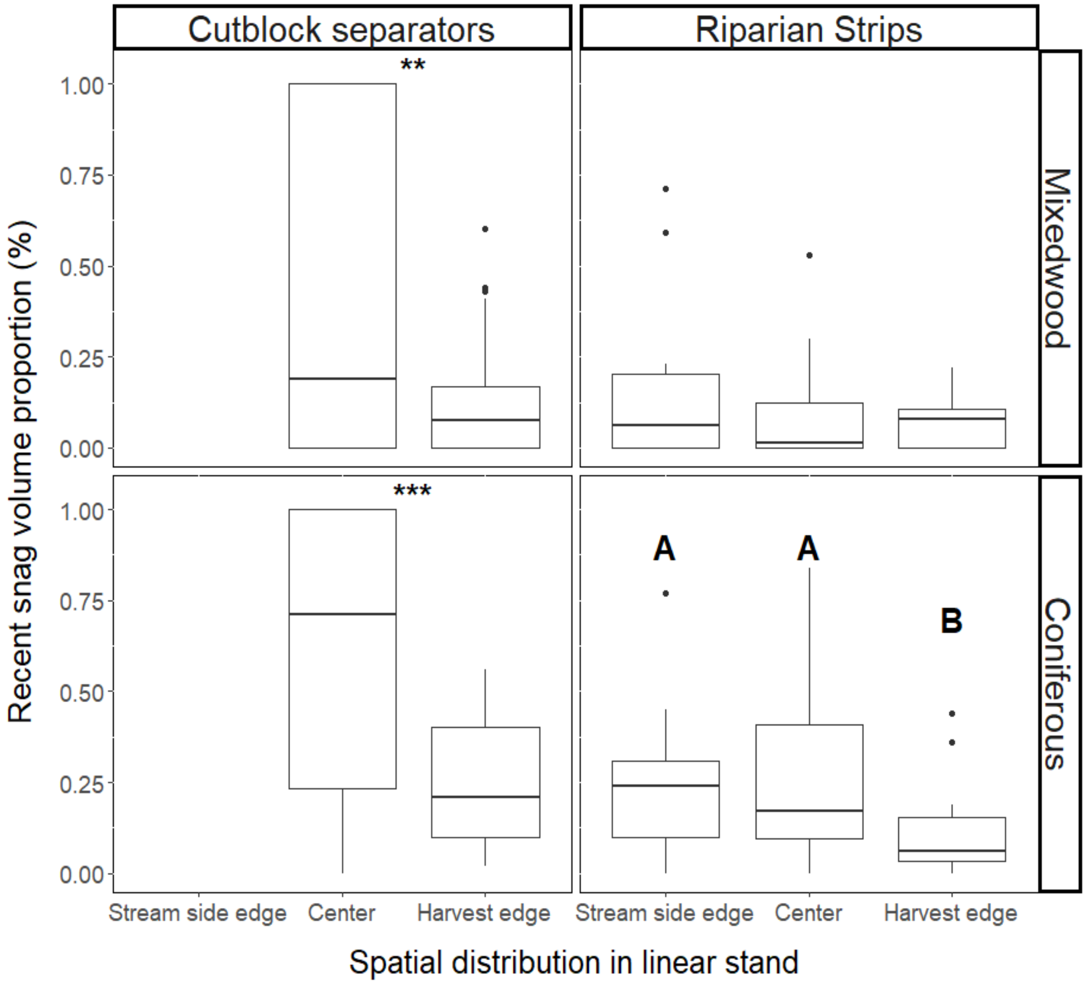

Figure 1.5 Recent snag volume as a proportion of recent deadwood across linear retention strips in cutblock separators and riparian buffer strips of harvested landscapes in boreal mixedwood and coniferous forests in northwestern Québec.

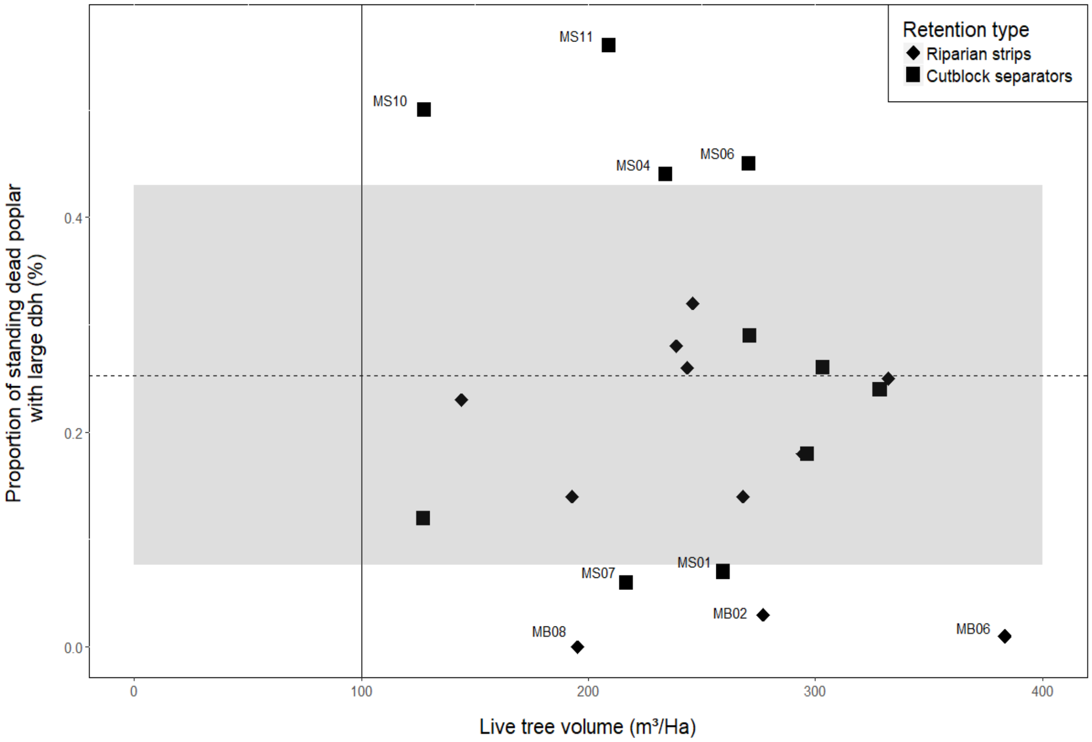

Figure 1.6 Volume proportion of large (dbh ⩾ 20cm) standing dead poplar (trembling aspen and balsam poplar) on total living tree volume. Only sites with at least 5 large aspen stems are presented. The dotted line represents the mean proportion found in natural forest (25.3%) and the grey zone represents the variability of large standing dead poplar in natural forest (SE = 17.7). Live tree volume on y-axis includes all species found in natural mixedwood stands and the threshold value of <100 m^3/ha represents the minimum live volume for a closed canopy.

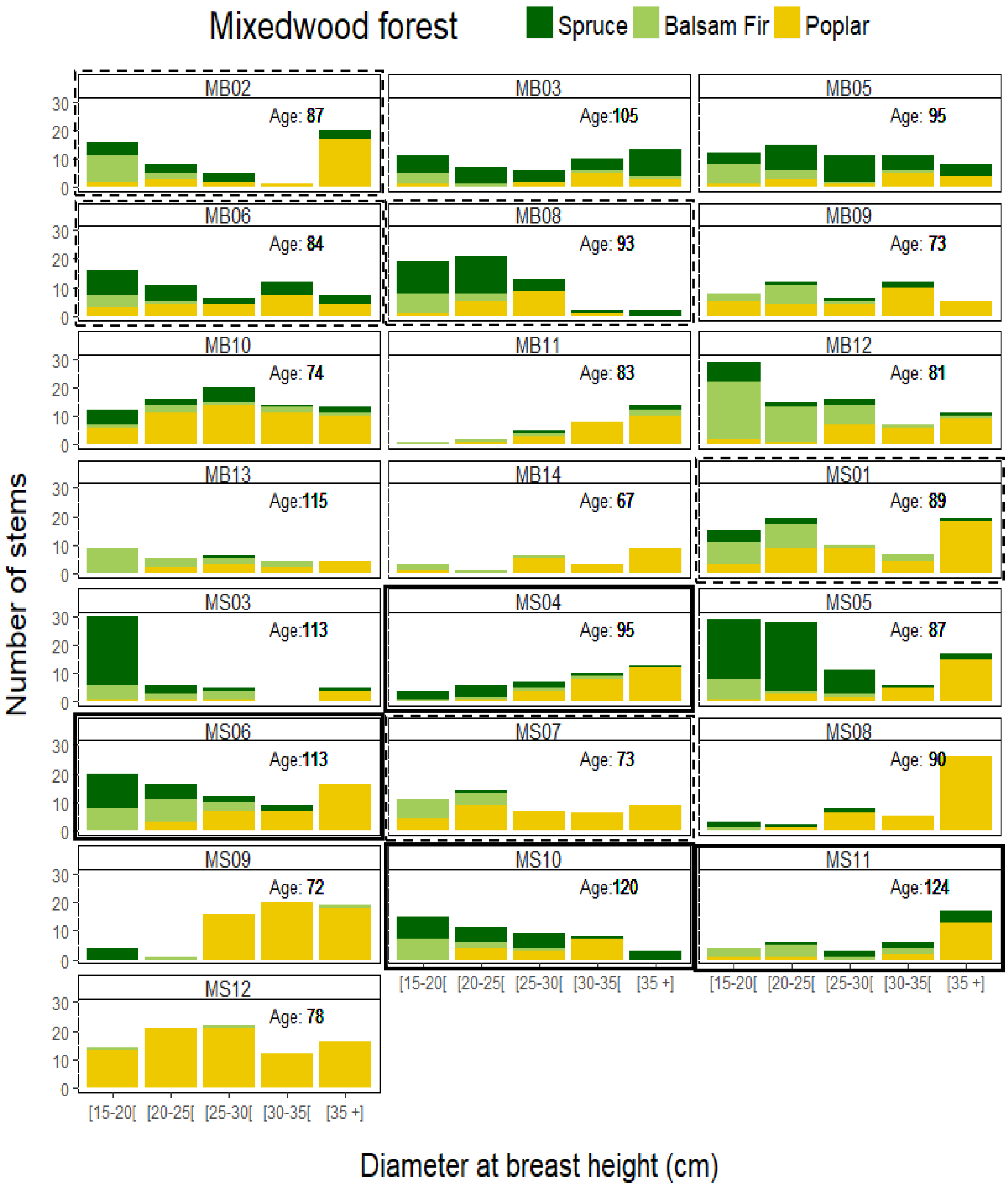

Figure 1.7 Tree diametrical distribution of each linear retention habitat sampled in the boreal mixedwood managed forest landscape. Poplar (yellow); balsam fir (light green); black and white spruces (dark green). Sites starting with PB are riparian strips whereas those starting with PS are cutblock separators. Stand age is also indicated on each diagram. Diagrams with a dark frame are sites showing a high proportion of large standing dead aspen whereas diagrams with dotted frame are sites with a low proportion of large standing dead aspen (see Figure 1.6).

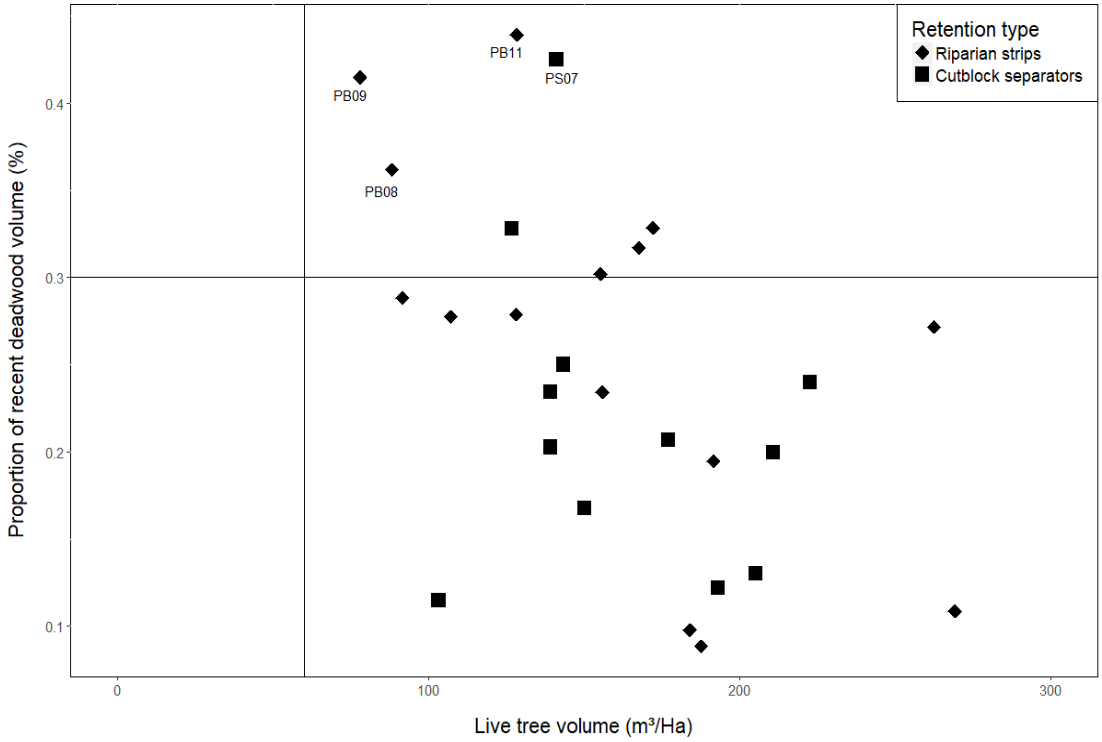

Figure 1.8 Relationship between the proportion of recent deadwood volume (ratio of recent deadwood volume to initial stand volume) and living tree volume in linear retention habitats sampled in the black spruce-feathermoss forest. Thresholds are based on natural forests. Proportion of recent deadwood should be within 30% of dead and live tree volume to be sustainable. Living tree volume should be higher than 60 m^3/ha to have a closed canopy and ensure long-term sustainability in deadwood recruitment.

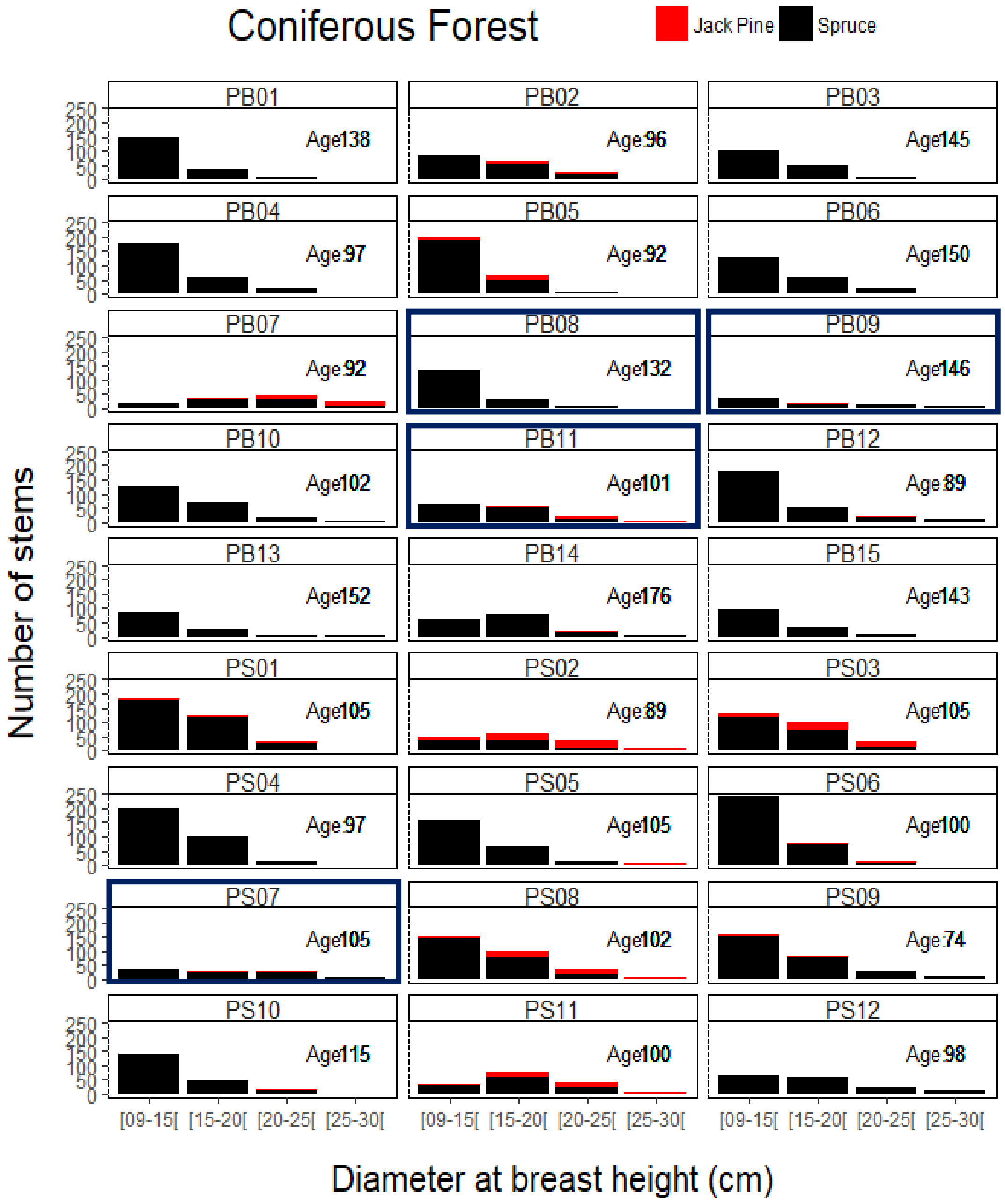

Figure 1.9 Tree diametrical distribution of each linear retention habitat sampled in the black spruce-feathermoss forest. Black and white spruces (black); jack pine (red). Site name starting with PB are riparian strips, whereas those starting with PS are cutblock separators. Stand age is also indicated on each diagram. Sites with a dark frame have very high proportion of recent deadwood volume (see Figure 1.8).

Table 1.1 Mean (range) of sample site characteristics. Initial stand volume, ISV; stand age, SA; site width, SW; recent deadwood volume, RDV.

Retention type	**SA** (Years)	**SW** (m)	**ISV** (m^3/Ha)	**RDV** (m^3/Ha)
Mixedwood forest				
Riparian strips	89 (67 – 115)	44.6 (13 – 110)	340.3 (131.1 – 604.6)	86.4 (0 – 234.5)
Cutblock separators	95 (72 – 124)	102.3 (51 – 197)	301.5 (85.4 – 553.2)	73.1 (0 – 208.5)
Coniferous forest				
Riparian strips	123 (89 – 176)	30.1 (15 – 80)	212.9 (62.5 – 427.9)	55.1 (0 – 190.5)
Cutblock separators	100 (74 – 115)	77.3 (40 – 108)	209.6 (65.9 – 377.4)	46.9 (0 – 201.0)

Table 1.2 Discrete characteristics of sample plots with detailed classification and number of observations for each class. Beaver occurrence, BO; Plot location, PL*; Organic layer thickness, OL; Orientation, OR.

Retention type	Parameter	Number of Class	Classification	n
		Mixedwood forest		
Riparian strips	BO	2	Present, Absent	27, 15
	PL	3	Harvest, Center, Stream	14, 14, 14
	OL(cm)	3	0-10;10-20;20+	29, 12, 1
	OR	4	N-S; NE-SO; E-O; SE-NO	16, 12, 5, 9
Cutblock separators	BO	2	Present, Absent	0, 56
	PL	2	Harvest, Center	28, 28
	OL(cm)	3	0-10;10-20;20+	35, 15, 6
	OR	4	N-S; NE-SO; E-O; SE-NO	18, 14, 12, 12
		Coniferous forest		
Riparian strips	PL	3	Harvest, Center, Stream	15, 15, 15
	OL(cm)	4	0-10;10-20;20 – 30; 30 +	3, 27, 8, 7
	OR	4	N-S; NE-SO; E-O; SE-NO	16, 7, 9, 13
Cutblock separators	PL	2	Harvest, Center	24, 22
	OL(cm)	4	0-10;10-20;20 – 30; 30 +	3, 25, 10, 8
	OR	4	N-S; NE-SO; E-O; SE-NO	11, 13, 18, 4

* Classification of plot location is the situation within the retention: harvest edge; center; stream side edge.

Table 1.3 Best model parameter estimates describing deadwood recruitment in mixedwood and coniferous forests with confidence intervals (CI) and degree of significance (P-value).

Forest	**Parameters**	**Estimate**	**Lower CI**	**Upper CI**	**P-Value**
Mixedwood	(Intercept)	0,43	-3,32	4,18	
	Initial stand volume	0,02	0,01	0,02	****
	Stand age	0,02	-0,02	0,06	
	Beaver occurrence	1,89	0,71	3,06	**
	(PL*) Harvest vs Stream edge	-2,55	-4,19	-0,90	**
	(PL) Harvest edge vs Center	-2,04	-3,12	-0,97	***
	Time since harvest	0,10	0,01	0,18	*
Coniferous	(Intercept)	-6,54	-11,18	-1,90	*
	Initial stand volume	0,03	0,02	0,03	****
	Stand age	0,06	0,03	0,10	**
	(PL) Center vs Stream edge	18,96	9,26	28,66	***
	(PL) Center vs Harvest edge	8,69	2,93	14,46	*
	ISV:Center vs Stream edge	-0,03	-0,05	-0,01	**
	ISV:Center vs Harvest edge	0,00	-0,01	0,02	

*Note that the level of reference for PL is harvest edge in mixedwood forest, and center in coniferous forest. This was chosen to better visualize the effect.

CHAPTER II

TREE MORTALITY, DEGRADATION AND DECOMPOSITION PATTERNS FOR TREMBLING ASPEN AND BLACK SPRUCE IN RIPARIAN BUFFERS OF MANAGED BOREAL FOREST LANDSCAPES IN NORTH-WESTERN QUEBEC

2.1 INTRODUCTION

Standing and downed deadwood play a crucial role in forest ecosystems from the moment of their creation to the last remaining fragments (Franklin et al. 1987). Every degradation stage serves either as habitat, food, drumming structure, germination substrate, or as movement corridors for a large variety of organisms (Elton 1966, Swift 1973, Speight 1989, Houle and Payette 1990, Berg et al. 1994, Bader et al. 1995, Eberhardt 1999, Kruys et al. 1999, Martin and Eadie 1999, Stokland 2001, Kimmins 2001, Imbeau and Desrochers 2002, Drapeau et al. 2009b, Nappi and Drapeau 2009, Ouellet-Lapointe et al. 2012, Robert et al. 2012). Stands with a variety of tree degradation stages provide quality habitats that contain complex vertical and horizontal structures which are important to maintain biodiversity, and particularly, deadwood dependent organisms (Grove 2002, Stokland et al. 2012). Such an environment naturally develops with the aging of forest stands as their structure becomes more heterogeneous and complex with a greater occurrence of large, decaying and dead trees (Cline et al. 1980, Harmon et al. 1986, Franklin et al. 1987, Krankina and Harmon 1995, Sturtevant et al. 1997, Lee 1998, Harper and Macdonald 2002, Aakala et al. 2007). In managed forest landscapes where residual unharvested forest is fragmented and exposed to windthrow, the decline and rarefication of old-growth features (old and dying standing trees) has been a key concern for biodiversity conservation planning. (Franklin et al. 2002, Boucher et al. 2006, Bergeron et al. 2007, Drapeau et al. 2009b, Stokland et al. 2012, Kuuluvainen et al. 2015).

Most of the commercial Canadian boreal forest is subject to timber harvesting under an even-aged clearcutting regime with variable dispersed retention (Bergeron and Harvey 1997, Drapeau et al. 2009a, Gauthier et al. 2009, 2015a). Linear remnant habitats such as riparian buffers are part of the retention habitats that can serve as lifeboats for organisms associated with old or mature forests (Franklin 1993, Franklin et al. 2000). Therefore, assessing their quality with regards to deadwood structure and dynamics is critical in a context of biodiversity conservation. These residual linear habitats consist of 20-meter wide forest strips remaining along each side of waterways (Quebec government, 2015). Such narrow stands, although adapted to the canopy opening due to local natural disturbance occurring in riparian ecotones, can be affected by edge creation after harvest (Darveau et al. 1994, Ruel et al. 2001, Mascarúa López et al. 2006). Furthermore, many studies have demonstrated how forest management can modify tree mortality and natural degradation patterns of dead trees (Cline et al. 1980, Storaunet and Rolstad 2002, MacDonald et al. 2004, Doyon et al. 2005, Garber et al. 2005, Vanderwel et al. 2006, Bladon et al. 2007, Bose et al. 2014). In addition, beaver activity in riparian mixedwood forests can strongly affect deciduous tree species, altering tree mortality and degradation processes by directly felling of healthy live trees (Naiman et al. 1986, Nummi and Kuuluvainen 2013). Because tree mortality and degradation pathways genuinely influence stand structural complexity, understanding tree species' degradation patterns is part of the quality assessment necessary in these retention habitats.

Cause of mortality is a determinant factor driving degradation pattern (Taylor and MacLean 2007, Parish et al. 2010). Standing dying trees have the potential to provide a large variety of structures along their degradation pathways (Parish et al. 2010, Angers et al. 2012a), whereas mortality by stem breakage can reduce the longevity of the snag's degradation state (Garber et al. 2005). Tree uprooting bypasses the chronosequence of degradation stages of snags from standing to downed wood while providing important microtopographic features (Schaetzl et al. 1989; Rich et al. 2007). Premature stem breakage can also diminish the availability of senescent trees. Quantifying average snag longevity of tree species allows to project their retention through time which is an important indicator of their long-term availability and thus habitat quality for snag users (Dahms 1949, Keen 1955, Bull 1983, Lee 1998, Everett et al. 1999, Storaunet and Rolstad 2004, Garber et al. 2005, Boulanger and Sirois 2006, Russell et al. 2006, Bond-Lamberty and Gower 2008, Angers et al. 2010, 2011). Persisting snags in linear features may be critical mesofilters (*sensu* Hunter 2005) in a biodiversity conservation strategy (Edworthy and Martin 2013) in aggregated clearcut landscapes. Decomposition rate for both snags and logs is also an important indicator of deadwood retention time and degradation patterns (Johnson and Greene 1991, Alban and Pastor 1993, Boulanger and Sirois 2006, Angers et al. 2010). This process is not constant during the whole degradation sequence, but changes over time and generally results in wood density loss (Johnson and Greene 1991, Harmon et al. 2000, Bond-Lamberty et al. 2002, Wang et al. 2002). Many studies have examined wood density distribution within a degradation classification scheme and assessed the correspondence between external appearance of decaying trees and the true state of internal wood decay (Cline et al. 1980, Krankina and Harmon 1995, Hale and Pastor 1998, Yatskov et al. 2003, Vanderwel et al. 2006, Robert et al. 2012, Angers et al. 2012a). Degradation processes can be influenced by several environmental conditions such as stand age, type, and density, productivity, humidity, and disturbance history (Bull et al. 1980, Harmon et al. 1986, Krankina and Harmon 1995, Lee et al. 1997, Spies 1998, Lee 1998, Siitonen et al. 2000). Other factors acting at the tree-level include tree species, size, height, position (downed or standing), humidity, and live crown ratio before death (Cline et al. 1980, Raphael and Morrison 1987, Morrison and Raphael 1993, Hale and Pastor 1998, Parish et al. 2010).

In this paper, we assess degradation pathways of standing dead trees of trembling aspen and black spruce, two of the main boreal species in remnant riparian strips in clearcut agglomerations of boreal mixedwood and coniferous landscapes in eastern North America. We evaluate how these patterns differ from those occurring in natural unharvested forest landscapes and assess the quality of linear retention habitats with regards to their capacity to maintain key structural features (standing dead trees) of mature and old forests in managed forest landscapes. More specifically, our three principal objectives were to (1) determine snag longevity and breakage patterns in black spruce and trembling aspen, (2) measure decomposition rates in those snags and, (3) assess the correlation between our degradation classification system, the decomposition rate (wood density loss) and time since death. We hypothesized that snag longevity would be shorter in our study sites than in natural forests, whereas decomposition rates would be slower since riparian strips have a greater exposure to openings than continuous forest stands in unharvested landscapes. We also predicted that ascending degradation classes (from fresh to well-decomposed) would positively correlate with density loss and time since death.

2.2 METHODS

2.2.1 Study area and species

The study was conducted in a vast territory (15 000 km^2) of managed boreal forest in northwestern Quebec in Abitibi and south of Nord-du-Quebec (78°30' – 79°30' W, 48° 00' – 50°00'N) (Figure 2.1) covering parts of two sub-bioclimatic domains. In the south, a mixedwood ecosystem, the balsam fir-white birch forest, and in the north, a coniferous ecosystem, the black spruce-feathermoss forest (Saucier et al. 2003). This study region is located in the Northern Clay Belt, a major physiographic region created by proglacial lake depositions of Ojibway and Barlow Lakes (Vincent and Hardy 1977). The region is characterized by a relatively flat topography; mean temperature varies between 0°C and 2.5°C, annual precipitation between 800 and 900 mm and the growing season lasts from 150 to 160 days (Harvey and Leduc 1999).

This study concentrates on the dominant tree species from each bioclimatic domain, i.e., trembling aspen (*Populus tremuloides*) for the balsam fir-white birch domain and black spruce (*Picea mariana*) for the black spruce-feathermoss domain. Both species play important ecological roles for deadwood-dependent species (Saint-Germain et al. 2007, Vaillancourt 2007, Drapeau et al. 2009b) and are commercially harvested in the region.

After disturbance, forest succession in the southern boreal mixedwood is initially dominated by shade-intolerant deciduous trembling aspen and white birch (*Betula papyrifera*). As the forest ages, these trees die, coniferous species balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), black spruce and northern-white cedar (*Thuja occidentalis*) gradually attain and dominate the canopy (Bergeron and Dubuc 1989, Harvey et al. 2002). The natural disturbance regime is primarily driven by fire (Bergeron et al. 2004a), and outbreaks of insects, such as spruce budworm (*Choristoneura fumiferana* (Clem.)) and forest tent caterpillar (*Malacosoma disstria* (Hbn.)) (Morin et al. 1993, Bergeron et al. 1998, Cooke and Lorenzetti 2006). The fire cycle in the mixedwood part of the study area vary from 100 to more than1000 years (Bergeron et al. 2001, Gauthier et al. 2015b); last major fires in this sector occurred in 1760 and 1923 (Bergeron 1991, Dansereau and Yves Bergeron 1993). Spruce budworm outbreaks tend to cause less tree mortality than in eastern Québec but still affect balsam fir growth and survival and, to some extent, that of black and white spruce (Bouchard et al. 2005). The last outbreak in this region occurred between 1972 and 1996 (Bouchard et al. 2005). Forest tent caterpillar can be a major cause of mortality for trembling aspen and other deciduous species. Outbreaks occur approximately every 10 years in this region, with the last major epidemic taking place in the late 1990’s – early 2000’s (Cooke and Lorenzetti 2006). Signs of an outbreak started to appear towards the end of our sampling season.

The black spruce-feathermoss forest is dominated by black spruce and jack pine (*Pinus banksiana*) with a lower occurrence of balsam fir and some intolerant deciduous species (Gauthier et al. 2000). Fire cycle in this region vary from 600 to 800 years (Gauthier et al. 2015b), and mean area burnt is larger in the coniferous forest than the mixedwood forest (Bergeron et al. 2004b). After fire, when present in the buried forest, jack pine dominates the regenerating stand in association with black spruce (Harper et al. 2003). As the stands age, paludification, which consists of an accumulation of organic matter, slow drainage and limited access to soil nutrients occurs on flat and lowland sites (Simard et al. 2007). These conditions tend to favorize black spruce a species tolerant to poorly drained and nutrient-poor site conditions (Gauthier et al. 2000). The relatively low presence of balsam fir diminishes the influence of spruce budworm outbreaks, and hence, in the absence of fire, secondary disturbances such as wind-related death, diseases, and senescence modify stand structure (Kneeshaw and Bergeron 1996, Gauthier et al. 2000, Harper et al. 2002).

The boreal forest is commercially harvested with an even-aged management system leaving retention habitats such as island patches, riparian strips, and linear cutblock separators. Our study concentrates on riparian strips along cutblock areas older than ten years of age.

2.2.2 Data collection

Sites were selected *a priori* using ArcGIS software and digital forest inventory provided by the government of Quebec (1:20 000). The selection was based on tree species composition (black spruce as dominant species in the coniferous forest; trembling aspen as dominant in the mixed forest), soil type, drainage, and canopy cover (≥60%). Selected sites had a minimum stand age of 80 years, and adjacent cutblocks were at least ten years old. To determine the exact stand age, we sampled cores below one meter in five dominant trees per site in our coniferous study sites and of ten dominant trees per site in the mixedwood sites. We also measured the organic layer thickness (cm) and the retention width (m) in the middle of each study plot (Table 2.1). Data collection was performed in the summer of 2015.

A 400 m^2 plot (20m x 20m) was placed randomly in every site, at least 30 meters from the closest road. Because riparian buffers are 20 meters wide, sampling plots were covering the whole retention width. All dead trees of the studied species whose base was situated inside the plot and having a diameter at breast height (dbh) over a minimal threshold (15 cm for trembling aspen, 10 cm for black spruce) was classified and samples. These dbh minimal thresholds were based on the growth rate of each species to ensure an adequate number of growth rings for dendrochronological crossdating analyses (Angers, V., personal communication). Characterization of standing trees consisted of measuring the diameter at breast height (dbh) and determining their degradation stage based on Imbeau and Desrochers'(2002) classification system for standing conifers and an adapted version for deciduous trees (Ouellet-Lapointe 2010). The classification system of Despont et al (2002) was used for downed logs. Table 2.2 provides a textual description of our degradation classification system. Sites in which less than 15 dead trees were sampled in the first plot had an additional adjacent plot established to raise the sample size. A total of seven plots were sampled in each forest type for a total of 112 in black spruce and 81 in trembling aspen stands.

Cross-section disks (5 cm thick) were collected at two locations on dead trees using a chain saw. The first one was taken close to the base of the tree and the second one was taken close to the crown (with a minimal diameter of six cm to ensure a minimum number of growth years). Two cross-sections per stem permitted cross-dating validation and increased the likelihood of capturing the last growth ring (Angers et al. 2012b). Sampling of disks generally avoided sections with advanced degradation. Disks were taped for identification and to keep sections intact. We sampled trees in advanced deterioration as long as stems could be dated.

2.2.3 Statistical analyses

2.2.3.1 Dendrochronological analysis

Dendrochronological analysis was used to determine the last year of growth for every dead tree. Samples were dried and sanded until early and late wood of annual rings could be distinguished. Broken samples were glued prior to sanding. Measurements of growth rings were performed on two perpendicular radii for every sample using CooRecorder Software. Samples were digitized at high resolution (1600dpi). Each series of measurements were cross validated using CDendro Software, first among the same-sample radii, and within the same-tree radii to detect missing or double rings. Each radius was then crossdated against a master series for the respective species to determine the last year of growth. Crossdating was confirmed using COFECHA (Holmes 1983). Master series were built using 5 to 10 cores from live trees sampled in study sites and validated with an existing master series for each species available at UQAT's dendrochronology lab for the same study region (Drobyshev, unpublished data). Datation was successful for 76% of our sampled dead trees. Over-decayed trees, cross sections missing the last growth ring, and trees younger than 50 years old were dismissed because crossdating was not feasible (33% of aspen, and 21% of black spruce). The difference between the last year of growth and the sampled year defines time since death (TSD).

2.2.3.2 Snag longevity

To evaluate snag longevity, we used the descriptive approach proposed by Angers et al. (2010). Proportion of snags still standing (ratio between the cumulative number of dead trees still standing and the total number of dead trees (standing and fallen)) was calculated for each year after death (i.e. at year 1, 2, 3, etc. after death for each individual stem). This proportion was then plotted graphically with time since death (TSD). These survival curves allow us to evaluate the occurrence of a lag-time before falling, and the slope translates the range span of survival time of snags between time of death and falling. Half-time, described as the time required for half of the dead trees to fall, can estimate an average survival time for snags to persist as standing stems. Uprooted trees and trees felled by beaver activity were not included in this analysis.

The influence of dbh on snag longevity (time exposed standing) was evaluated using linear regression, and statistical assumptions were verified graphically.

2.2.3.3 Decomposition rate analysis

Annual loss in wood density can be interpreted as the decomposition rate. Dry weight and volume of cross-section disks were measured to undertake a chronosequence analysis for each species. This analysis was only done on cross sections collected at the base of stems. Disks were oven-dried at 60°C until they stopped losing weight for at least 24 hours; weight measures were taken with a 0.01g precision balance. Bark, moss, and other plant residue were removed from samples prior to weight and volume measurements. Insect galleries were also noted for each cross-section and classed as none, little or large. Volume was calculated using cylinder volume equation, where average diameter and height were calculated using the longest and the shortest measurements of cross-section (measured to 0.1cm precision). When pieces of disk were missing, we estimated this volume and subtracted it from the calculated cylindrical volume.

The negative exponential model has been widely used to evaluate degradation rate (Foster and Lang 1982, Yatskov et al. 2003, Brais et al. 2006, Angers et al. 2012b):

$$D_t = D_0 * e^{-k*TSD}$$

where D_t is the wood density (g/cm^3) at a given TSD (year), D_0 is the initial density, and k is the degradation rate (year^{-1}) constant (Olsen 1963). Simple linear model has also been reported to adequately represent this relationship (Graham and Cromack 1982, Angers et al. 2012b):

$$D_t = m * TSD + D_0,$$

where m is the proportion of density that is lost each year. We computed both models for snags and logs separately, with site as a random effect.

Degradation rate increases considerably when stems are in direct contact with the ground (Mattson et al. 1987, Johnson and Greene 1991, Wei et al. 1997, Næsset 1999, Wang et al. 2002, Boulanger and Sirois 2006). Determining the decomposition rate of logs without knowing the time since tree fall can therefore lead to an important underestimation (Storaunet and Rolstad 2002). Some studies have utilized snag falling rate to approximate time since fall (Johnson and Greene 1991, Boulanger and Sirois 2006). However, several studies have also pointed out that decomposition rates in logs vary with decay class making the decomposition rate analyses in logs difficult to extrapolate to the stand level (Hale and Pastor 1998, Harmon et al. 2000, Bond-Lamberty et al. 2002, Wang et al. 2002, Bond-Lamberty and Gower 2008).

Consequently, we decided to analyze the decomposition rate on snags only and pursue with an analysis on degradation classification and density loss for logs.

Our snag longevity and decomposition rates are compared with those of Angers et al (2010, 2012b). These authors used a similar sampling protocol on the same species and their values represent a control in forests originating from natural disturbances in our study region.

2.2.3.4 Degradation stages, wood density loss and time since death

Deadwood is often categorized with an ordered classification depicting their degree of degradation using apparent gross attributes. For standing dead trees, stems with many branches, intact bark, hard wood, and full height are in the early degradation stage, and as they lose these attributes, they are classified into subsequent degradation stages (Imbeau and Desrochers 2002). Downed deadwood is categorized according to wood hardness, portion of bark retention and the amount of the stem that is buried (Desponts et al. 2002). Degradation classifications may vary slightly among studies but are generally based on the same characteristics as those in our study (Cline et al. 1980, Triska and Cromack. 1980, Yatskov et al. 2003, Boulanger and Sirois 2006). We evaluated the relationship between degradation class, wood density and as time since death in order to evaluate the capacity of these classification systems to truly represent the state of wood decomposition. We performed multiple comparisons of average wood density and average time since death among degradation stages using least square means for unbalanced samples (lsmeans package by Russell Lenth) to assess how these two variables change along the classification system and within individual classes. Some classes were poorly represented, in which case we merged them to the most similar class in terms of density mean and range.

2.3 RESULTS

2.3.1 General mortality patterns

Riparian buffers do not appear to be subject to high tree mortality immediately following their creation. Although no site indicated a significant difference in annual mortality between pre and post harvest (data not shown), two sites, one in mixedwood forests and one in coniferous forests, showed a marked input in tree mortality a few years after harvest (MB05, Figure 2.2). One site (PB03) harvested in 1982 was too old to detect any datable dead trees prior to harvest (Figure 2.2).

Our results show a general view of tree degradation pathways. Trembling aspen trees that die standing do not remain intact for very long (3.67 years, see table 2.3). Once the trunk breaks, trees tend to be more stable as most of our sampled snags were in this form (n =28; TSD = 11.47). While only one snag was created as a result of girdling by beavers, most of downed aspen logs were the results of beaver activity (n=17). Average time since death (TSD) in logs resulting from breakage was similar to that of logs downed by beaver. Uprooting was not an important cause of death in trembling aspen (Table 2.3).

Intact standing dead trees in black spruce were more abundant than intact trembling aspen, and their average TSD was twice that of intact aspen snags (Table 2.3). Broken snags constituted 40% of spruce snags. Broken spruce logs were more abundant than uprooted, although uprooting was an important cause of death (54.8%, Table 2.3). In general, the average value of TSD was higher for black spruce than for trembling aspen.

2.3.2 Survival curves

Survival curves of trembling aspen and black spruce showed somewhat different patterns (Figure 2.3). Trembling aspen exhibited a lag time of 2 years, indicating a delay during which dead stems tend to remain standing whereas black spruce showed no lag time and entered the falling period from the year of death. Once trembling aspen snags start to fall, recruitment of downed logs was nearly constant through time, as the linear model indicates that annual probability of falling is 3.54%. Black spruce snags showed a shorter half-time and a steeper slope of downed dead tree recruitment over the first two decades. However, after 18 years recruitment slowed considerably as indicated by the reverse sigmoid curve (Figure 2.3B). The highest fall rate suggested by the model, 30.7%, occurred between 10 and 20 years after tree death. This indicates that spruce snags which stood more than 20 years after death are more likely to persist for a longer period. No relationship was observed between time since death and dbh among snags of either species ($P = 0.318$ for trembling aspen; $P =0.861$ for black spruce).

2.3.3 Decomposition rates

Both regression models, negative exponential and simple linear, presented a similar fit with our data and showed similar p-values (Table 2.4). Decomposition rate of trembling aspen snags was slightly slower than in natural forests of the same region (Table 2.4). Decomposition rate in black spruce snags was, however, one order of magnitude higher in riparian buffers than in natural forests (Table 2.4).

2.3.4 Degradation stage and density loss

Distribution of wood density values according to degradation stage showed that snags and logs were two distinct components in our system and that they deteriorated at different rates. Recently downed deadwood (class 9) had a higher average density than most advanced snag degradation stages (class 7-8, table 2.2) for both tree species (see Figure 2.4A and 2.5A). This difference was significant in trembling aspen (P-value = 0.005) and marginally significant in black spruce (P-value = 0.073), indicating that recently downed deadwood was more likely to be recruited from degradation classes 4 to 6, whereas standing stems in degradation classes 7 and 8 may have fallen to the ground directly as class 10 or greater.

Density loss along the degradation trajectory of snags was similar for both species presenting a gradual decrease with advanced degradation (Figure 2.4A and 2.5A). In both species, degradation classes 4 and 5 were grouped because of low representation and variability in average density. In trembling aspen, degradation classes 6 and 7 were also grouped for the same reasons, whereas black spruce had no snag in the last snag degradation class (stage 8) making the comparison between species difficult. Overall, the pattern and the decrease of wood density along the degradation classification were similar.

Average time since death in degradation classes 4-5 and 9 of trembling aspen was lower than the others, however the overall pattern showed no significant differences among degradation classes for this species (Figure 2.4B). In black spruce, the pattern observed with time since death among degradation classes indicate that, in general, dead stems go through the degradation classes in a chronological order (from 4 to 10+). (Figure 2.5B).

Once on the ground, dead stems of aspen and black spruce appear to undergo density loss and apparent degradation at similar rates (Figure 2.4 and 2.5). While, density loss between degradation stage 9 and 10+ was significant, indicating a fast decomposition rate, it should be noted that 10+ includes advanced degradation stages 11 and 12.

2.4 DISCUSSION

Our objective in this chapter was to assess the quality of riparian buffers in managed forest landscapes with regards to their capacity to maintain key structural features (standing dead trees). For trembling aspen, standing dead trees tended to experience stem breakage in the first few years after death, followed by a period during which snags remain relatively stable (Qinghong and Hytteborn 1991, Lee et al. 1997, Siitonen et al. 2000). This may be partly explained by its capacity to reproduce by clonal suckering creates a complex and well-developed root network that makes this species less prone to uprooting (Peterson and Peterson 1992, Angers et al. 2010). Uprooting rate in the unmanaged forest is around 12-18% (Hill et al. 2005, Angers et al. 2010). In riparian buffers, we found a rate considerably lower (3.7%) suggesting a root adaptation to wind exposure owing to existing opening in water courses. On the other hand, aspen in mixedwood riparian retention was vulnerable to girdling by beaver (see Chapter 1). Logs downed by beaver tend to supplant the uprooting disturbance in stands adjacent to a watercourse (Kuuluvainen et al. 2002). Beaver is considered a keystone species as it profoundly modifies its environment by felling trees and flooding terrestrial zones (Naiman et al. 1986, Nummi and Kuuluvainen 2013). Its preference for deciduous species, in particular poplar (Naiman et al. 1986), may directly affect habitat availability for cavity users in riparian buffer strips in mixedwood forests.

Standing dead black spruce trees appear to remain intact (little or no snapping) for longer periods than trembling aspen in the riparian buffers, a pattern similar to that found in natural forests (Aakala et al. 2008, Angers et al. 2010). However, its shallow root system combined with the accumulation of organic matter in the Clay Belt region makes this species highly susceptible to uprooting in our study area (Smith et al. 1987, Harper et al. 2003). Also, the opening created by the adjacent clearcut of our riparian buffers appears to increase the uprooting events as our results (54.8%) were considerably higher than what was found in natural forest (17.9%) for the same study region (Angers et al. 2010). Uprooting in managed coniferous landscapes has been reported to be largely influenced by initial stand conditions prior to harvest, such as topography, stand density and surrounding species in the stand (Elie and Ruel 2005, Riopel et al. 2010, Lavoie et al. 2012). Although riparian buffers do not seem threatened with an excessive mortality, discrepancies in principal causes of death produce a different vertical and horizontal structure in these linear habitats than in unharvested forest blocks.

2.4.1 Snag survival

Our results on snag survival for both species were very similar to those measured in natural forests of the same region and forest cover types. In fact, Angers et al. (2010) found a lag time followed by a linear relationship with time since death for trembling aspen, and a reverse sigmoidal relationship with no lag time for black spruce.

In trembling aspen, however, our lag time was shorter compared with other studies in natural forests where it was reported to be 5 to 8 years (Lee 1998, Angers et al. 2010), thus suggesting a shorter stability period in riparian buffers. However, the half-time estimate in our linear retention in managed ecosystems was similar to the 15-19 years found in natural forests (Lee 1998, Angers et al. 2010). Lee (1998) reported a reverse sigmoidal survival curve, starting with a slower falling rate for the first 20 years followed by a rapid fall, and the overall fall rate was 9-20%, a somewhat higher rate than the one obtained from our linear regression. Our result on trembling aspen fall rate was similar to the one found in boreal old-growth forest in Ontario (Bond-Lamberty and Gower 2008) whereas black spruce fall rate was also similar to fall rates of coniferous species in Canada's western forests (Dahms 1949, Keen 1955, Bull 1983).

The occurrence of lag time in snag survival curves has been reported in many studies and it is highly variable depending on species, ecosystems and landscape (Keen 1929, 1955, Dahms 1949, Cline et al. 1980, Bull 1983, Lee 1998, Garber et al. 2005, Russell et al. 2006, Angers et al. 2010, 2011). The shorter lag time in our study could be explained by the opening created by the even-aged harvest influencing the degradation processes in exposed riparian buffers. Although trembling aspen in riparian buffers might start with a falling period earlier than in natural forests, its falling pattern indicates a similar retention time as the one observed in unharvested natural forests.

Several studies reported no lag-time period on the survival curve of the genus *Picea* (Everett et al. 1999, Storaunet and Rolstad 2004, Boulanger and Sirois 2006, Angers et al. 2010, 2011). The absence of lag-time in black spruce survival curve could be a result of the intrinsic biology of this species with a degradation pattern that starts promptly after death and makes it harder to detect. A reverse sigmoidal shaped survival curve for spruce was also found in other studies for natural and managed forests (Lee 1998, Garber et al. 2005, Russell et al. 2006, Parish et al. 2010). Half-time in black spruce for our riparian buffers was slightly shorter than in other studies conducted in natural mature and old spruce forest stands or recently burned stands which reported 16 to 18 years (Boulanger and Sirois 2006, Angers et al. 2010). However, it was longer than the six years found in intensively managed stands (Garber et al. 2005). Black spruce snag longevity was moderately reduced in riparian buffers compare to natural forests yet enhanced compared to other intensively managed black spruce stands.

2.4.2 Decomposition rates

Aspen decomposition rate was not altered by the even-aged harvest opening, whereas black spruce snags experienced an important increase in decomposition rate in riparian buffers. The lower rate found in natural forest for black spruce could be explained by the occurrence of very old black spruce snags in Angers et al (2012b) resulting in a low mean decomposition rate.

Contrary to our results, previous studies have found a higher decomposition rate in aspen than in spruce (Alban and Pastor 1993, Angers et al. 2012b). Others have reported a decomposition rate in coniferous snags close to zero (Johnson and Greene 1991, Boulanger and Sirois 2006). Riparian buffers are inclined to higher humidity, a major factor influencing snag decomposition rate (Harmon et al. 1986), which could explain our result. Black spruce's higher decomposition rate could also be explained by the occurrence of saproxylic insect galleries in advanced decay snags. Wood-boring insects in trees remove an important amount of wood, thus reducing the measured density. In effect, spruce cross sections had a greater frequency of insect galleries than aspen cross sections (unpublished data). High decomposition rates in black spruce snags could also explain their reduced longevity compared with snags in natural forests.

2.4.3 Degradation classes, wood density, and time since death

As expected, there was an important change in the degradation pattern once dead stems transited from snags to logs (Johnson and Greene 1991, Krankina and Harmon 1995, Storaunet and Rolstad 2002). Dead stems enter the downed dead wood pool in a range of wood densities and time since death. Furthermore, the significant density differences between log degradation stages suggest rapid decomposition rates. This fast degradation is partly due to the 10+class grouping classes 10, 11, and 12 in one. However, most of our datable downed logs were in the recent degradation stages (9 and 10); as advanced degradation classes were too decomposed to successfully cross-date.

The relationship between degradation stage and wood density loss for both species suggests that physical degradation and decomposition processes are operating in parallel. As decomposition processes take place, wood density of dead stems and distinctive visual attributes, like branches and height decreases. This relationship has also been observed in other studies (Harmon et al. 1987, Krankina and Harmon 1995, Yatskov et al. 2003).

There were no major differences observed between species regarding density loss pattern. However, average time since death according to degradation class showed different schemes between the two species and was strongly related to the cause of trees mortality. The absence of a relationship between degradation stage and time since death in trembling aspen suggests that the degradation process begins prior to death. Dead trembling aspen stems entered the downed wood pool from any decay stage (live or snag). This degradation timeline for deciduous species was also found in other studies (Hale and Pastor 1998, Yatskov et al. 2003, Vanderwel et al., 2006) and was attributed to species susceptibility to heart rot (Hale and Pastor 1998, Siitonen 2001). A similar analysis on trembling aspen in natural mixedwood boreal forest indicated a slightly stronger relationship between degradation stage and time since death (Angers et al. 2012a). This discrepancy could be due to the greater exposition of live trees to wind in riparian buffers making them more susceptible to stem breakage, and thus subject to directly entering the deadwood pool in class 6 or greater.

Black spruce degradation patterns correlated both with time since death and wood density loss. This relationship between time since death and degradation class has also been observed in other studies involving coniferous species (Cline et al. 1980, Aakala et al. 2008, Angers et al. 2012a). In most cases, black spruce entered the deadwood pool in the first degradation stage (class 9) and evolved through the degradation process and the successive degradation classes.

While our results suggest that the creation of riparian buffers did not systematically increase tree mortality in the years following harvest some sites, however, showed higher mortality rates after harvest. This could partly be due to limitations in our capacity to detect mortality with our protocol since data collection was performed at one point in time, and therefore older death may be underestimated. Trees that died by uprooting or stem breakage near the base would tend to quickly enter the downed deadwood trajectory with accelerated degradation compared to standing dead stems (Mattson et al. 1987, Johnson and Greene 1991, Wei et al. 1997, Næsset 1999, Wang et al. 2002). Also, well decomposed stems could have been missed in our sampling protocol, or some samples may have been dismissed because of their poor quality for dendrochronology analyses.

2.4.4 Conclusion

Tree mortality, rate of fall, degradation, and decomposition pathways define stands' vertical and horizontal structure. Understanding these patterns in retention habitats of managed forest landscapes is critical for assessing the quality and sustainability of these habitats for deadwood dependent species. Our study on riparian buffers showed slight differences with natural forests of trembling aspen and black spruce but does not indicate that these remnant habitats are at risk with regards to the overall sustainability and recruitment of deadwood. Although the interconnected root system of trembling aspen provides a strong resistance to uprooting in linear retention habitats, the species' vulnerability to stem breakage is amplified. Snag longevity is not diminished, but the diversity of snag degradation stages could be reduced in the long term. In contrast, black spruce showed a strong vulnerability to uprooting, which is a mortality cause for trees that bypasses the snag phase. Decomposition and fall rate in snags were also slightly higher in riparian buffers compared with natural forests, possibly indicating a lower amount of standing dead wood in boreal coniferous riparian buffers as time since harvest increases. An increase in riparian buffer width would likely reduce wind exposure at the core and increase sustainability and diversity of vertical stand structure in linear riparian buffers, thus improving their functional role as lifeboats for many deadwood dependent organisms in old forests.

1.5 REFERENCES

Aakala, T., Kuuluvainen, T., Gauthier, S., et De Grandpré, L. 2008. Standing dead trees and their decay-class dynamics in the northeastern boreal old-growth forests of Quebec. For. Ecol. Manage. **255**(3–4): 410–420. doi:10.1016/j.foreco.2007.09.008.

Aakala, T., Kuuluvainen, T., De Grandpré, L., et Gauthier, S. 2007. Trees dying standing in the northeastern boreal old-growth forests of Quebec: spatial patterns, rates, and temporal variation. Can. J. For. Res. **37**: 50–61. doi:10.1139/x06-201.

Alban, D.H., et Pastor, J. 1993. Decomposition of aspen, spruce, and pine boles on two sites in Minnesota. Can. J. For. Res. (23): 1744–1749.

Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat : a review. Oikos **71**(3): 355–366.

Angers, V.A. 2011. Snag Dynamics in Boreal Mixedwood and Coniferous Forests. Thèse de doctorat, Université du Québec à Montréal.

Angers, V.A., Bergeron, Y., et Drapeau, P. 2012a. Morphological attributes and snag classification of four North American boreal tree species: Relationships with time since death and wood density. For. Ecol. Manage. **263**: 138–147.

Angers, V.A., Drapeau, P., et Bergeron, Y. 2010. Snag degradation pathways of four North American boreal tree species. For. Ecol. Manage. **259**(3): 246–256. doi:10.1016/j.foreco.2009.09.026.

Angers, V.A., Drapeau, P., et Bergeron, Y. 2012b. Mineralization rates and factors influencing snag decay in four North American boreal tree species. Can. J. For. Res. **42**(1): 157–166. doi:10.1139/x11-167.

Angers, V.A., Gauthier, S., Drapeau, P., Jayen, K., et Bergeron, Y. 2011. Tree mortality and snag dynamics in North American boreal tree species after a wildfire: A long-term study. Int. J. Wildl. Fire **20**(6): 751–763. doi:10.1071/WF10010.

Bader, P., Jansson, S., et Jonsson, B.G. 1995. Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. Biol. Conserv. **72**(3): 355–362. doi:10.1016/0006-3207(94)00029-P.

Berg, A., Ehnstrom, B., Gustafsson, L., Hallingback, T., Jonsell, M., et Weslien, J. 1994. Threatened plant, animal, and fungus species in swedish forests : distribution and habitat associations. Soc. Conserv. Biol. **8**(3): 718–731.

Bergeron, Y. 1991. The influence of island and mainland lakeshore landscapes on boreal forest fire regimes. Ecology **72**(6): 1980–1992.

Bergeron, Y., Drapeau, P., Gauthier, S., et Lecomte, N. 2007. Using knowledge of natural disturbances to support sustainable forest management in the northern Clay Belt. For. Chron. **83**(3): 326–337. doi:10.5558/tfc83326-3.

Bergeron, Y., et Dubuc, M. 1989. Succession in the southern part of the Canadian boreal forest. Vegetatio **79**: 51–63.

Bergeron, Y., Engelmark, O., Harvey, B., Morin, H., et Sirois, L. 1998. Key issues in disturbance dynamics in boreal forests. J. Veg. Sci. **9**: 463–610. doi:10.1111/j.1654-1103.1998.tb00931.x.

Bergeron, Y., Flannigan, M., Gauthier, S., Leduc, A., et Lefort, P. 2004a. Past, current and future fire frequency in the Canadian Boreal Forest: Implications for sustainable forest management. AMBIO A J. Hum. Environ. **33**(6): 356. doi:10.1639/0044-7447(2004)033[0356:PCAFFF]2.0.CO;2.

Bergeron, Y., Gauthier, S., Flannigan, M., et Kafka, V. 2004b. Fire regimes at the transition between mixed wood and coniferous boreal forest in Northwestern Quebec. Ecology **85**(7): 1916–1932. doi:10.1890/02-0716.

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

Bergeron, Y., et Harvey, B.D. 1997. Basing silviculture on natural ecosystem dynamics: An approach applied to the southern boreal mixedwood forest of Quebec. For. Ecol. Manage. **92**(1–3): 235–242. doi:10.1016/S0378-1127(96)03924-2.

Bladon, K.D., Silins, U., Landhäusser, S.M., Messier, C., et Lieffers, V.J. 2007. Carbon isotope discrimination and water stress in trembling aspen following variable retention harvesting. Tree Physiol. **27**(7): 1065–1071. doi:10.1093/treephys/27.7.1065.

Bond-Lamberty, B., et Gower, S.T. 2008. Decomposition and fragmentation of coarse woody debris: re-visiting a boreal black spruce chronosequence. Ecosystems **11**(6): 831–840. doi:10.1007/s10021-008-9163-y.

Bond-Lamberty, B., Wang, C., et Gower, S.T. 2002. Annual carbon flux from woody debris for a boreal black spruce fire chronosequence. J. Geophys. Res. Atmos. **107**(D23): 1–10. doi:10.1029/2001JD000839.

Bose, A.K., Harvey, B.D., et Brais, S. 2014. Sapling recruitment and mortality dynamics following partial harvesting in aspen-dominated mixedwoods in eastern Canada. For. Ecol. Manage. **329**: 37–48. Elsevier B.V. doi:10.1016/j.foreco.2014.06.004.

Bouchard, M., Kneeshaw, D.D., et Bergeron, Y. 2005. Mortality and stand renewal patterns following the last spruce budworm outbreak in mixed forests of western Quebec. For. Ecol. Manage. **204**(2–3): 297–313. doi:10.1016/j.foreco.2004.09.017.

Boucher, D., Gauthier, S., et 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**(2): 172–180. doi:10.2980/i1195-6860-13-2-172.1.

Boulanger, Y., et Sirois, L. 2006. Postfire dynamics of black spruce coarse woody debris in northern boreal forests of Quebec. Can. J. For. Res. **36**(7): 1770–1780. doi:10.1139/x06-070.

Brais, S., Paré, D., et Lierman, C. 2006. Tree bole mineralization rates of four species of the Canadian eastern boreal forest: implications for nutrient dynamics following stand-replacing disturbances. Can. J. For. Res. **36**(9): 2331–2340. doi:10.1139/x06-136.

Bull, E.L. 1983. Longevity of Snags and Their Use by Woodpeckers. *In* Snag Habitat Management Symposium. Arizona. pp. 64–67.

Bull, E.L., Twombly, A.D., et Quigley, T.M. 1980. Perpetuating snags in managed mixed conifer forests of Blue Montain, Oregon. USDA For. Serv. Gen. Tech. Rep.: 325–336.

Cline, S.P., Berg, A.B., et Wight, H.M. 1980. Snag characteristics and dynamics in Douglas-Fir forests, western Oregon. J. Wildl. Manage. **44**(4): 773–786.

Cooke, B.J., et Lorenzetti, F. 2006. The dynamics of forest tent caterpillar outbreaks in Québec, Canada. For. Ecol. Manage. **226**: 110–121. doi:10.1111/j.1600-0587.2011.07083.x.

Dahms, W.G. 1949. How long do ponderosa pine snags stand? Pacific Northwest For. Range Exp. Stn. **57**: 3.

Dansereau, P.-R., et Yves Bergeron. 1993. Fire history in the southern boreal forest of northwestern Quebec. Can. J. For. Res. **23**: 25–32.

Darveau, M., Bélanger, L., et Ruel, J.-C. 1994. Mid-term effects of windfall on bird use of riparian forest strips. Int. Congr. Game Biol. **21**(2): 104–109.

Desponts, M., Desrochers, A., Bélanger, L., et Huot, J. 2002. Structure de sapinières aménagées et anciennes du massif des Laurentides (Québec) et diversité des plantes invasculaires. Can. J. For. Res. **32**(12): 2077–2093. doi:10.1139/x02-127.

Doyon, F., Gagnon, D., et Giroux, J.F. 2005. Effects of strip and single-tree selection cutting on birds and their habitat in a southwestern Quebec northern hardwood forest. For. Ecol. Manage. **209**(1–2): 101–116. doi:10.1016/j.foreco.2005.01.005.

Drapeau, P., Leduc, A., et Bergeron, Y. 2009a. Bridging ecosystem and multiple species approaches for setting conservation targets in managed boreal landscapes. *In* Villard, M.A., Gunnar-Jonsson, B.G., (Eds), Setting conservation targets for managed forest landscapes. Cambridge University Press, Cambridge, UK, pp. 129-160, 426pages

Drapeau, P., Nappi, A., Imbeau, L., et Saint-Germain, M. 2009b. Standing deadwood for keystone bird species in the eastern boreal forest: Managing for snag dynamics. For. Chron. **85**(2): 227–234. doi:10.5558/tfc85227-2.

Eberhardt, L.S. 1999. A test of an environmental advertisement hypothesis for the function of drumming in yellow-bellied sapsuckers. Condor: 798–803.

Edworthy, A.B., et Martin, K. 2013. Persistence of tree cavities used by cavity-nesting vertebrates declines in harvested forests. J. Wildl. Manage. **77**(4): 770–776. doi:10.1002/jwmg.526.

Elie, J.-G., et Ruel, J.-C. 2005. Windthrow hazard modelling in boreal forests of black spruce and jack pine. Can. J. For. Res. **35**: 2655–2663. doi:10.1139/X05-189.

Elton, C. 1966. Dying and dead wood. *In* The pattern of animal communities. Methuen, London, et Wiley, New York. p 279-305

Everett, R., Lehmkuhl, J., Schellhaas, R., Ohison, P., Keenum, D., Riesterer, H., et Spurbeck, D. 1999. Snag dynamics in a chronosequence of 26 wildfires on the east slope of the Cascade Range in Washington State, USA. J. Wildl. Fire **9**(4): 223–234.

Foster, J.R., et Lang, G.E. 1982. Decomposition of red spruce and balsam fir boles in the White Mountains of New Hampshire. Can. J. For. Res. **12**: 617–626.

Franklin, J.F. 1993. Preserving Biodiversity : Species, ecosystems, or landscapes ? Ecol. Appl. **3**(2): 202–205.

Franklin, J.F., Lindenmayer, D.B., Macmahon, J.A., Mckee, A., Magnuson, J., Perry, D.A., Waide, R., et Foster, D.R. 2000. Threads of continuity. Conserv. Pract. 1:9-16.

Franklin, J.F., Shugart, H., et Harmon, M.E. 1987. Tree death as an ecological process. Bioscience **37**(8): 550–556.

Franklin, J.F., Spies, T.A., Pelt, R. Van, Carey, A.B., Thornburgh, D. a, Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., et Chen, J. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For. Ecol. Manage. **155**(1–3): 399–423. doi:10.1016/S0378-1127(01)00575-8.

Garber, S.M., Brown, J.P., Wilson, D.S., Maguire, D. A, et Heath, L.S. 2005. Snag longevity under alternative silvicultural regimes in mixed-species forests of central Maine. Can. J. For. Res. **35**(4): 787–796. doi:10.1139/x05-021.

Gauthier, S., Bernier, P.Y., Boulanger, Y., Guo, J., Guindon, L., Beaudoin, A., et Boucher, D. 2015a. Vulnerability of timber supply to projected changes in fire regime in Canada's managed forests. Can. J. For. Res. **1447**: 1–33. doi:10.1139/cjfr-2015-0079.

Gauthier, S., Raulier, F., Ouzennou, H. et Saucier, J.-P. 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.

Gauthier, S., DeGrandpré, L., et Bergeron, Y. 2000. Differences in forest composition in two boreal forest ecoregions of Quebec. J. Veg. Sci. **11**(6): 781–790.

Gauthier, S., Vaillancourt, M.-A., Kneeshaw, D.D., Drapeau, P., DeGrandpré, L., Claveau, Y., et Pare, D. 2009. Forest Ecosystem Management: Origins and Foundations. *In* Ecosystem management in the boreal forest. Presses de l'Université du Québec, Québec, Qc. pp. 13–38.

Graham, R.L., et Cromack, K. 1982. Mass, nutrient content, and decay rate of dead boles in rain forests of Olympic National Park. Canadian J. For. Res. **12**: 511–521.

Grove, S.J. 2002. Saproxylic Insect Ecology and the Sustainable management of forests. Annu. Rev. Ecol. Syst. **33**(1): 1–23. doi:10.1146/annurev.ecolsys.33.010802.150507.

Hale, C.M., et Pastor, J. 1998. Nitrogen content, decay rates, and decompositional dynamics of hollow versus solid hardwood logs in hardwood forests of Minnesota, U.S.A. Can. J. For. Res. **28**(9): 1276–1285. doi:10.1139/x98-097.

Harmon, M.E., Franklin, J.F., Swanson, F., Sollins, P., Gregory, S. V., Lattin, J.D., Anderson, N.., Cline, S.P., Aumen, N.., Sedell, J.., Lienkaemper, G.., Cromack Jr, K., et Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. (15): 133–302.

Harmon, M.E., Jr, K.C., et Smith, B.G. 1987. Coarse woody debris in mixed-conifer forests, Sequoia National Park, California. Can. J. For. Res. **17**: 1265–1272.

Harmon, M.E., Krankina, O.N., et Sexton, J. 2000. Decomposition vectors: a new approach to estimating woody detritus decomposition dynamics. Can. J. For. Res. **30**(1): 76–84. doi:10.1139/cjfr-30-1-76.

Harper, K.A., Bergeron, Y., Gauthier, S., et 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.

Harper, K.A., Boudreault, C., DeGrandpré, L., Drapeau, P., Gauthier, S., et Bergeron, Y. 2003. Structure, composition, and diversity of old-growth black spruce boreal forest of the Clay Belt region in Quebec and Ontario. Environ. Rev. **11**(S1): S79–S98. doi:10.1139/a03-013.

Harper, K.A., et Macdonald, S.E. 2002. Structure and composition of edges next to regenerating clear-cuts in mixed-wood boreal forest. J. Veg. Sci. **13**: 535–546.

Harvey, B.D., et Leduc, A. 1999. Plan général d'aménagement - Forêt d'enseignement et de recherche du lac Duparquet (1998-2023). Université du Québec en Abitibi-Témiscamingue.153 pages

Harvey, B.D., Leduc, A., Gauthier, S., et Bergeron, Y. 2002. Stand-landscape integration in natural disturbance-based management of the southern boreal forest. For. Ecol. Manage. **155**(1–3): 369–385. doi:10.1016/S0378-1127(01)00573-4.

Hill, S.B., Mallik, A.U., et Chen, H.Y. 2005. Canopy gap disturbance and succession in trembling aspen dominated boreal forests in northeastern Ontario. Can. J. For. Res. **35**(8): 1942–1951. doi:10.1139/x05-126.

Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bull. **43**: 69–78.

Houle, G., et Payette, S. 1990. Seed dynamics deciduous of Betula alleghaniensis in forest of north-eastern North America. J. Ecol. **78**(3): 677–690.

Hunter, M.L. 2005. A mesofilter conservation strategy to complement fine and coarse filters. Conserv. Biol. **19**(4): 1025–1029. doi:10.1111/j.1523-1739.2005.00172.x.

Imbeau, L., et Desrochers, A. 2002. Foraging ecology and use of drumming trees by three-toed woodpeckers. J. Wildl. Manage. **66**(1): 222–231.

Johnson, E.A., et Greene, D. 1991. A method for studying dead bole dynamics in Pinus contorta var. latifolia-Picea engelmannii forests. J. Veg. Sci. **2**(4): 523–530. Available from http://onlinelibrary.wiley.com/doi/10.2307/3236034/abstract.

Keen, F.P. 1929. How soon do yellow pine snags fall? J. For. (27): 735–737.

Keen, F.P. 1955. The rate of natural falling of beetle-killed ponderosa pine snags. J. For. (53): 720–723.

Kimmins, J.P. 2001. Balancing act: environmental issues in forestry. *In* 2nd Editio. University of British Columbia Press, Vancouver.

Kneeshaw, D.D., et Bergeron, Y. 1996. Ecological factors affecting the abundance of advance regeneration in Quebec’s southwestern boreal forest. Can. J. For. Res. **26**: 888–898.

Krankina, O.N., et Harmon, M.E. 1995. Dynamics of the dead wood carbon pool in Northwestern Russian Boreal Forests. Water, Air Soil Pollut. **82**: 227–238.

Kruys, N., Fries, C., Jonsson, B.G., Lämås, T., et Ståhl, G. 1999. Wood-inhabiting cryptogams on dead Norway spruce (Picea abies) trees in managed Swedish boreal forests. Can. J. For. Res. **29**(2): 178–186. doi:10.1139/x98-191.

Kuuluvainen, T., Aapala, K., Ahlroth, P., Kuusinen, M., Lindholm, T., Sallantaus, T., Siitonen, J., et Tukia, H. 2002. Principles of ecological restoration of boreal forested ecosystems: Finland as an example. Silva Fenn. **36**(1): 409–422.

Kuuluvainen, T., Bergeron, Y., et Coates, K.D. 2015. Restoration and ecosystem-based management in the circumboreal forest: background, challenges, and opportunities. *In* Restoration of Boreal and Temperate Forests, Second Edi. CRC Press. pp. 251–270.

Lavoie, S., Ruel, J.-C., Bergeron, Y., et Harvey, B.D. 2012. Windthrow after group and dispersed tree retention in eastern Canada. For. Ecol. Manage. **269**: 158–167. doi:10.1016/j.foreco.2011.12.018.

Lee, P. 1998. Dynamics of snags in aspen-dominated midboreal forests. For. Ecol. Manage. **105**(1–3): 263–272. doi:10.1016/S0378-1127(97)00286-7.

Lee, P., Crites, S., Nietfeld, M., Guyen, H. Van, et Stelfox, J.B. 1997. Characteristics and origins of deadwood material in aspend-dominated boreal forests. Ecol. Appl. **7**(2): 691–701.

MacDonald, G.B., Cherry, M.L., et Thompson, D.J. 2004. Effect of harvest intensity on development of natural regeneration and shrubs in an Ontario boreal mixedwood stand. For. Ecol. Manage. **189**(1–3): 207–222. doi:10.1016/j.foreco.2003.08.010.

Martin, K., et Eadie, J.M. 1999. Nest webs: A community-wide approach to the management and conservation of cavity-nesting forest birds. For. Ecol. Manage. **115**(2–3): 243–257. doi:10.1016/S0378-1127(98)00403-4.

Mascarúa López, L.E., Harper, K.A., et Drapeau, P. 2006. Edge influence on forest structure in large forest remnants, cutblock separators, and riparian buffers in managed black spruce forests. Ecoscience **13**(2): 226–233. doi:10.2980/i1195-6860-13-2-226.1.

Mattson, K.G., Swank, W.T., et Waide, J.B. 1987. Decomposition of woody debris in a regenerating, clear-cut forest in the Southern Appalachians. Can. J. For. Res. **17**: 712–721.

Morin, H., Laprise, D., et Bergeron, Y. 1993. Chronology of spruce budworm outbreaks near Lake Duparquet, Abitibi region, Quebec. Can. J. For. Res. **23**: 1497–1506.

Morrison, M.L., et Raphael, M.G. 1993. Modeling the dynamics of snags. Ecol. Soc. Am. **3**(2): 322–330.

Næsset, E. 1999. Decomposition rate constants of *Picea abies* logs in southeastern Norway. Can. J. For. Res. **29**(3): 372–381. doi:10.1139/cjfr-29-3-372.

Naiman, R.J., Melillo, J.M., et Hobbie, J.E. 1986. Ecosystem Alteration of Boreal Forest Streams by Beaver (Castor canadensis). Ecol. Soc. Am. **67**(5): 1254–1269.

Nappi, A., et Drapeau, P. 2009. Reproductive success of the black-backed woodpecker (Picoides arcticus) in burned boreal forests: Are burns source habitats? Biol. Conserv. **142**(7): 1381–1391. Elsevier Ltd. doi:10.1016/j.biocon.2009.01.022.

Nummi, P., et Kuuluvainen, T. 2013. Forest disturbance by an ecosystem engineer: beaver in boreal forest landscapes. Boreal Environ. Res. **18**: 13–24..

Olsen, J.S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology **44**(2): 322–331.

Ouellet-Lapointe, U. 2010. Le maintien des espèces cavicoles dans les paysages aménagés en forêt boréale mixte de l'est du Canada. Mémoire de maîtrise. Universite du Quebec à Montréal.

Ouellet-Lapointe, U., Drapeau, P., Cadieux, P., et Imbeau, L. 2012. Woodpecker excavations suitability for and occupancy by cavity users in the boreal mixedwood forest of Eastern Canada. Ecoscience **19**(4): 391–397. doi:10.2980/19-4-3582.

Parish, R., Antos, J. a., Ott, P.K., et Lucca, C.M. Di. 2010. Snag longevity of Douglas-fir, western hemlock, and western redcedar from permanent sample plots in coastal British Columbia. For. Ecol. Manage. **259**(3): 633–640. doi:10.1016/j.foreco.2009.11.022.

Peterson, E.B., et Peterson, N.M. 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces. Disponible à http://www.cfs.nrcan.gc.ca/bookstore_pdfs/12011.pdf .

Qinghong, L., et Hytteborn, H. 1991. Gap structure, disturbance and regeneration in a primeval Picea abies forest. J. Veg. Sci. **2**: 391–402. doi:10.2307/3235932.

Québec Government. 2015. Règlement sur les normes d'intervention forestières, chapter A-18.1, r. 7 (mise à jour le 1 June 2017).

R Core Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Raphael, M.G., et Morrison, M.L. 1987. Decay and dynamics of snags in the Sierra Nevada, California. For. Sci. **33**(3): 774–783.

Rich RL, Frelich LE et Reich, PB (2007) Wind-throw mortality in the southern boreal forest: effects of species, diameter and stand age. J Ecology 95: 1261-1273

Riopel, M., Bégin, J., et Ruel, J.-C. 2010. Probabilités de pertes des tiges individuelles, cinq ans après des coupes avec protection des petites tiges marchandes, dans des forêts résineuses du Québec. Can. J. For. Res. **40**(7): 1458–1472. doi:10.1139/X10-059.

Robert, E., Brais, S., Harvey, BD et Greene, DF. 2012. Seedling establishment and survival on decaying logs in boreal mixedwood stands following a mast year. Can. J. For. Res. 42 (8): 1446–1455

Ruel, J.-C., Pin, D., et Cooper, K. 2001. Windthrow in riparian buffer strips: effect of wind exposure, thinning and strip width. For. Ecol. Manage. **143**(1–3): 105–113. doi:10.1016/S0378-1127(00)00510-7.

Russell, R.E., Saab, V. a., Dudley, J.G., et Rotella, J.J. 2006. Snag longevity in relation to wildfire and postfire salvage logging. For. Ecol. Manage. **232**(1–3): 179–187. doi:10.1016/j.foreco.2006.05.068.

Saint-Germain, M., Drapeau, P., et 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 (Cop.). **30**(6): 737–748. doi:10.1111/j.2007.0906-7590.05080.x.

Schaetzl, R.J., Burns, S.F., Johnson, D.L., et Small, T.W. 1989. Tree uprooting : Review of impacts on forest Ecology. Vegetatio **79**(3): 165–176.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms : Fennoscandian Boreal Forests as an Example. Oikos (49): 11–41.

Siitonen, J., Martikainen, P., Punttila, P., et Rauh, J. 2000. Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. For. Ecol. Manage. **128**(3): 211–225. doi:10.1016/S0378-1127(99)00148-6.

Simard, M., Lecomte, N., Bergeron, Y., Bernier, P.Y., et Paré, D. 2007. Forest productivity decline caused by successional paludification of boreal soils. Ecol. Appl. **17**(6): 1619–1637. doi:10.1890/06-1795.1.

Smith, V.G., Watts, M., et James, D.F. 1987. Mechanical stability of black spruce in the clay belt region of northern Ontario. Can. J. For. Res. **17**: 1080–1091.

Speight, M.C.D. 1989. Saproxylic invertebrates and their conservation. Nat. Environ. **42**: 1–79.

Spies, T.A. 1998. Forest structure : A key to the ecosystem. Northwest Sci. **72**(2): 34–39.

Stokland, J., Siitonen, J., et Jonsson, B.G. 2012. Biodiversity in dead wood. Cambridge University Press, Cambridge.

Stokland, J.N. 2001. The coarse woody debris profile : An archive of recent forest history and an important biodiversity indicator. Oikos (49): 71–83.

Storaunet, K.O., et Rolstad, J. 2002. Time since death and fall of Norway spruce logs in old-growth and selectively cut boreal forest. Can. J. For. Res. **32**(10): 1801–1812. doi:10.1139/x02-105.

Storaunet, K.O., et Rolstad, J. 2004. How long do Norway spruce snags stand? Evaluating four estimation methods. Can. J. For. Res. **34**(2): 376–383. doi:10.1139/x03-248.

Sturtevant, B.R., Bissonette, J.A., Long, J.N., et Roberts, D.W. 1997. Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland Ecol. Appl. **7**(2): 702–712.

Swift, M.J. 1973. The estimation of mycelial biomass by determination of the hexoamine content of wood tissue decayed by fungi. Soil Biol. Biochem. **5**: 321–332.

Taylor, S.L., et MacLean, D. a. 2007. Dead wood dynamics in declining balsam fir and spruce stands in New Brunswick, Canada. Can. J. For. Res. **37**(4): 750–762. doi:10.1139/X06-272.

Triska, F.J., et Kermit Cromack Jr. 1980. The role of wood debris in forests and streams. *In* Forests: Fresh Perspectives from Ecosystem Analysis. pp. 171–190.

Vaillancourt, M.-A. 2007. Caractérisation de la disponibilité des arbres potentiels à la nidification du Garrot d'Islande dans la forêt boréale de l'est du Québec. Mémoire de maîtrise, Université du Québec à Montréal, 99 pages.

Vanderwel, M.C., Caspersen, J.P., et Woods, M.E. 2006. Snag dynamics in partially harvested and unmanaged northern hardwood forests. Can. J. For. Res. **36**(11): 2769–2779. doi:10.1139/x06-173.

Vincent, J.-S., et Hardy, L. 1977. L'évolution et l'extension des lacs glaciaires Barlow et Ojibway en territoire québécois. Géographie Phys. Quat. **31**(3–4): 357. doi:10.7202/1000283ar.

Wang, C., Bond-Lamberty, B., et Gower, S. 2002. Environmental controls on carbon dioxide flux from black spruce coarse woody debris. Oecologia **132**(3): 374–381. doi:10.1007/s00442-002-0987-4.

Wei, X., Kimmins, J.P., Peel, K., et Steen, O. 1997. Mass and nutrients in woody debris in harvested and wildfire-killed lodgepole pine forests in the central interior of British Columbia. Can. J. For. Res. **27**(2): 148–155. doi:10.1139/x96-169.

Yatskov, M., Harmon, M.E., et Krankina, O.N. 2003. A chronosequence of wood decomposition in the boreal forests of Russia. Can. J. For. Res. **33**(7): 1211–1226. doi:10.1139/x03-033.

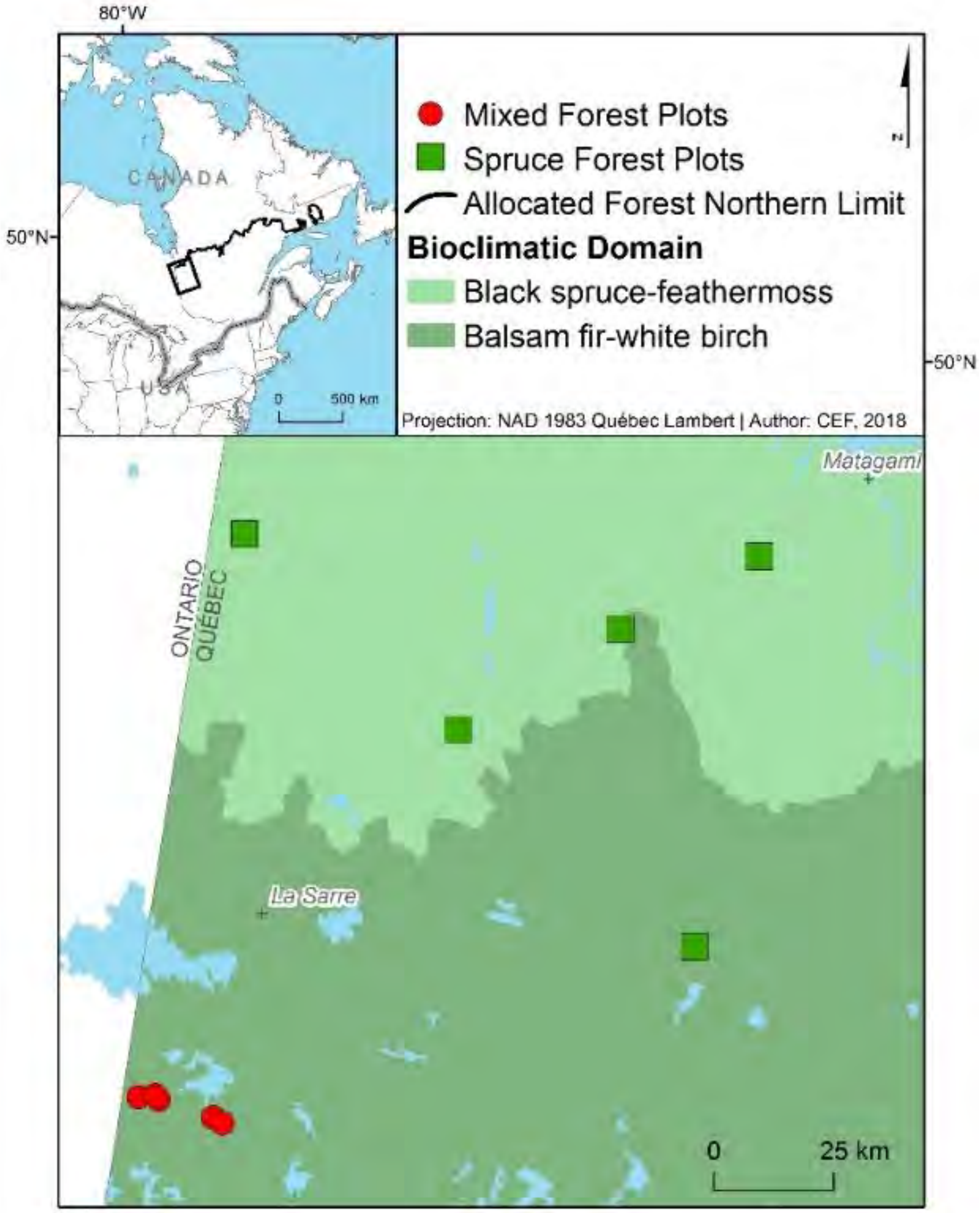

Figure 2.1 Location of study area and sample sites.

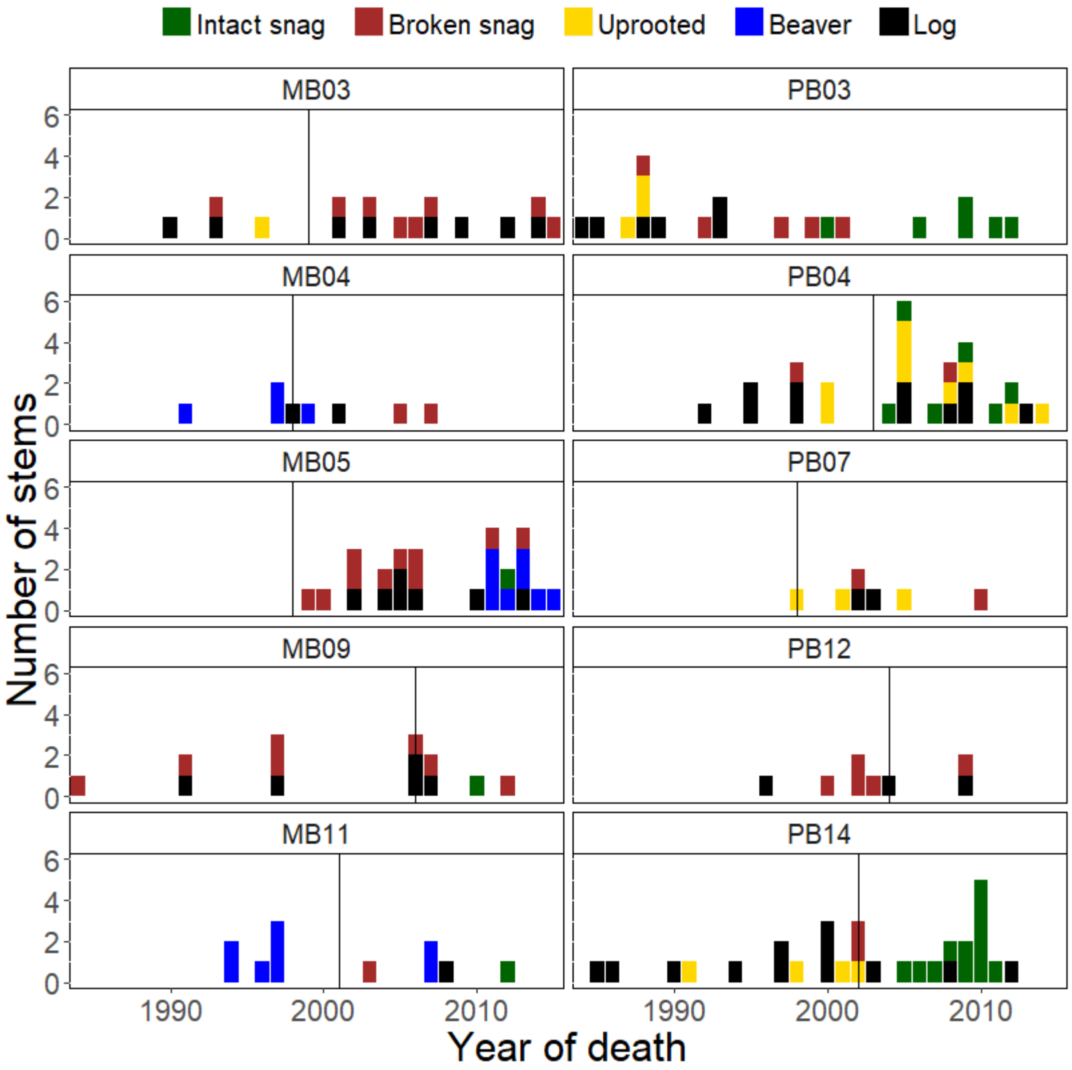

Figure 2.2 Mortality count per year for trembling aspen and black spruce. Vertical lines indicate year of retention creation by harvest adjacent to each site. PB03 was harvested in 1982 which was too old to detect any datable dead trees prior to harvest Mixedwood forest plots are on left column and coniferous forest plots on the right. ANOVA analyses were performed on each site identifying no significant difference between pre- and post-harvest

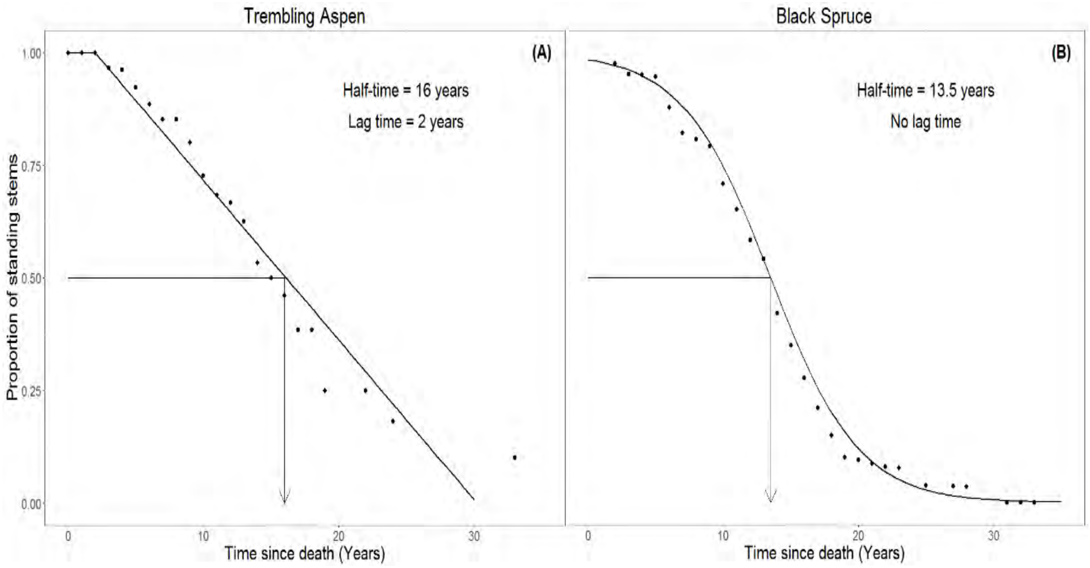

Figure 2.3 Survival curves for trembling aspen in mixedwood forest and black spruce in coniferous forest. Linear model equation for trembling aspen is Y = 1.0707 – 0.03544*x R^2 = 0.944. Reverse sigmoidal function for black spruce is Y= 1/ (1+exp(0.3069*(TDM-13.5))).

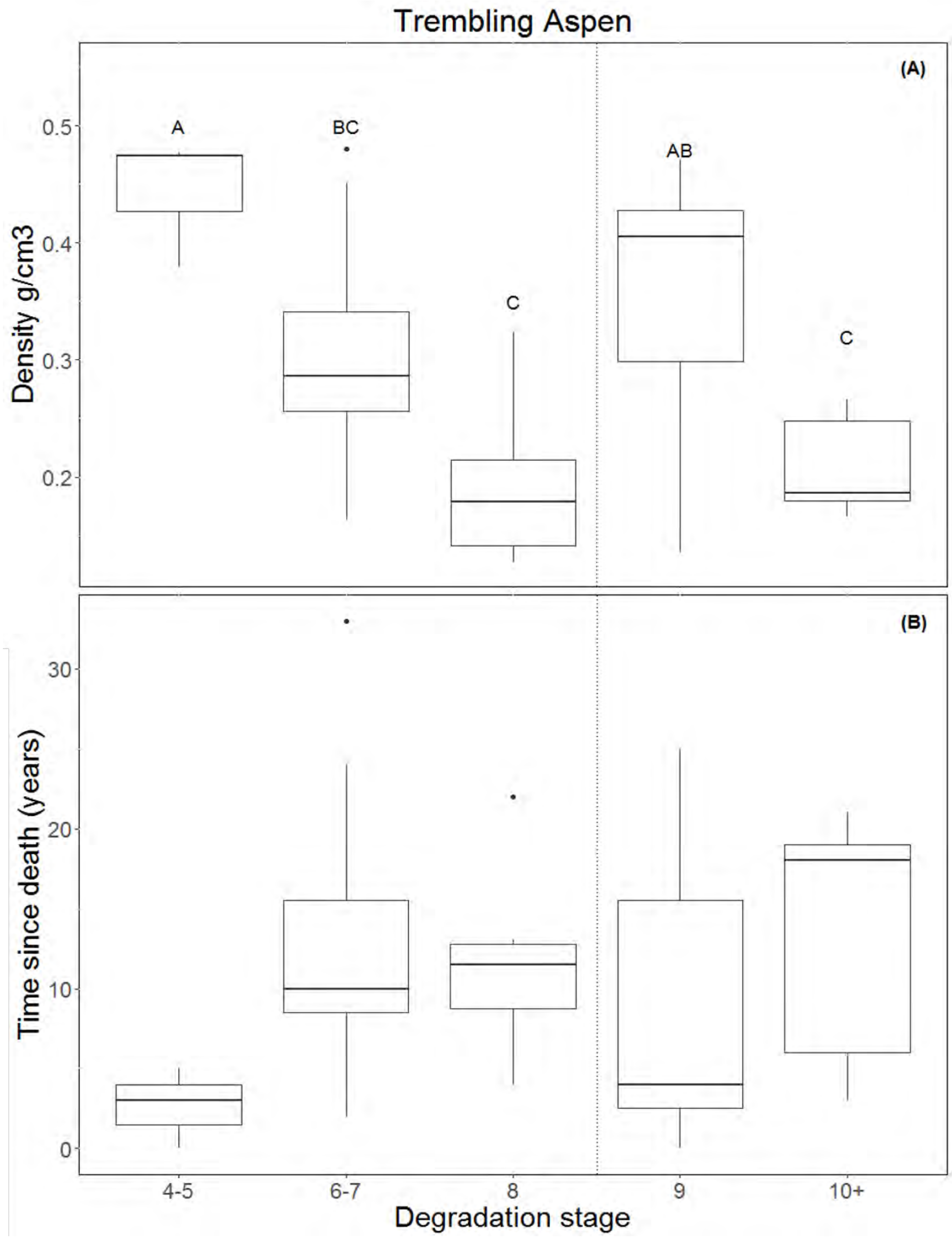

Figure 2.4 Wood density and time since death relative to degradation stage distributions for trembling aspen. Capital letters on top of boxplots indicate the significant difference among them resulting from multiple comparison test using least square means for unbalanced samples (lsmeans package). Vertical dotted lines separate snag from log degradation stages. No significant difference was observed among TSD distribution.

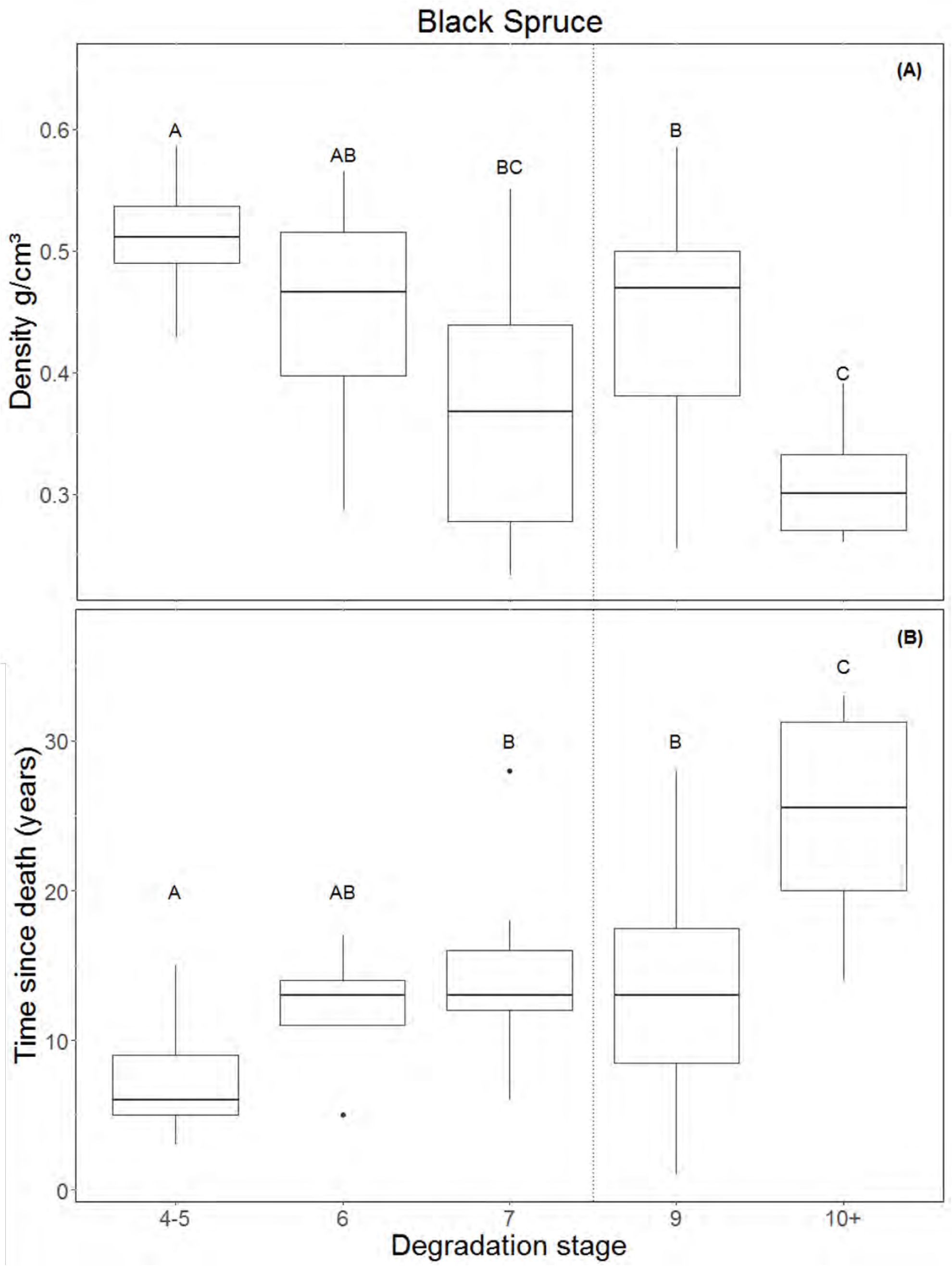

Figure 2.5 Wood denstiy and time since death relative to degradation stage distributions for black spruce. Capital letters on top of boxplots indicate the significant difference among them resulting from multiple comparison test using least square means for unbalanced samples (lsmeans package). Vertical dotted lines separate snag from log degradation stages.

Table 2.1 Sample site characteristics.

Site	**Time since harvest (years)**	**Stand age (years)**	**Retention width (m)**	**Organic layer thickness (cm)**
Mixedwood Forest				
MB03	17	105	37	12
MB04	18	99	30	9
MB05	18	95	31	6
MB09	10	73	32	2
MB11	15	83	25	8
Coniferous Forest				
PB03	33	145	34	40
PB04	13	97	25	14
PB07	18	92	23	10
PB12	12	89	34	16
PB14	14	176	18	43

Table 2.2 Degradation classification system with description of each stage. *

Degradation stage	**Characteristics**
1	Live, sound, more than 95% of leaves (needles) still present; no visible signs of senescence.
2	Live, signs of senescence, between 20-95% of leaves (needles) still present.
3	Live but advanced signs of senescence, less than 20% of leaves (needles) remaining.
4	Recently dead, hard wood, bark mostly intact, no green leaves (needles), some twigs remaining.
5	Dead, no leaves, hard wood, no twigs, some large branches remaining.
6	Dead, hard wood, bark starting to peel off, stem broken above 50% of original height (based on surrounding live trees with similar dbh).
7	Dead, soft wood and partially decomposed, stem broken below 50% of original height (based on surrounding live trees with similar dbh).
8	Stump with height less than 2 meters.
9	Recently fallen, hard wood, intact bark, crown remaining.
10	Hard wood, bark starting to peel off, light moss cover.
11	Hardwood, moss cover on more than 50% of the stem.
12	Soft wood, completely covered with moss.

* From Imbeau and Desrochers (2002), Ouellet-Lapointe (2010), Desponts et al. (2002).

Table 2.3 Description of dated dead stems. Time since death (TSD) mean and standard error (SE), and number of samples of each species.

Species	**Condition**	**State**	**TSD (Years)**		**n**
			Mean	**SE**	
Trembling Aspen	Snag	Intact	3.67	0.67	3
		Broken	11.46	1.35	28
		Beaver	8.00	NA	1
	Log	Broken	10.67	2.32	9
		Beaver	11.35	2.14	17
		Uprooted	19.00	0.00	1
Black Spruce	Snag	Intact	6.67	0.59	24
		Broken	14.13	1.46	16
	Log	Broken	17.67	1.56	31
		Uprooted	13.71	1.91	17

Table 2.4 Decomposition rate in snags for trembling aspen and black spruce according to an negative exponential model and a linear regression model.

		Trembling Aspen		Black Spruce	
		Our study	Natural forest	Our study	Natural forest
Models	n	28	50	38	63
Neg. exponential	k	**0.0335**	0.0274	**0.0196**	0.0058
	P-value	0.00021		0.00076	
Linear	m	**-0.0081**	-0.0088	**-0.0092**	-0.0021
	R^2	0.319		0.263	
	P-value	0.0023		0.001	

Comparison with natural forest was done using data from Angers et al. (2012b).

CONCLUSION GÉNÉRALE

Afin d'atteindre efficacement les objectifs de conservation de la biodiversité, l'aménagement forestier doit assurer une rétention forestière de qualité. Les organismes dépendant de forêts d'intérieur ou d'attributs spécifiques comme le bois sénescent et mort doivent se résoudre à habiter les peuplements maintenus au travers un territoire fragmenté ou morcelé qui peut s'étendre sur des centaines de km^2 (Franklin 1993; Franklin et al. 2000). Au Québec, les bandes riveraines et les séparateurs de coupe font oeuvre de rétention forestière depuis plus de trente ans (Gouvernement du Québec, 2015). Ce type de rétention offre une connectivité structurelle importante des écosystèmes forestiers et riverains pour la dispersion des espèces (Andren, 1994; Debinski and Holt, 2000; Franklin et al. 2000, Bennet 2003). En contrepartie, la forme linéaire génère un effet de lisière important qui peut s'étendre sur l'ensemble de l'habitat de rétention compte tenu de la largeur conservée (Harper et al. 2016, Mascarua-Lopez et al. 2006). L'objectif de ce mémoire était donc d'évaluer la dynamique de bois mort dans ces habitats linéaires résiduels, soit la principale stratégie de rétention dans les agglomérations de coupe. L'étude s'est effectuée à deux niveaux d'organisation biologique, d'abord le premier chapitre a présenté la dynamique à l'échelle du peuplement où l'on y a traité les facteurs de recrutement, ainsi que la durabilité de ces habitats en termes de disponibilité structurelle de bois vivant et mort. Au deuxième chapitre, l'étude s'est concentrée sur la dynamique à l'échelle de l'arbre pour deux espèces dominantes des forêts boréales mixte et coniférienne, soit le peuplier faux-tremble et l'épinette noire. Dans cette section, une approche d'analyse dendrochronologique a été utilisée pour évaluer les taux de chute et les patrons de dégradation pour chacune de ces espèces d'arbre.

En plus de l'âge des peuplements, des conditions initiales et de la présence du castor, les principaux facteurs influençant la mortalité des arbres en rétention linéaire étaient leur position dans le peuplement (au centre ou en bordure de l'habitat linéaire) et le temps depuis la coupe. En effet, les arbres en bordure de l'aire de coupe présentaient une plus grande vulnérabilité à l'exposition au vent que ceux situés en bordure riveraine ou au centre de la rétention linéaire. Le déracinement et la rupture au tronc étaient les causes de mortalité les plus fréquentes, engendrant une abondance de bois mort au sol plus importante et une plus faible présence d'arbres morts sur pied intacts en bordure de coupe qu'au centre des peuplements. Les deux premières décennies suivant la récolte forestière ont montré une certaine instabilité dans la dynamique de mortalité des arbres. Cette période était marquée par une grande variabilité dans les taux de recrutement de bois mort sur pied, suivie d'une réduction importante et, d'une stabilité de la mortalité.

Quelques sites ont montré une mortalité « excessive » pouvant mener à un effondrement du peuplement vers un habitat ouvert. Toutefois, la majorité des bandes de rétention linéaire échantillonnées dans cette étude, tant en forêt boréale mixte que coniférienne, persistent en tant qu'habitats forestiers plus de 30 ans après la coupe. Malgré un effet de lisière important, ces écosystèmes apparaissent résilients, les processus de mortalité et de dégradation des arbres montrent une réponse similaire à celle des peuplements âgés en forêt naturelle. Ceci dit, les bandes de rétention linéaire de faible largeur ne fournissent pas d'habitat d'intérieur pour autant.

Les patrons de mortalité des arbres, de dégradation et de décoposition du bois à l'échelle de l'arbre définissent en partie la structure verticale et horizontale retrouvée dans les peuplements. L'analyse dendrochronologique sur le peuplier faux-tremble et l'épinette noire n'a pas démontré de hausse exceptionnelle de la mortalité des arbres dans les bandes riveraines au cours des premières années après la coupe. Les patrons de mortalité montrent une petite différence avec ceux reportés dans d'autres études en forêt naturelle, sans pour autant menacer la durabilité de la dynamique et du recrutement du bois mort sur pied. Un chicot de peuplier faux-tremble dans une bande riveraine a une période de stabilité plus courte avant d'entamer la période de chute au sol, par contre, sa longévité moyenne est similaire à celle observée en forêt naturelle. Sa vulnérabilité aux champignons causant la pourriture du cœur de l'arbre, engendre le processus de dégradation avant sa mort, ce qui accélère son passage dans les stades de dégradation des systèmes de classification. De plus, la forte mortalité des tiges de peupliers par le castor suscite une inquiétude par rapport à la pression que peut exercer cet animal dans les bandes riveraines et son impact possible sur les utilisateurs de cavités sur les tiges de peupliers dans ces milieux. Pour l'épinette noire, l'absence de période de stabilité sur la courbe de survie des chicots est commune à plusieurs études menées sur le genre *Picea.* Cependant, une réduction de sa longévité par rapport à la forêt naturelle a été observée. De plus, l'occurrence du déracinement de cette espèce est fortement augmentée en forêt aménagée, ce qui a pour conséquence de tronquer le passage des arbres morts sur pied à tous les stades de dégradation.

Finalement, la persistance de la complexité structurelle verticale et horizontale des bandes riveraines montre qu'en général, les sites ne sont pas sujets à un déclin et peuvent persister en tant que legs biologiques de forêts âgés à long terme. Par conséquent, on peut supposer que ces habitats peuvent supporter une communauté d'organismes dépendants du bois mort sur pied. Cependant, dans le contexte de l'aménagement durable des écosystèmes forestiers, les aménagistes devraient planifier des séparateurs de coupe avec une largeur minimale de 100 mètres pour les deux domaines bioclimatiques afin d'assurer une forêt n'étant pas entièrement sous l'effet de lisière. Quant aux bandes riveraines, bien que plusieurs études aient démontré leur adaptabilité aux ouvertures due à la présence de cours d'eau (Mascarua-Lopez et al, 2006; Harper, 1999; Harper and MacDonald, 2001) nos résultats suggèrent une certaine vulnérabilité et un seuil minimal de leur largeur devrait être investigué. Une augmentation de la largeur permettrait de rencontrer plus efficacement les objectifs de conservation de biodiversité en territoire aménagée. De plus, ces rétentions devraient être conservées pour toute la durée de la révolution des forêts avoisinantes, c'est-à-dire jusqu'au retour d'un couvert forestier mature dans les agglomérations de coupe. Ces recommandations sont fondées sur le principe d'améliorer la qualité des rétentions forestières afin que celles-ci conservent les attributs de forêts âgées indispensables à plusieurs organismes et que ces habitats améliorent leur rôle fonctionnel de refuges dans les paysages aménagés.

BIBLIOGRAPHIE

Aakala, T., Kuuluvainen, T., Gauthier, S., et De Grandpré, L. 2008. Standing dead trees and their decay-class dynamics in the northeastern boreal old-growth forests of Quebec. For. Ecol. Manage. **255**(3–4): 410–420. doi:10.1016/j.foreco.2007.09.008.

Aakala, T., Kuuluvainen, T., De Grandpré, L., et Gauthier, S. 2007. Trees dying standing in the northeastern boreal old-growth forests of Quebec: spatial patterns, rates, and temporal variation. Can. J. For. Res. **37**: 50–61. doi:10.1139/x06-201.

Aitchison, J., et Silvey, S.D. 1957. The generalization of probit analysis to the case of multiple responses. Biometrika Trust **44**(1): 131–140.

Alban, D.H., et Pastor, J. 1993. Decomposition of aspen, spruce, and pine boles on two sites in Minnesota. Can. J. For. Res. (23): 1744–1749.

Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat : a review. Oikos **71**(3): 355–366.

Angers, V.A. 2009. L’enjeu écologique du bois mort - Complément au Guide pour la description des principaux enjeux écologiques dans les plans régionaux de développement intégré des ressources et du territoire. Ministère des Ressources naturelles et de la Faune, Direction de l'environnement et de la protection des forêts

Angers, V.A. 2011. Snag Dynamics in Boreal Mixedwood and Coniferous Forests. Thèse de doctorat, Université du Québec à Montréal.

Angers, V.A., Bergeron, Y., et Drapeau, P. 2012a. Morphological attributes and snag classification of four North American boreal tree species: Relationships with time since death and wood density. For. Ecol. Manage. **263**: 138–147.

Angers, V.A., Drapeau, P., et Bergeron, Y. 2010. Snag degradation pathways of four North American boreal tree species. For. Ecol. Manage. **259**(3): 246–256. doi:10.1016/j.foreco.2009.09.026.

Angers, V.A., Drapeau, P., et Bergeron, Y. 2012b. Mineralization rates and factors influencing snag decay in four North American boreal tree species. Can. J. For. Res. **42**(1): 157–166. doi:10.1139/x11-167.

Angers, V.A., Gauthier, S., Drapeau, P., Jayen, K., et Bergeron, Y. 2011. Tree mortality and snag dynamics in North American boreal tree species after a wildfire: A long-term study. Int. J. Wildl. Fire **20**(6): 751–763. doi:10.1071/WF10010.

Bader, P., Jansson, S., et Jonsson, B.G. 1995. Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. Biol. Conserv. **72**(3): 355–362. doi:10.1016/0006-3207(94)00029-P.

Bebber, D.P., Cole, W.G., Thomas, S.C., Balsillie, D., et Duinker, P. 2005. Effects of retention harvests on structure of old-growth Pinus strobus L. stands in Ontario. For. Ecol. Manage. **205**(1–3): 91–103. doi:10.1016/j.foreco.2004.10.048.

Bennett, A.F. 2003. Linkages in the landscape: The role of corridors and connectivity in wildlife conservation. *In* Iucn. doi:10.2305/IUCN.CH.2004.FR.1.en.

Berg, A., Ehnstrom, B., Gustafsson, L., Hallingback, T., Jonsell, M., et Weslien, J. 1994. Threatened plant, animal, and fungus species in swedish forests : distribution and habitat associations. Soc. Conserv. Biol. **8**(3): 718–731.

Bergeron, Y. 1991. The influence of island and mainland lakeshore landscapes on boreal forest fire regimes. Ecology **72**(6): 1980–1992.

Bergeron, Y., Drapeau, P., Gauthier, S., et Lecomte, N. 2007. Using knowledge of natural disturbances to support sustainable forest management in the northern Clay Belt. For. Chron. **83**(3): 326–337. doi:10.5558/tfc83326-3.

Bergeron, Y., et Dubuc, M. 1989. Succession in the southern part of the Canadian boreal forest. Vegetatio **79**: 51–63.

Bergeron, Y., Engelmark, O., Harvey, B., Morin, H., et Sirois, L. 1998. Key issues in disturbance dynamics in boreal forests. J. Veg. Sci. **9**: 463–610. doi:10.1111/j.1654-1103.1998.tb00931.x.

Bergeron, Y., Flannigan, M., Gauthier, S., Leduc, A., et Lefort, P. 2004a. Past, current and future fire frequency in the Canadian Boreal Forest: Implications for sustainable forest management. AMBIO A J. Hum. Environ. **33**(6): 356. doi:10.1639/0044-7447(2004)033[0356:PCAFFF]2.0.CO;2.

Bergeron, Y., Gauthier, S., Flannigan, M., et Kafka, V. 2004b. Fire regimes at the transition between mixed wood and coniferous boreal forest in Northwestern Quebec. Ecology **85**(7): 1916–1932. doi:10.1890/02-0716.

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

Bergeron, Y., et Harvey, B.D. 1997. Basing silviculture on natural ecosystem dynamics: An approach applied to the southern boreal mixedwood forest of Quebec. For. Ecol. Manage. **92**(1–3): 235–242. doi:10.1016/S0378-1127(96)03924-2.

Bergeron, Y., Irulappa Pillai Vijayakumar, D., Ouzennou, H., Raulier, F., Leduc, A., et 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. For. An Int. J. For. Res. **90**(4): 485–495.

Bergeron, Y., Leduc, A., Harvey, B.D., et Gauthier, S. 2002. Natural fire regime : A guide for sustainable management of the canadian boreal forest. Silva Fenn. **36** (January): 81–95.

Bladon, K.D., Lieffers, V.J., Silins, U., Landhäusser, S.M., et Blenis, P. V. 2008. Elevated mortality of residual trees following structural retention harvesting in boreal mixedwoods. For. Chron. **84**(1): 70–75. doi:10.5558/tfc84070-1.

Bladon, K.D., Silins, U., Landhäusser, S.M., Messier, C., et Lieffers, V.J. 2007. Carbon isotope discrimination and water stress in trembling aspen following variable retention harvesting. Tree Physiol. **27**(7): 1065–1071. doi:10.1093/treephys/27.7.1065.

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., et Gower, S.T. 2008. Decomposition and fragmentation of coarse woody debris: re-visiting a boreal black spruce chronosequence. Ecosystems **11**(6): 831–840. doi:10.1007/s10021-008-9163-y.

Bond-Lamberty, B., Wang, C., et Gower, S.T. 2002. Annual carbon flux from woody debris for a boreal black spruce fire chronosequence. J. Geophys. Res. Atmos. **107**(D23): 1–10. doi:10.1029/2001JD000839.

Bose, A.K., Harvey, B.D., et Brais, S. 2014. Sapling recruitment and mortality dynamics following partial harvesting in aspen-dominated mixedwoods in eastern Canada. For. Ecol. Manage. **329**: 37–48. Elsevier B.V. doi:10.1016/j.foreco.2014.06.004.

Bouchard, M., Kneeshaw, D.D., et Bergeron, Y. 2005. Mortality and stand renewal patterns following the last spruce budworm outbreak in mixed forests of western Quebec. For. Ecol. Manage. **204**(2–3): 297–313. doi:10.1016/j.foreco.2004.09.017.

Boucher, D., Gauthier, S., et 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**(2): 172–180. doi:10.2980/i1195-6860-13-2-172.1.

Boulanger, Y., et Sirois, L. 2006. Postfire dynamics of black spruce coarse woody debris in northern boreal forests of Quebec. Can. J. For. Res. **36**(7): 1770–1780. doi:10.1139/x06-070.

Brais, S., Sadi, F., Bergeron, Y., et Grenier, Y. 2005. Coarse woody debris dynamics in a post-fire jack pine chronosequence and its relation with site productivity. For. Ecol. Manage. 220(1-3):216-226.

Brais, S., Paré, D., et Lierman, C. 2006. Tree bole mineralization rates of four species of the Canadian eastern boreal forest: implications for nutrient dynamics following stand-replacing disturbances. Can. J. For. Res. **36**(9): 2331–2340. doi:10.1139/x06-136.

Braithwaite, N.T., et Mallik, A.U. 2012. Edge effects of wildfire and riparian buffers along boreal forest streams. J. Appl. Ecol. **49**(1): 192–201. doi:10.1111/j.1365-2664.2011.02076.x.

Bull, E.L. 1983. Longevity of Snags and Their Use by Woodpeckers. *In* Snag Habitat Management Symposium. Arizona. pp. 64–67.

Bull, E.L., Twombly, A.D., et Quigley, T.M. 1980. Perpetuating snags in managed mixed conifer forests of Blue Montain, Oregon. USDA For. Serv. Gen. Tech. Rep.: 325–336.

Burnham, K.P., et Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach (2nd ed). *In* Ecological Modelling. Springler Verlag, New York, NY. doi:10.1016/j.ecolmodel.2003.11.004.

Burton, P.J. 2002. Effects of clearcut edges on trees in the sub-boreal spruce zone of Northwest-Central British Columbia. Silva Fenn. **36**(1): 329–352.

Cadieux, P. 2011. Dynamique de la faune cavicole le long d'un gradient d'âge en forêt boréale mixte de l'Est de l'Amérique du Nord Mémoire de maîtrise. Université du Québec à Montréal.

Cadieux, P., et Drapeau, P. 2017. Are old boreal forests a safe bet for the conservation of the avifauna associated with decayed wood in eastern Canada? For. Ecol. Manage. **385**: 127–139. Elsevier B.V. doi:10.1016/j.foreco.2016.11.024.

Chen, J., Franklin, J.F., et Lower, J.S. 1995. Comparison of abiotic and structurally defined patch patterns in a hypothetical forest landscape. Conserv. Biol. **10**(3): 854–862.

Chen, J., Franklin, J.F., et Spies, T.A. 1992. Vegetation responses to edge environments in old-growth douglas-fir forests. Ecol. Appl. **2**(4): 387–396.

Clark, D.F., Kneeshaw, D.D., Burton, P.J., et Antos, J. a. 1998. Coarse woody debris in sub-boreal spruce forests of west-central British Columbia. Can. J. For. Res. **28**(2): 284–290. doi:10.1139/cjfr-28-2-284.

Cline, S.P., Berg, A.B., et Wight, H.M. 1980. Snag characteristics and dynamics in Douglas-Fir forests, western Oregon. J. Wildl. Manage. **44**(4): 773–786.

Cooke, B.J., et Lorenzetti, F. 2006. The dynamics of forest tent caterpillar outbreaks in Québec, Canada. For. Ecol. Manage. **226**: 110–121. doi:10.1111/j.1600-0587.2011.07083.x.

Cyr, D., Gauthier, S., Bergeron, Y., et Carcaillet, C. 2009. Forest management is driving the eastern North American boreal forest outside its natural range of variability. Front. Ecol. Environ. **7**(10): 519–524. doi:10.1890/080088.

Dahms, W.G. 1949. How long do ponderosa pine snags stand? Pacific Northwest For. Range Exp. Stn. **57**: 3.

Dansereau, P.-R., et Yves Bergeron. 1993. Fire history in the southern boreal forest of northwestern Quebec. Can. J. For. Res. **23**: 25–32.

Darveau, M., Bélanger, L., et Ruel, J.-C. 1994. Mid-term effects of windfall on bird use of riparian forest strips. Int. Congr. Game Biol. **21**(2): 104–109.

Debinski, D.M., et Holt, R.D. 2000. A Survey and overview of habitat fragmentation experiments. Conserv. Biol. **14**(2): 342–355. doi:10.1046/j.1523-1739.2000.98081.x.

Delong, S.C., et Tanner, D. 1996. Managing the pattern of forest harvest: lessons from wildfire. Biodivers. Conserv. **5**: 1191–1205.

Desponts, M., Desrochers, A., Bélanger, L., et Huot, J. 2002. Structure de sapinières aménagées et anciennes du massif des Laurentides (Québec) et diversité des plantes invasculaires. Can. J. For. Res. **32**(12): 2077–2093. doi:10.1139/x02-127.

DeWalle, D.R. 1983. Wind damage around clearcuts in the Ridge and Valley province of Pennsylvania. J. For. **81**(3): 158–172.

Doyon, F., Gagnon, D., et Giroux, J.F. 2005. Effects of strip and single-tree selection cutting on birds and their habitat in a southwestern Quebec northern hardwood forest. For. Ecol. Manage. **209**(1–2): 101–116. doi:10.1016/j.foreco.2005.01.005.

Dragotescu, I., et Kneeshaw, D.D. 2012. A comparison of residual forest following fires and harvesting in boreal forests in Quebec , Canada. Silva Fenn. **46**(3): 365–376.

Drapeau, P., Leduc, A., et Bergeron, Y. 2009a. Bridging ecosystem and multiple species approaches for setting conservation targets in managed boreal landscapes. *In* Villard, M.A., Gunnar-Jonsson, B.G., (Eds), Setting conservation targets for managed forest landscapes. Cambridge University Press, Cambridge, UK, pp. 129-160, 426pages

Drapeau, P., Leduc, A., Giroux, J., Savard, J.L., et Vickery, W.L. 2000. Landscape-scale disturbances and changes in bird communities of boreal mixed-wood forests. Ecol. Monogr. **70**(3): 423–444.

Drapeau, P., Nappi, A., Giroux, J., Leduc, A., et Savard, J.-P. 2002. Distribution patterns of birds associated with snags in natural and managed eastern boreal forests. *In* Reno, N.V. (Eds WF Laudenslayer, PJ Shean, BE Valentine, CP Weatherspoon, TE Lisle) Proceeding of symposium on the ecology and management of dead wood in western forests, USDA For. Serv. Gen. Tech. Rep. PSW-GTR-181, Albany, CA, p: 193–205.

Drapeau, P., Nappi, A., Imbeau, L., et Saint-Germain, M. 2009b. Standing deadwood for keystone bird species in the eastern boreal forest: Managing for snag dynamics. For. Chron. **85**(2): 227–234. doi:10.5558/tfc85227-2.

Drapeau, P., Villard, M.A., Leduc, A., et Hannon, S.J. 2016. Natural disturbance regimes as templates for the response of bird species assemblages to contemporary forest management. Divers. Distrib. **22**(4): 385–399. doi:10.1111/ddi.12407.

Dupuch, A., et Fortin, D. 2013. The extent of edge effects increases during post-harvesting forest succession. Biol. Conserv. **162**: 9–16. Elsevier Ltd. doi:10.1016/j.biocon.2013.03.023.

Eberhardt, L.S. 1999. A test of an environmental advertisement hypothesis for the function of drumming in yellow-bellied sapsuckers. Condor: 798–803.

Edworthy, A.B., et Martin, K. 2013. Persistence of tree cavities used by cavity-nesting vertebrates declines in harvested forests. J. Wildl. Manage. **77**(4): 770–776. doi:10.1002/jwmg.526.

Elie, J.-G., et Ruel, J.-C. 2005. Windthrow hazard modelling in boreal forests of black spruce and jack pine. Can. J. For. Res. **35**: 2655–2663. doi:10.1139/X05-189.

Elton, C. 1966. Dying and dead wood. *In* The pattern of animal communities. Methuen, London, et Wiley, New York. p 279-305

Erickson, H.E., Edmonds, R.L., et Peterson, C.E. 1985. Decomposition of logging residues in Douglas-fir, western hemlock, Pacific silver fir, and ponderosa pine ecosystems. Can. J. For. Res. (15): 914–921..

Esseen, P.-A. 1994. Tree mortality patterns after experimental fragmentation of an old-growth conifer forest. Biol. Conserv. **68**: 19–28.

Everett, R., Lehmkuhl, J., Schellhaas, R., Ohison, P., Keenum, D., Riesterer, H., et Spurbeck, D. 1999. Snag dynamics in a chronosequence of 26 wildfires on the east slope of the Cascade Range in Washington State, USA. J. Wildl. Fire **9**(4): 223–234.

Fenton, N.J., et Bergeron, Y. 2008. Does time or habitat make old-growth forests species rich? Bryophyte richness in boreal Picea mariana forests. Biol. Conserv. **141**(5): 1389–1399. doi:10.1016/j.biocon.2008.03.019.

Ferguson, S.H., et Archibald, D.J. 2002. The 3/4 power law in forest management: how to grow dead trees. For. Ecol. Manage. **169**(3): 283–292. doi:10.1016/S0378-1127(01)00766-6.

Fortin, M., DeBlois, J., Bernier, S., et Blais, G. 2007. Mise au point d’un tarif de cubage général pour les forêts québécoises: Une approche pour mieux évaluer l’incertitude associée aux prévisions. For. Chron. **83**(5): 754–765. doi:10.5558/tfc83754-5.

Foster, J.R., et Lang, G.E. 1982. Decomposition of red spruce and balsam fir boles in the White Mountains of New Hampshire. Can. J. For. Res. **12**: 617–626.

Franklin, J.F. 1993. Preserving Biodiversity : Species, ecosystems, or landscapes ? Ecol. Appl. **3**(2): 202–205.

Franklin, J.F., Lindenmayer, D.B., Macmahon, J.A., Mckee, A., Magnuson, J., Perry, D.A., Waide, R., et Foster, D.R. 2000. Threads of continuity. Conserv. Pract. 1:9-16.

Franklin, J.F., Shugart, H., et Harmon, M.E. 1987. Tree death as an ecological process. Bioscience **37**(8): 550–556.

Franklin, J.F., Spies, T.A., Pelt, R. Van, Carey, A.B., Thornburgh, D. a, Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., et Chen, J. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For. Ecol. Manage. **155**(1–3): 399–423. doi:10.1016/S0378-1127(01)00575-8.

Garber, S.M., Brown, J.P., Wilson, D.S., Maguire, D. A, et Heath, L.S. 2005. Snag longevity under alternative silvicultural regimes in mixed-species forests of central Maine. Can. J. For. Res. **35**(4): 787–796. doi:10.1139/x05-021.

Gardiner, B.A., Stacey, G.R., Belcher, R.E., et Wood, C.J. 1997. Field and wind tunnel assessments of the implications of respacing and thinning for tree stability. Forestry **70**(3): 233–252. doi:10.1093/forestry/70.3.233.

Gauthier, S., Bernier, P.Y., Boulanger, Y., Guo, J., Guindon, L., Beaudoin, A., et Boucher, D. 2015a. Vulnerability of timber supply to projected changes in fire regime in Canada's managed forests. Can. J. For. Res. **1447**: 1–33. doi:10.1139/cjfr-2015-0079.

Gauthier, S., Raulier, F., Ouzennou, H. et Saucier, J.-P. 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.

Gauthier, S., DeGrandpré, L., et Bergeron, Y. 2000. Differences in forest composition in two boreal forest ecoregions of Quebec. J. Veg. Sci. **11**(6): 781–790.

Gauthier, S., Vaillancourt, M.-A., Kneeshaw, D.D., Drapeau, P., DeGrandpré, L., Claveau, Y., et Pare, D. 2009. Forest Ecosystem Management: Origins and Foundations. *In* Ecosystem management in the boreal forest. Presses de l'Université du Québec, Québec, Qc. pp. 13–38.

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

Graham, R.L., et Cromack, K. 1982. Mass, nutrient content, and decay rate of dead boles in rain forests of Olympic National Park. Canadian J. For. Res. **12**: 511–521.

Grove, S.J. 2002. Saproxylic Insect Ecology and the Sustainable management of forests. Annu. Rev. Ecol. Syst. **33**(1): 1–23. doi:10.1146/annurev.ecolsys.33.010802.150507.

Hale, C.M., et Pastor, J. 1998. Nitrogen content, decay rates, and decompositional dynamics of hollow versus solid hardwood logs in hardwood forests of Minnesota, U.S.A. Can. J. For. Res. **28**(9): 1276–1285. doi:10.1139/x98-097.

Hannon, S.J., Paszkowski, C.A., Boutin, S., DeGroot, J., Macdonald, S.E., Wheatley, M., et Eaton, B.R. 2002. Abundance and species composition of amphibians, small mammals, and songbirds in riparian forest buffer strips of varying widths in the boreal mixedwood of Alberta. Can. J. For. Res. **32**(10): 1784–1800. doi:10.1139/x02-092.

Harmon, M.E., Franklin, J.F., Swanson, F., Sollins, P., Gregory, S. V., Lattin, J.D., Anderson, N.., Cline, S.P., Aumen, N.., Sedell, J.., Lienkaemper, G.., Cromack Jr, K., et Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. (15): 133–302.

Harmon, M.E., Jr, K.C., et Smith, B.G. 1987. Coarse woody debris in mixed-conifer forests, Sequoia National Park, California. Can. J. For. Res. **17**: 1265–1272.

Harmon, M.E., Krankina, O.N., et Sexton, J. 2000. Decomposition vectors: a new approach to estimating woody detritus decomposition dynamics. Can. J. For. Res. **30**(1): 76–84. doi:10.1139/cjfr-30-1-76.

Harmon, M.E., et Sexton, J. 1996. Guidelines for measurements of woody detritus in forest ecosystems.

Harper, K.A. 1999. Variability in forest structure and composition along edge-to-interior gradients from lakeshore and clearcut edges and in riparian buffers in the aspen- dominated mixedwood boreal forest. Dissertation. University of Alberta. Edmonton, Alberta, Canada.

Harper, K.A., Bergeron, Y., Gauthier, S., et 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.

Harper, K.A., Boudreault, C., DeGrandpré, L., Drapeau, P., Gauthier, S., et Bergeron, Y. 2003. Structure, composition, and diversity of old-growth black spruce boreal forest of the Clay Belt region in Quebec and Ontario. Environ. Rev. **11**(S1): S79–S98. doi:10.1139/a03-013.

Harper, K.A., Drapeau, P., Lesieur, D., et Bergeron, Y. 2014. Forest structure and composition at fire edges of different ages: Evidence of persistent structural features on the landscape. For. Ecol. Manage. **314**: 131–140. Elsevier B.V. doi:10.1016/j.foreco.2013.12.009.

Harper, K.A., Drapeau, P., Lesieur, D., et Bergeron, Y. 2016. Negligible structural development and edge influence on the understorey at 16–17-yr-old clear-cut edges in black spruce forest. Appl. Veg. Sci. **19**(3): 462–473. doi:10.1111/avsc.12226.

Harper, K.A., Lesieur, D., Bergeron, Y., et Drapeau, P. 2004. Forest structure and composition at young fire and cut edges in black spruce boreal forest. Can. J. For. Res. **34**(2): 289–302. doi:10.1139/x03-279.

Harper, K.A., et Macdonald, S.E. 2001. Structure and composition of riparian boreal forest: New methods for analyzing edge influence. Ecology **82**(3): 649–659.

Harper, K.A., et Macdonald, S.E. 2002. Structure and composition of edges next to regenerating clear-cuts in mixed-wood boreal forest. J. Veg. Sci. **13**: 535–546.

Harper, K.A., Macdonald, S.E., Burton, P.J., Chen, J., Brosofske, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D., Jaiteh, M.S., et Esseen, P.-A. 2005. Edge influence on forest structure and composition in fragmented landscapes. Conserv. Biol. **19**(3): 768–782. doi:10.1111/j.1523-1739.2005.00045.x.

Harvey, B.D., et Leduc, A. 1999. Plan général d'aménagement - Forêt d'enseignement et de recherche du lac Duparquet (1998-2023). Université du Québec en Abitibi-Témiscamingue.153 pages

Harvey, B.D., Leduc, A., Gauthier, S., et Bergeron, Y. 2002. Stand-landscape integration in natural disturbance-based management of the southern boreal forest. For. Ecol. Manage. **155**(1–3): 369–385. doi:10.1016/S0378-1127(01)00573-4.

Hély, C., Bergeron, Y., et Flannigan, M.D. 2000. Coarse woody debris in the southeastern Canadian boreal forest: composition and load variations in relation to stand replacement. Can. J. For. Res. **30**(5): 674–687. doi:10.1139/x99-256.

Hill, S.B., Mallik, A.U., et Chen, H.Y. 2005. Canopy gap disturbance and succession in trembling aspen dominated boreal forests in northeastern Ontario. Can. J. For. Res. **35**(8): 1942–1951. doi:10.1139/x05-126.

Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bull. **43**: 69–78.

Houle, G., et Payette, S. 1990. Seed dynamics deciduous of Betula alleghaniensis in forest of north-eastern North America. J. Ecol. **78**(3): 677–690.

Huggard, D.J. 1999. Static life-table analysis of fall rates of subalpine fir snags. Ecol. Appl. **9**(3): 1009–1016.

Hunter, M.L. 2005. A mesofilter conservation strategy to complement fine and coarse filters. Conserv. Biol. **19**(4): 1025–1029. doi:10.1111/j.1523-1739.2005.00172.x.

Imbeau, L., et Desrochers, A. 2002. Foraging ecology and use of drumming trees by three-toed woodpeckers. J. Wildl. Manage. **66**(1): 222–231.

Johnson, E.A., et Greene, D. 1991. A method for studying dead bole dynamics in Pinus contorta var. latifolia-Picea engelmannii forests. J. Veg. Sci. **2**(4): 523–530. Available from http://onlinelibrary.wiley.com/doi/10.2307/3236034/abstract.

Johnson, E.A., et Van Wagner, C.E. 1985. The theory and use of two fire history models. Can. J. For. Res. **15**: 214–220.

Kapos, V. 1989. Effects of isolation on the water status of forest patches in the brazilian amazon. J. Trop. Ecol. **5**(2): 173–185.

Keen, F.P. 1929. How soon do yellow pine snags fall? J. For. (27): 735–737.

Keen, F.P. 1955. The rate of natural falling of beetle-killed ponderosa pine snags. J. For. (53): 720–723.

Kimmins, J.P. 2001. Balancing act: environmental issues in forestry. *In* 2nd Editio. University of British Columbia Press, Vancouver.

Kneeshaw, D.D., et Bergeron, Y. 1996. Ecological factors affecting the abundance of advance regeneration in Quebec's southwestern boreal forest. Can. J. For. Res. **26**: 888–898.

Kneeshaw, D.D., et Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. Ecology **79**(3): 783–794.

Krankina, O.N., et Harmon, M.E. 1995. Dynamics of the dead wood carbon pool in Northwestern Russian Boreal Forests. Water, Air Soil Pollut. **82**: 227–238.

Kruys, N., Fries, C., Jonsson, B.G., Lämås, T., et Ståhl, G. 1999. Wood-inhabiting cryptogams on dead Norway spruce (Picea abies) trees in managed Swedish boreal forests. Can. J. For. Res. **29**(2): 178–186. doi:10.1139/x98-191.

Kuuluvainen, T., Aapala, K., Ahlroth, P., Kuusinen, M., Lindholm, T., Sallantaus, T., Siitonen, J., et Tukia, H. 2002. Principles of ecological restoration of boreal forested ecosystems: Finland as an example. Silva Fenn. **36**(1): 409–422.

Kuuluvainen, T., Bergeron, Y., et Coates, K.D. 2015. Restoration and ecosystem-based management in the circumboreal forest: background, challenges, and opportunities. *In* Restoration of Boreal and Temperate Forests, Second Edi. CRC Press. pp. 251–270.

Lassauce, A., Paillet, Y., Jactel, H., et Bouget, C. 2011. Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. Ecol. Indic. **11**(5): 1027–1039. Elsevier Ltd. doi:10.1016/j.ecolind.2011.02.004.

Laurance, W.F., Ferreira, L. V., Rankin-de Merona, J.M., et Laurance, S.G. 1998. Rain forest fragmentation and the dynamics of Amazonian tree communities. Ecology **79**(6): 2032–2040. doi:10.2307/176707.

Lavoie, S., Ruel, J.-C., Bergeron, Y., et Harvey, B.D. 2012. Windthrow after group and dispersed tree retention in eastern Canada. For. Ecol. Manage. **269**: 158–167. doi:10.1016/j.foreco.2011.12.018.

Lecomte, N., Simard, M., Fenton, N., et Bergeron, Y. 2006. Fire severity and long-term ecosystem biomass dynamics in coniferous boreal forests of eastern Canada. Ecosystems **9**(8): 1215–1230. doi:10.1007/s10021-004-0168-x.

Lee, P. 1998. Dynamics of snags in aspen-dominated midboreal forests. For. Ecol. Manage. **105**(1–3): 263–272. doi:10.1016/S0378-1127(97)00286-7.

Lee, P., Crites, S., Nietfeld, M., Guyen, H. Van, et Stelfox, J.B. 1997. Characteristics and origins of deadwood material in aspend-dominated boreal forests. Ecol. Appl. **7**(2): 691–701.

Linder, P., et Ostlund, L. 1998. Structural changes in three mid-boreal Swedish forest landscapes, 1885-1996. Biol. Conserv. (85): 9–19.

Lussier, J.-M., Morin, H., et Gagnon, R. 2002. Mortality in black spruce stands of fire or clear-cut origin. Can. J. For. Res. **32**(3): 539–547. doi:10.1139/x01-201.

MacDonald, G.B., Cherry, M.L., et Thompson, D.J. 2004. Effect of harvest intensity on development of natural regeneration and shrubs in an Ontario boreal mixedwood stand. For. Ecol. Manage. **189**(1–3): 207–222. doi:10.1016/j.foreco.2003.08.010.

Martin, K., et Eadie, J.M. 1999. Nest webs: A community-wide approach to the management and conservation of cavity-nesting forest birds. For. Ecol. Manage. **115**(2–3): 243–257. doi:10.1016/S0378-1127(98)00403-4.

Mascarúa López, L.E., Harper, K.A., et Drapeau, P. 2006. Edge influence on forest structure in large forest remnants, cutblock separators, and riparian buffers in managed black spruce forests. Ecoscience **13**(2): 226–233. doi:10.2980/i1195-6860-13-2-226.1.

Mattson, K.G., Swank, W.T., et Waide, J.B. 1987. Decomposition of woody debris in a regenerating, clear-cut forest in the Southern Appalachians. Can. J. For. Res. **17**: 712–721.

McCarthy, J., 2001. Gap dynamics of forest trees: a review with particular attention to boreal forests. Environ. Rev. 9, 1-59.

MFFP, Ministère des Ressources naturelles. 2005. Plans généraux d'aménagement forestier 2007-2012 - Document de mise en œuvre. Available from http://www.mrn.gouv.qc.ca/publications/forets/consultation/document-oeuvre.pdf.

Morin, H., Laprise, D., et Bergeron, Y. 1993. Chronology of spruce budworm outbreaks near Lake Duparquet, Abitibi region, Quebec. Can. J. For. Res. **23**: 1497–1506.

Morrison, M.L., et Raphael, M.G. 1993. Modeling the dynamics of snags. Ecol. Soc. Am. **3**(2): 322–330.

Moussaoui, L., Fenton, N.J., Leduc, A., et Bergeron, Y. 2016. Deadwood abundance in post-harvest and post-fire residual patches: An evaluation of patch temporal dynamics in black spruce boreal forest. For. Ecol. Manage. **368**: 17–27. Elsevier B.V. doi:10.1016/j.foreco.2016.03.012.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Tree **10**(2): 58–62.

Næsset, E. 1999. Decomposition rate constants of *Picea abies* logs in southeastern Norway. Can. J. For. Res. **29**(3): 372–381. doi:10.1139/cjfr-29-3-372.

Naiman, R.J., Melillo, J.M., et Hobbie, J.E. 1986. Ecosystem Alteration of Boreal Forest Streams by Beaver (Castor canadensis). Ecol. Soc. Am. **67**(5): 1254–1269.

Nappi, A., et Drapeau, P. 2009. Reproductive success of the black-backed woodpecker (Picoides arcticus) in burned boreal forests: Are burns source habitats? Biol. Conserv. **142**(7): 1381–1391. Elsevier Ltd. doi:10.1016/j.biocon.2009.01.022.

Nappi, A., Drapeau, P., et Leduc, A. 2015. How important is dead wood for woodpeckers foraging in eastern North American boreal forests? For. Ecol. Manage. **346**: 10–21. Elsevier B.V. doi:10.1016/j.foreco.2015.02.028.

Nummi, P., et Kuuluvainen, T. 2013. Forest disturbance by an ecosystem engineer: beaver in boreal forest landscapes. Boreal Environ. Res. **18**: 13–24..

Olsen, J.S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology **44**(2): 322–331.

Ouellet-Lapointe, U. 2010. Le maintien des espèces cavicoles dans les paysages aménagés en forêt boréale mixte de l'est du Canada. Mémoire de maîtrise. Universite du Quebec à Montréal.

Ouellet-Lapointe, U., Drapeau, P., Cadieux, P., et Imbeau, L. 2012. Woodpecker excavations suitability for and occupancy by cavity users in the boreal mixedwood forest of Eastern Canada. Ecoscience **19**(4): 391–397. doi:10.2980/19-4-3582.

Paré, D., et Bergeron, Y. 1995. Above-Ground Biomass Accumulation along a 230-Year Chronosequence in the Southern Portion of the Canadian Boreal Forest. J. Ecol. **83**(6): 1001–1007.

Parish, R., Antos, J. a., Ott, P.K., et Lucca, C.M. Di. 2010. Snag longevity of Douglas-fir, western hemlock, and western redcedar from permanent sample plots in coastal British Columbia. For. Ecol. Manage. **259**(3): 633–640. doi:10.1016/j.foreco.2009.11.022.

Perron, N. 2003. Peut-on et doit-on s'inspirer de la variabilité naturelle des feux pour élaborer une stratégie écosystemique de répartition des coupes à l'échelle du paysage? Thèse de doctorat. Université Laval.

Peterson, E.B., et Peterson, N.M. 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces. Disponible à http://www.cfs.nrcan.gc.ca/bookstore_pdfs/12011.pdf .

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., et the R Development Core Team. 2008. The nlme package. Available at http://cran.stat.sfu.ca/.

Pham, A.T., Grandpré, L. De, Gauthier, S., et Bergeron, Y. 2004. Gap dynamics and replacement patterns in gaps of the northeastern boreal forest of Quebec. Can. J. For. Res. **34**(2): 353–364. doi:10.1139/x03-265.

Pothier, D., Raulier, F. et Riopel, M., 2004. Ageing and decline of trembling aspen stands in Quebec. Can. J. Forest Res. 34, 1251–1258. http://dx.doi.org/10.1139/x04-017.

Potvin, F., et Bertrand, N. 2004. Leaving forest strips in large clearcut landscapes of boreal forest: A management scenario suitable for wildlife? For. Chron. **80**(1): 44–53. doi:10.5558/tfc80044-1.

Poulin, J., et Messier, C. 2006. Rapport de paramétrisation du modèle de simulation de la dynamique forestière SORTIE-ND pour la forêt boréale et sub-boréale de l'ouest du Québec. [Rapport non publié] Montréal, QC

Qinghong, L., et Hytteborn, H. 1991. Gap structure, disturbance and regeneration in a primeval Picea abies forest. J. Veg. Sci. **2**: 391–402. doi:10.2307/3235932.

Gouvernement du Québec. 2015. Règlement sur les normes d'intervention forestières, chapter A-18.1, r. 7 (mise à jour le 1 June 2017).

R Core Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Ranney, J.W., Bruner, M.C., et Levenson, J. 1981. The importance of edge in the structure and dynamics of forest islands. pp. 67–69 *In* Forest islands in man dominated landscapes. *Edited by* R. Burgess and D. Sharp. Springler Verlag, New York, NY..

Raphael, M.G., et Morrison, M.L. 1987. Decay and dynamics of snags in the Sierra Nevada, California. For. Sci. **33**(3): 774–783.

Rich RL, Frelich LE et Reich, PB (2007) Wind-throw mortality in the southern boreal forest: effects of species, diameter and stand age. J Ecology 95: 1261-1273

Riopel, M., Bégin, J., et Ruel, J.-C. 2010. Probabilités de pertes des tiges individuelles, cinq ans après des coupes avec protection des petites tiges marchandes, dans des forêts résineuses du Québec. Can. J. For. Res. **40**(7): 1458–1472. doi:10.1139/X10-059.

Roberge, J.-M., Angelstam, P., et Villard, M. 2008. Specialised woodpeckers and naturalness in hemiboreal forests – Deriving quantitative targets for conservation planning. Biol. Conserv. **141**(4): 997–1012. doi:10.1016/j.biocon.2008.01.010.

Robert, E., Brais, S., Harvey, BD et Greene, DF. 2012. Seedling establishment and survival on decaying logs in boreal mixedwood stands following a mast year. Can. J. For. Res. 42 (8): 1446–1455

Ruel, J.-C. 1995. Understanding windthrow : Silvicultural implications. For. Chron. **71**(4): 434–445.

Ruel, J.-C., Pin, D., et Cooper, K. 2001. Windthrow in riparian buffer strips: effect of wind exposure, thinning and strip width. For. Ecol. Manage. **143**(1–3): 105–113. doi:10.1016/S0378-1127(00)00510-7.

Russell, R.E., Saab, V. a., Dudley, J.G., et Rotella, J.J. 2006. Snag longevity in relation to wildfire and postfire salvage logging. For. Ecol. Manage. **232**(1–3): 179–187. doi:10.1016/j.foreco.2006.05.068.

Saint-Germain, M., Drapeau, P., et 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 (Cop.). **30**(6): 737–748. doi:10.1111/j.2007.0906-7590.05080.x.

Saucier, J.-P., Grondin, P., Robitaille, A., et Bergeron, J.-F. 2003. Zone de végétation et domaines bioclimatiques du Québec. Ressources naturelles, Faune et Parcs.

Schaetzl, R.J., Burns, S.F., Johnson, D.L., et Small, T.W. 1989. Tree uprooting : Review of impacts on forest Ecology. Vegetatio **79**(3): 165–176.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms : Fennoscandian Boreal Forests as an Example. Oikos (49): 11–41.

Siitonen, J., Martikainen, P., Punttila, P., et Rauh, J. 2000. Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. For. Ecol. Manage. **128**(3): 211–225. doi:10.1016/S0378-1127(99)00148-6.

Simard, M., Lecomte, N., Bergeron, Y., Bernier, P.Y., et Paré, D. 2007. Forest productivity decline caused by successional paludification of boreal soils. Ecol. Appl. **17**(6): 1619–1637. doi:10.1890/06-1795.1.

Smith, V.G., Watts, M., et James, D.F. 1987. Mechanical stability of black spruce in the clay belt region of northern Ontario. Can. J. For. Res. **17**: 1080–1091.

Speight, M.C.D. 1989. Saproxylic invertebrates and their conservation. Nat. Environ. **42**: 1–79.

Spies, T.A. 1998. Forest structure : A key to the ecosystem. Northwest Sci. **72**(2): 34–39.

Spies, T.A., Franklin, J.F., et Thomas, T.B. 1988. Coarse woody debris in douglas-fir forests of western Oregon and Washington. Ecology **69**(6): 1689–1702.

Ste-Marie, G. 2009. Interactions entre le peuplier faux-tremble et l'épinette noire en forêt boréale de l'ouest du Québec. Mémoire de maîtrise, Université du Québec à Montréal. 91 pages

Stokland, J., Siitonen, J., et Jonsson, B.G. 2012. Biodiversity in dead wood. Cambridge University Press, Cambridge.

Stokland, J.N. 2001. The coarse woody debris profile : An archive of recent forest history and an important biodiversity indicator. Oikos (49): 71–83.

Storaunet, K.O., et Rolstad, J. 2002. Time since death and fall of Norway spruce logs in old-growth and selectively cut boreal forest. Can. J. For. Res. **32**(10): 1801–1812. doi:10.1139/x02-105.

Storaunet, K.O., et Rolstad, J. 2004. How long do Norway spruce snags stand? Evaluating four estimation methods. Can. J. For. Res. **34**(2): 376–383. doi:10.1139/x03-248.

Sturtevant, B.R., Bissonette, J.A., Long, J.N., et Roberts, D.W. 1997. Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland Ecol. Appl. **7**(2): 702–712.

Swift, M.J. 1973. The estimation of mycelial biomass by determination of the hexoamine content of wood tissue decayed by fungi. Soil Biol. Biochem. **5**: 321–332.

Taylor, S.L., et MacLean, D. a. 2007. Dead wood dynamics in declining balsam fir and spruce stands in New Brunswick, Canada. Can. J. For. Res. **37**(4): 750–762. doi:10.1139/X06-272.

Thorpe, H.C., et Thomas, S.C. 2007. Partial harvesting in the Canadian boreal: Success will depend on stand dynamic responses. For. Chron. **83**(3): 319–325. doi:10.5558/tfc83319-3.

Triska, F.J., et Kermit Cromack Jr. 1980. The role of wood debris in forests and streams. *In* Forests: Fresh Perspectives from Ecosystem Analysis. pp. 171–190.

Urban, S.T., Lieffers, V.J., et Macdonald, S.E. 1994. Release in radial growth in the trunk and structural roots of white spruce as measured by dendrochronology. Can. J. For. Res. **24**: 1550–1556.

Urgenson, L.S., Halpern, C.B., et Anderson, P.D. 2013. Level and pattern of overstory retention influence rates and forms of tree mortality in mature, coniferous forests of the Pacific Northwest, USA. For. Ecol. Manage. **308**: 116–127. Elsevier B.V. doi:10.1016/j.foreco.2013.07.021.

Vaillancourt, M.-A. 2007. Caractérisation de la disponibilité des arbres potentiels à la nidification du Garrot d'Islande dans la forêt boréale de l'est du Québec. Mémoire de maîtrise, Université du Québec à Montréal, 99 pages.

Vanderwel, M.C., Caspersen, J.P., et Woods, M.E. 2006. Snag dynamics in partially harvested and unmanaged northern hardwood forests. Can. J. For. Res. **36**(11): 2769–2779. doi:10.1139/x06-173.

Villard, P. 1994. Foraging behavior of Black-backed and Three-toed woodpeckers during spring and summer in a Canadian boreal forest. Can. J. Zool. (72): 1957–1959.

Vincent, J.-S., et Hardy, L. 1977. L'évolution et l'extension des lacs glaciaires Barlow et Ojibway en territoire québécois. Géographie Phys. Quat. **31**(3–4): 357. doi:10.7202/1000283ar.

Wang, C., Bond-Lamberty, B., et Gower, S. 2002. Environmental controls on carbon dioxide flux from black spruce coarse woody debris. Oecologia **132**(3): 374–381. doi:10.1007/s00442-002-0987-4.

Wei, X., Kimmins, J.P., Peel, K., et Steen, O. 1997. Mass and nutrients in woody debris in harvested and wildfire-killed lodgepole pine forests in the central interior of British Columbia. Can. J. For. Res. **27**(2): 148–155. doi:10.1139/x96-169.

Whitney, R.D., 1989. Root-rot damage in naturally regenerated stands of spruce and balsam fir in Ontario. Can J. For. Res. 19, 295-308.

Yatskov, M., Harmon, M.E., et Krankina, O.N. 2003. A chronosequence of wood decomposition in the boreal forests of Russia. Can. J. For. Res. **33**(7): 1211–1226. doi:10.1139/x03-033.