TABLE DES MATIÈRES

CHAPITRE I

CHAPITRE II

CHAPITRE IV

CHAPITRE V

LISTE DES FIGURES

LISTE DES TABLEAUX

Tableau Page

LISTE DES ABRÉVIATIONS

C	Continuous forest stand
CPRS	Coupe à protection de la régénération et des sols
DBH	Diameter at breast height
EXT	Exposure time to the disturbed matrix
FSC	Forest Stewardship Council
LT	Large timber (DBH > 17 cm)
MSI	Average shape index
MT	Medium timber (13 cm > DBH ≤ 17 cm)
OCi	Old island retention patch
OCs	Old separator retention patch
OF	Old fire residual patch
ST	Small timber (9 cm > DBH ≥ 13 cm)
TOL	Thickness of the organic layer
TSF	Time since last fire
YCc	Young clump retention patch
YCi	Young island retention patch
YF	Young fire residual patch.

RÉSUMÉ

La préoccupation de la préservation des forêts et de l'avenir de la foresterie s'est traduite par l'essor de nombreux projets de loi et certifications axés sur la gestion durable des forêts. Il s'agit de comprendre les mécanismes et dynamiques de perturbations naturelles afin de minimiser les écarts entre paysage naturels et paysages aménagés. La rétention des attributs structuraux (arbres vivants et morts, débris ligneux) à l'intérieur des zones aménagées est l'outil privilégié au Québec à cet effet. Toutefois, les modalités de rétention n'y sont pas encore bien définies et celles déjà existantes (bouquets, séparateurs) ou à l'essai (îlots) génèrent des peuplements de taille et de volume relativement arbitraires. Dans l'optique d'aménagement forestier écosystémique, l'objectif principal de cette thèse était d'évaluer le succès des coupes à rétention verte en pessière noire et de documenter la dynamique post-perturbation des îlots résiduels issus de feu et d'îlots de rétention créés par les traitements sylvicoles.

Trois types de peuplements en pessière à mousses ont été étudiés, soit, 41 placettes provenant d'îlots résiduels post-feu, 45 placettes de rétentions post-coupe et 37 placettes provenant de forêts continues (témoins). Les îlots résiduels post-feu et post-coupe ont été considérés selon leur temps d'exposition à la matrice perturbée comme jeunes (< 20 ans), ou vieux (≥ 20 ans). Les conditions forestières (diamètre, hauteur et volume des arbres et des chicots, volume de bois mort au sol, densité de régénération et des gaules, épaisseur de la matière organique, superficie et âge du peuplement) de chaque site à l'intérieur et en lisière ont été échantillonnées. Les peuplements ont été datés soit par une approche dendrochronologique ou au Carbone 14.

Le premier chapitre consistait à évaluer l'abondance post-perturbation du bois mort récent des îlots résiduels post-feu et de rétention post-coupe en fonction du volume de bois initial et à comparer leur dynamique temporelle. Les îlots résiduels post-feu ayant un volume de bois initial supérieur à 60 m^3ha^{-1} génèrent du bois mort d'une façon soutenable. Parfois, bien que les îlots résiduels post-feu apparaissent durables à moyen terme, leurs faibles volumes de bois sur pied fait en sorte qu'ils génèrent très peu de bois mort. En contexte aménagé, les grands îlots de rétention et les séparateurs secs avaient, généralement, une dynamique de recrutement de bois mort semblable à celle d'îlot post-feu. Toutefois, les bouquets figuraient parmi les îlots de rétention des plus vulnérables à l'écroulement même s'ils étaient peu volumétriques en raison de leur petite taille. Afin d'augmenter la durée de vie post-coupe d'îlots de rétention, nous

recommandons la sélection de parcelles de forêts à fort volume de bois (entre 60 et 300 m^3ha^{-1}) et de grandes superficies, sous la forme d'îlot ou de séparateur.

Le deuxième chapitre consistait en une classification des structures d'îlots résiduels post-feu et post-coupe en faisant le lien avec l'abondance du bois mort. Notre approche de classification structurale, basée sur l'analyse de la distribution de la taille des tiges marchandes, a permis d'identifier six types structuraux distincts. Les structures diamétrales en j-inversé (type 1) et unimodale tronquée (type 2) caractérisaient les peuplements dominés par le petit bois. À l'opposé, les peuplements de type 6 avaient une structure irrégulière et principalement composée de gros bois. La comparaison des types structuraux entre les îlots résiduels post-feu et post-coupe ont montré que généralement, les rétentions de coupe maintenaient bien la variété structurale naturelle observée dans les îlots de feu et la forêt continue. Toutefois, même si les peuplements de types 1 et 2 étaient présents dans les peuplements naturels, seuls les peuplements de types 3 à 6 comportaient d'une part, du bois moyen et gros longtemps après coupe et d'autre part, garantissaient le recrutement de nouvelles tiges marchandes. Afin d'éviter la simplification de la structure, nous recommandons que les îlots de rétention soient intentionnellement orientés vers les types dominés par des arbres intermédiaires et grands.

Le troisième chapitre a abordé la notion d'effet de lisière. En quoi les îlots créés par l'homme y seraient plus exposés que les îlots post-feu ? Les effets de lisière sur les attributs structuraux d'îlots résiduels post-feu et post-coupe apparaissaient, en général, similaires et dans les deux cas, ces effets dépendaient surtout des conditions initiales pré-perturbation de l'îlot résiduel et de leur temps d'exposition à la matrice perturbée environnante. Les résultats de ce chapitre suggèrent que les trois facteurs, un volume initial en bois marchand faible, l'écroulement de la lisière et la régénération du parterre de coupe, pourraient expliquer les faibles effets de lisières sur les attributs structuraux d'îlots résiduels présents au moment de l'échantillonnage. Un faible volume initial en bois marchand pourrait expliquer les faibles effets de lisières sur les attributs structuraux d'îlots résiduels. Certaines rétentions de coupe sous la forme de bouquet, en raison de leur petite taille et de leur fort volume de bois initial, se sont en partie écroulées. Nous recommandons donc la rétention de grands îlots de forêt fermée dans le parterre de coupe ce qui permettrait aux effets de lisière de se stabiliser avant d'atteindre leur centre tout en continuant d'assurer, à moyen et long terme, le recrutement de bois mort et d'arbres vivants.

À l'issue de cette thèse, nous démontrons l'influence de la structure initiale des peuplements ayant subit les feux et les coupes sur leur dynamique post-perturbation. Les conclusions soulèvent l'importance d'utiliser les îlots résiduels post-feu comme outils dans les stratégies d'aménagement écosystémique puisqu'ils maintiennent la variabilité structurelle portée par la forêt continue. En forêt boréale aménagée, maintenir une variabilité structurelle comparable à celle rencontrée en forêt naturelle

est susceptible de jouer un rôle dans la régénération des parterres de coupe et dans la préservation des espèces forestières.

Mots clés : forêt boréale, perturbation, rétention variable, coupe totale, attributs structuraux, aménagement forestier écosystémique, conservation de la biodiversité, habitat de qualité, dynamique de bois mort, durabilité d'îlot résiduel.

CHAPITRE I

INTRODUCTION GÉNÉRALE

1.1 Problématique

Depuis plus de deux décennies, la préservation de la forêt et l'avenir de la foresterie sont devenus des enjeux écologiques et socioéconomiques d'envergure de la communauté internationale (MEA, 2005; FAO, 2011). Ceci s'est traduit par l'impulsion donnée à la certification forestière et à l'adoption de projets de loi sur l'aménagement durable des forêts exigeant, particulièrement, le maintien de leur productivité et de leur résilience (Loyche Wilkie *et al.*, 2003). Pour assurer la gestion durable de ses forêts, le Québec privilégie désormais l'aménagement écosystémique dans sa récente Loi sur l'aménagement durable de son territoire forestier.

L'aménagement écosystémique des forêts s'appuie sur la compréhension des patrons spatiaux et dynamiques de la forêt naturelle afin de pratiquer une foresterie plus respectueuse de son fonctionnement et du maintien de sa biodiversité (Coulombe *et al.*, 2004). Il s'agit de favoriser dans le paysage aménagé le maintien d'une structure et d'une composition de peuplements semblables à celles caractérisant le paysage naturel (Franklin, 1993; Gauthier *et al.*, 1996). Parce que le feu constitue l'agent principal de perturbation naturelle en forêt boréale (Payette, 1992; Haeussler et Kneeshaw, 2003), et puisqu'il agit de manière non sélective en laissant des îlots intacts de végétation sur place (DeLong et Tanner, 1996; Bergeron *et al.*, 2001; Lindenmayer, 2006), il est le plus souvent utilisé comme modèle pour aménager de façon durable la forêt boréale. Toutefois, l'évaluation de la pérennité de ces îlots résiduels de végétation pose un défi de l'évaluation préalable de leur dynamique temporelle (Franklin, 1993; Gauthier *et al.*, 1996).

Alors que le feu constitue une partie intégrante du fonctionnement et de l'évolution de la forêt boréale (Payette, 1992; Hunter, 1993; Bergeron *et al.*, 1998), la coupe forestière lui reste une perturbation complètement étrangère. Un paysage aménagé présente généralement une organisation spatiale différente de celle caractérisant un paysage naturel (Belleau *et al.*, 2007; Bergeron *et al.*, 2007; Gauthier *et al.*, 2008b). Cette différence est principalement liée à la taille, la forme et l'arrangement après perturbation des legs biologiques dans le paysage. La coupe forestière telle qu'elle est actuellement pratiquée reproduit habituellement la même sévérité uniformément partout (Belleau *et al.*, 2007; Bergeron *et al.*, 2007). En revanche, la sévérité des feux est spatialement beaucoup plus variable, les zones épargnées ou faiblement affectées par le feu peuvent recouvrir jusqu'à 51 % de la superficie consumée (Bergeron *et al.*, 2007). C'est pourquoi on se questionne sur le maintien de rétention suffisante à l'intérieur des paysages aménagés. D'autant plus que la rétention de legs biologiques est susceptible de jouer un rôle important dans la recolonisation des parterres de coupe.

En forêt boréale canadienne, les études scientifiques s'intéressant à ces aspects sont rares et les comparaisons directes entre îlots de feu versus îlots de coupe sont fragmentaires. Afin de bénéficier davantage des services écosystémiques de la forêt boréale, il importe, désormais, de mettre au point des stratégies alternatives d'aménagement qui soient centrées sur le maintien de la biodiversité. La problématique générale de cette thèse s'inscrit dans cette perspective. Afin de comprendre jusqu'à quel point les rétentions générées par la coupe sylvicole s'apparentent aux îlots résiduels post-feu, nous comparons la structure et la dynamique des peuplements d'îlots résiduels post-feu et de rétentions post-coupe de taille et âges variables, autant à l'intérieur qu'en lisière en considérant les structures de la forêt continue d'origine comme témoins.

1.2 Intérêt d'étudier la dynamique de structure forestière

La structure interne d'un peuplement forestier se définit comme étant l'arrangement vertical et horizontal des arbres (Brokaw et Lent, 1999). Elle peut aussi être caractérisée par des attributs structuraux, à savoir les arbres vivants et morts debout (chicots) et les débris ligneux au sol. Ces attributs reçoivent un intérêt particulier, car ils sont facilement mesurables (surface terrière, volume, diamètre moyen) et sont souvent considérés comme des indicateurs de la biodiversité (McElhinny *et al.*, 2005). Les arbres de grand diamètre (vivants et morts), et le bois mort au sol peuvent fournir pour la faune des sources d'alimentation, des sites de reproduction, des aires d'hivernage et des abris contre les prédateurs et les aléas climatiques (Thompson et Curran, 1995; Økland, 1996; Spence *et al.*, 1996).

En contexte naturel, la configuration et composition des mosaïques forestières boréales est essentiellement déterminée par les régimes de perturbations naturelles comme les feux (Hunter Jr, 1990). La complexification de la structure interne des peuplements se fait au fil du temps. La complexité structurale est donc liée à la sénescence du peuplement forestier ou de l'occurrence des perturbations naturelles secondaires telles que les chablis et les épidémies d'insectes. En forêt boréale, la dynamique de maturation et de succession d'un peuplement forestier se traduit d'une part, par un remplacement d'essences pionnières par des essences de succession plus compétitives et tolérantes à l'ombre, puis par une dominance d'espèces de fin de succession supposée être stable sur le plan de la structure et de la composition (Larson et Oliver, 1996; Frelich, 2002), et d'autre part, par un apport continuel de débris ligneux grossiers au sol. Simultanément, des changements structuraux dans la taille des arbres se traduisent par un passage d'une structure diamétrale unimodale dépourvue de gros arbres à bimodale puis multimodale incluant des arbres de diamètre et âge variables (Larson et Oliver, 1996; Brassard et Chen, 2006). Plusieurs facteurs sont susceptibles d'influencer la dynamique de la structure forestière, à savoir le type de perturbation d'origine (Hunter Jr, 1990); le temps passé depuis la dernière perturbation et les caractéristiques du sol (Lindenmayer *et al.*, 1999); ou les conditions initiales du peuplement avant perturbation (Smith, 2010; Ouarmim *et al.*, 2014a; Bolton *et al.*, 2015).

Du point de vue floristique et faunique, ces changement de structure peuvent avoir des conséquences sur plusieurs organismes, à savoir les plantes et les mousses occupant le sol forestier (Fenton et Frego, 2005; Lachance *et al.*, 2013), ou les espèces d'oiseaux et d'insectes associées, surtout, aux gros arbres ou au bois mort grossier (Gandhi *et al.*, 2004; Bouchard et Hébert, 2016). Il est donc de plus en plus reconnu que la préservation de la biodiversité dans le paysage aménagé passe par le maintien des attributs structuraux de l'habitat forestier (Hunter Jr, 1990; Kuuluvainen, 2002; Kimmins, 2004).

1.3 Intérêt de considérer la forêt continue comme témoin

La forêt boréale continue provient majoritairement de feux survenus à des périodes diverses. Par conséquent, la matrice forestière naturelle y est généralement constituée de peuplement de différents âges. En raison de cycle des feux relativement long en forêt boréale de l'est, la proportion de vieux peuplements de plus de 150 ans peut dépasser les 50 % du paysage (Bélisle et al., 2011). De plus, plusieurs études s'accordent sur le fait que les attributs structuraux uniques aux vieilles forêts (gros arbres et bois mort sénescent) procurent une diversité d'habitats assurant la survie de plusieurs espèces vulnérables, notamment, d'oiseaux et de petits mammifères (Ferron et St-Laurent, 2005; Schmiegelow et al., 2006; Nappi et al., 2015), et le maintien de la régénération, de la productivité et de l'humidité du sol relativement stable de la forêt (Gagnon et Morin, 2001; Lee et Canada, 2003; Lee, 2007).

1.4 Îlots résiduels post-feu

Les feux brûlent rarement tout sur leur passage en forêt boréale (Perron et al., 2008; Perera et al., 2009; Madoui et al., 2011). Ceci se traduit par une mosaïque de peuplements d'âges, de compositions et de structures variables à l'échelle du paysage (Payette, 1992; Cyr et al., 2009). Le périmètre du feu inclut des peuplements entièrement brûlés, d'autres brûlés à différents degrés, et des peuplements épargnés (Van Wagner, 1983; Turner et al., 1997; Kafka et al., 2001; Perron et al., 2008; Madoui et al., 2011).

Les peuplements épargnés à l'intérieur du périmètre du feu, ici qualifiés d'îlots résiduels, sont également appelées forêts ou habitats résiduels (Gasaway et DuBois, 1985; Eberhart et Woodard, 1987; DeLong et Tanner, 1996; Stuart-Smith et Hendry, 1998; Dragotescu et Kneeshaw, 2012), et ils enferment en plus des arbres vivants, des chicots et des débris ligneux, des plantes arbustives et herbacées. Certains de ces îlots résiduels pourraient avoir été épargnés par les feux depuis des millénaires, et n'avoir été brûlés que lors d'un feu particulièrement sévère (Cyr *et al.*, 2005; Bergeron et Harper, 2009; Ouarmim *et al.*, 2015), dans ce cas, ils peuvent être considérés comme des refuges permanents avec plus de complexité structurelle, c.-à-d., *hotspot* de biodiversité. D'autres ont échappé uniquement au dernier feu, probablement d'une façon aléatoire (Ouarmim *et al.*, 2014b) par des événements fortuits, comme le changement de direction de vent ou l'absence de combustibles limitant la propagation du feu.

Il est généralement admis que la sévérité, la fréquence et la taille des feux varient en réponse à une combinaison de facteurs, qui en retour modélise de façon hétérogène le paysage forestier (DeLong et Tanner, 1996; Turner *et al.*, 1998; Miller et Urban, 1999; Bergeron *et al.*, 2001). Parmi ces facteurs environnementaux, la topographie (configuration du terrain), le climat (le vent et l'humidité du sol) et les facteurs biotiques (qualité du combustible) sont les plus souvent avancés (Van Wagner, 1968; Hély *et al.*, 2000; McRae *et al.*, 2001; Cyr *et al.*, 2007). En forêt boréale, la distance à un coupe-feu peut être à l'origine de la persistance d'îlots résiduels (Larsen, 1997; Kafka *et al.*, 2001; Cyr *et al.*, 2007). Il appert aussi dans d'autres études que les caractéristiques des peuplements de la forêt avant feu peuvent également être à l'origine de la présence ou de la persistance d'îlots résiduels (Foster, 1985; DeLong et Kessler, 2000; Kafka *et al.*, 2001; Madoui *et al.*, 2011; Ouarmim *et al.*, 2014a).

Bien que l'étude des îlots résiduels post-feu remonte à un peu plus d'une trentaine d'années, on s'y intéressât davantage à leur configuration spatiale (Eberhart et Woodard, 1987; DeLong et Tanner, 1996; Stuart-Smith et Hendry, 1998; Madoui *et al.*, 2011; Dragotescu et Kneeshaw, 2012; Madoui *et al.*, 2015) et moins à leur dynamique après-feu. La proportion et la superficie d'îlots résiduels dans le périmètre brûlé peuvent varier dépendamment de la taille des feux, du territoire, ou des conditions locales (Eberhart et Woodard, 1987; DeLong et Tanner, 1996; Smyth *et al.*, 2005). Même si la moitié des feux produisent généralement des îlots de superficies inférieures à 2 ha, les grands feux consumant des milliers d'hectares produisent des îlots pouvant atteindre une dizaine d'hectares. De plus, à cause de leur forte probabilité à rencontrer des coupe-feux (colline, ruisseau), les grands feux épargnent généralement une proportion plus élevée d'îlots résiduels, alors que les petits feux en renferment rarement (Eberhart et Woodard, 1987; DeLong et Tanner, 1996). Les études rapportent des valeurs allant généralement de 1 à 37% de la superficie des feux en îlots résiduels en forêt boréale (Eberhart et Woodard, 1987; DeLong et Tanner, 1996; Perron *et al.*, 2008; Madoui *et al.*, 2011; Dragotescu et Kneeshaw, 2012).

En préservant les attributs structuraux de la forêt continue d'origine avant-feu, entre autres de vieilles forêts, les îlots résiduels pourraient servir, d'une part, comme habitat refuge critique pour de nombreuses espèces forestières (Schmiegelow *et al.*, 2006; Perhans *et al.*, 2009; Hylander et Johnson, 2010) à savoir, les microorganismes, les insectes, les oiseaux et les mammifères (Gasaway et DuBois, 1985; Gandhi *et al.*, 2001). D'autre part, les îlots résiduels constituent une source de propagules qui pourrait assurer la recolonisation post-feu du périmètre brûlé et le rétablissement de certaines espèces (DeLong et Kessler, 2000; Madoui *et al.*, 2011).

Malgré ces pistes intéressantes, pour la forêt boréale canadienne, les caractéristiques structurales d'îlots résiduels ne sont pas encore bien documentées (Schmiegelow *et al.*, 2006). De plus, aucune étude n'a jusqu'ici, comparé la dynamique de structure de forêt boréale continue à celle d'îlots résiduels post-feu. La prise en considération de la présence dans le paysage forestier d'îlots résiduels dans les plans de gestion de la biodiversité bénéficierait d'une étude comparant la dynamique de structure des îlots résiduels issus de feu aux îlots de rétention créés par la coupe forestière. Si les feux n'opèrent aucune sélection et que les îlots post-feu sont représentatifs de la variabilité de la forêt continue, on peut s'en inspirer pour établir notre référant. Si par contre, les îlots post-feu constituent un échantillon biaisé de la forêt continue, on se doit alors utiliser la forêt continue comme référant surtout qu'elle est à risque en forêt aménagée.

1.5 Îlots de rétention post-coupe

Au Québec, les pratiques d'exploitation conventionnelles telles que les coupes à blanc ou les coupes totales ont été remplacées, depuis la fin des années 1980, par la coupe totale avec protection de la régénération et des sols (CPRS), qui consiste essentiellement en la récolte de toutes les tiges marchandes (DHP > 9 cm) en minimisant l'impact sur les sols. Les coupes forestières totales présentent alors une taille maximale de 250 ha et les forêts résiduelles se retrouvent entre autres sous la forme de séparateurs de coupe (séparateurs secs) d'une largeur de 60 à 100 m et d'îlots à orignaux (*Alces americanus*) de 3 à 10 ha (Gouvernement du Québec, 1988). La présence de ces séparateurs de coupe et d'îlots dans les parterres de coupe facilite notamment le déplacement de la faune et leur procurer des refuges contre les prédateurs (Desrochers et Hannon, 1997). Dans sa nouvelle loi sur l'aménagement durable de son territoire forestier, le Québec privilège désormais un aménagement écosystémique en vue d'assurer le maintien de la biodiversité et la variabilité des écosystèmes. Il s'agit d'un aménagement visant à réduire les écarts entre la forêt aménagée et la forêt naturelle, une forêt qui a évolué selon une dynamique générée par les perturbations naturelles.

Cependant, l'usage unique de la coupe totale ainsi qu'une absence de considération des effets cumulatifs qui en découlent à l'échelle du paysage sont à l'origine du rajeunissement et de la simplification de sa structure forestière (Harper *et al.*, 2004; Bergeron *et al.*, 2007; Kuuluvainen *et al.*, 2015). Dans une mosaïque forestière soumise à des révolutions de coupe relativement courtes, les massifs de vieilles forêts continues sont progressivement remplacés par des forêts résiduelles de plus faibles superficies dispersées dans une matrice dominée par des peuplements en régénération (Gauthier *et al.*, 1996; Bergeron *et al.*, 2002). En territoire aménagé, ces forêts résiduelles risquent d'être les seuls héritages structuraux de la forêt d'origine. Puisque plusieurs espèces dépendent partiellement ou entièrement des forêts anciennes (Drapeau *et al.*, 2000), leur diminution est susceptible d'influencer autant la flore que la faune (Franklin *et al.*, 1997).

Depuis un peu plus d'une décennie, la rétention forestière, connue aussi sous d'autres noms à savoir rétention verte, variable ou de legs biologiques (Franklin *et al.*, 1997; Barg et Hanley, 2001), est la stratégie proposée au Québec pour limiter les impacts de la coupe sur la biodiversité en forêt boréale aménagée et ainsi, améliorer l'acceptabilité sociale des activités de récolte forestière (Gustafsson *et al.*, 2012; Lindenmayer *et al.*, 2012). La rétention forestière consiste à favoriser le maintien d'une grande diversité structurale dans les parterres de coupe et éventuellement dans la forêt régénérée (Gauthier *et al.*, 2001; Beese *et al.*, 2003; Gauthier *et al.*, 2008b). Ainsi, la faune trouverait refuge et sources de nourriture dans le bois mort debout ou au sol, et sa décomposition permettrait au sol de rester fertile. De plus, les arbres vivants permettraient d'une part d'augmenter la capacité de rétablissement post-coupe des espèces et ainsi, préserver la diversité génétique. D'autre part, la rétention d'arbres pourrait réduire l'érosion du sol. La rétention post-coupe des attributs structuraux de la forêt d'origine se fait, généralement, de façon isolée ou regroupée en îlots (Franklin *et al.*, 1997; Doyon et Sougavinski, 2003; Work *et al.*, 2004). Elle peut donc s'agencer à plusieurs régimes sylvicoles (Franklin *et al.*, 1997; Beese *et al.*, 2003; Gustafsson *et al.*, 2012).

Or, au Québec, les modalités de rétention ne sont pas encore bien définies et les rétentions actuelles, qui sont pour la plupart purement expérimentales, préconisent des peuplements de taille relativement arbitraires (ex., îlots, séparateurs) maximisant souvent le volume de bois récolté (DeLong, 2002). De plus, la rétention est souvent réalisée selon des critères opérationnels, comme la faible valeur marchande de l'îlot, son accessibilité, sa proximité aux plans d'eau et son âge. Depuis une dizaine d'années, avec la réforme de la foresterie, notamment, par un aménagement écosystémique, on recherche surtout à améliorer les modalités actuelles de rétention variable, telle que les CPRS (coupe avec protection de la génération et des sols) sous la forme de bouquet ou d'îlot en faisant en sorte de se rapprocher davantage des patrons laissés par les perturbations naturelles (feux), surtout en matière de taille et de caractéristiques structurales (Bergeron *et al.*, 1999b; Harvey *et al.*, 2002). Pour pallier ces changements, l'amélioration des modalités actuelles de rétention après coupe bénéficierait d'une comparaison de leur structure et de leur dynamique à celles d'îlots résiduels laissés après feu.

1.6 Effet de lisière

Qu’ils soient issus de feu ou de coupe, les îlots résiduels ou de rétention se retrouvent relativement, d’une part avec peu de forêt d’intérieure héritée de la forêt d’origine, qui est une partie de forêt qui n’a pas subi l'influence des ouvertures et d’autre part, avec plus de proportions de lisières exposées au nouvel environnement perturbé (coupé ou brûlé) (Harper *et al.*, 2005). La lisière forestière correspond à la zone de transition entre l’îlot résiduel et la matrice perturbée qui présente des conditions climatiques et écologiques particulières. Elle est pour cette raison soumise à une dynamique spatiale propre qu’on nomme effet de lisière. Il s’agit d’un gradient continu de la limite forêt-milieu ouvert verts la forêt d’intérieure de l’îlot (Harper *et al.*, 2005). L’effet de lisière était d’abord estimé visuellement (Chen et al. 1995), puis, depuis une quinzaine d’années, par des méthodes statistiques. Il n’y a donc pas de consensus quant à la méthode de mesure de l’effet de lisière. De manière générale, on mesure les effets de lisière par deux critères : leur étendue spatiale ou profondeur d’influence et leur amplitude ou magnitude (Harper et al. 2005 ; Chen et al 1995). La profondeur d’influence (DEI) est la distance sur laquelle des modifications de la variable réponse sont observées. Elle permet d’estimer la surface totale d’habitat ou d’un paysage sous l’influence de l’effet de lisière. La magnitude (MEI) se définit par le contraste entre les valeurs de la variable réponse, mesurée de la lisière vers la forêt d’intérieure.

Les effets de lisière peuvent être à l’origine de différences de structure, de composition et de fonction des habitats de lisière par rapport aux forêts intérieures. En raison d’une perturbation récente, ces différences peuvent augmenter la vulnérabilité des îlots de rétention au risque d’écroulement et ainsi, influencer, à court ou à long terme la survie de plusieurs espèces qui en dépendent (McGarigal et Marks, 1995). De plus, les caractéristiques d’îlots de rétention et d’îlots résiduels comme la densité des tiges et la densité des gaules peuvent influencer leur susceptibilité au chablis (Riopel *et al.*, 2010). Par contre, comparées au nombre d’études effectuées après feu, maintes d’études ont examiné la réaction, à court terme, des îlots de rétention dans les coupes (Rosenvald et Lohmus, 2008; Perhans *et al.*, 2009; Gustafsson *et al.*, 2010). En revanche, la plupart des îlots de rétention étudiés sont de petites tailles et les espèces qu'on y rencontre sont souvent associées à un habitat de lisière (Harper *et al.*, 2004; Fenton et Frego, 2005; Boudreault *et al.*, 2008). Les îlots de petite taille des paysages aménagés peuvent présenter des effets de lisière importants, à savoir, une plus grande mortalité d'arbres et une réduction du couvert forestier, et donc une forêt intérieure d'étendue restreinte (Rheault *et al.*, 2003; Mascarúa López *et al.*, 2006). En outre, les îlots de rétention, souvent de forme linéaire, peuvent subir des événements importants de chablis (Lavoie et al., 2012) dépendamment de leur contexte environnant, de leur orientation et des caractéristiques structurales du peuplement (Dragotescu et Kneeshaw, 2012; Lavoie *et al.*, 2012). Ceci laisse penser que la plupart des îlots de rétention après coupe ne pourraient pas remplir leurs rôles durant toute la prochaine rotation forestière.

Néanmoins, les lisières sont rarement prises en compte dans les plans d'aménagement et de conservation de la biodiversité. De plus, les lisières naturelles sont moins bien documentées que les lisières créées par la coupe forestière (Harper et al., 2004). En outre, en forêt boréale, on a commencé à s'intéresser aux lisières forestières que récemment (Harper *et al.*, 2004; Mascarúa López *et al.*, 2006; Larrivée *et al.*, 2008; Braithwaite et Mallik, 2012). D'où l'originalité de ce projet qui compare les deux types d'îlots résiduels en ce qui concerne leurs structures et leurs dynamique spatiale et temporelle, à l'échelle du peuplement, tant en forêt d'intérieur qu'en lisière.

1.7 Objectifs de la thèse

Afin d'orienter la rétention du matériel végétal à retenir dans les parterres de coupe permettant de préserver la matrice forestière et les espèces qui lui sont associées, il est indispensable d'établir non seulement le nombre de rétentions, mais aussi les types de structures, tout en ayant une idée sur leur éventuelle dynamique post-coupe. Dans le but d'améliorer les techniques actuelles de rétention en forêt boréale, il importe alors de comparer la structure et la dynamique des îlots de rétention post-coupe à celles d'îlots résiduels post-feu.

L'objectif général de la présente thèse consiste à documenter les mécanismes ou les différences possibles entre les îlots naturels et les îlots de rétention créés par la coupe en pessière à mousses de l'ouest du Québec. Notre étude est basée sur l'analyse à l'échelle du peuplement des caractéristiques structurales et dynamiques de trois types de peuplements post-perturbation, soit des îlots résiduels post-feu, des îlots de rétention post-coupe et de la forêt continue non perturbée. Plus spécifiquement, la thèse s'articule autour des objectifs suivants faisant objet de trois chapitres distincts :

- Évaluer et comparer l'abondance du bois mort entre les peuplements provenant d'îlots de rétention post-coupe et d'îlots post-feu et comparer leur durabilité post-perturbation. Nous soupçonnions qu'indépendamment de la perturbation d'origine, les jeunes îlots résiduels (exposés récemment à un nouvel environnement plus ouvert) présenteraient plus de volume de bois mort que les vieux (exposés très longtemps à une matrice perturbée). De plus, les conditions intiales susceptibles d'expliquer les variations en volume de bois mort ont été identifiées. Les facteurs potentiels étaient : le temps depuis le dernier feu dans l'îlot, c.-à-d. l'âge de la forêt d'origine, l'âge de l'îlot (le temps d'exposition de l'îlot à une matrice perturbée), la superficie et la forme de l'îlot, l'ancrage des arbres (estimé par l'épaisseur de la matière organique) et le diamètre à hauteur de poitrine et la hauteur moyens des arbres dans l'îlot (Chapitre 2).
- Déterminer si la variété structurale rencontrée dans les peuplements forestiers naturels (îlots post-feu ou forêt continue) se compare bien à celle observée au sein de la rétention post-coupe. La classification structurale des îlots résiduels post-feu et post-coupe a été établie en fonction de la distribution diamétrale de la densité et

de la surface terrière marchande des peuplements. La comparaison des caractéristiques structurales (taille des arbres et des chicots, densité et volume des arbres et du bois mort récent et ancien, épaisseur de la matière organique, et forme, taille et âge minimum des peuplements) permettant de différencier les îlots de rétention de ceux issus de feu a été également effectuée. Enfin le lien entre la dynamique temporelle des îlots résiduels et leurs types structuraux a été examiné (Chapitre 3).

- Comparer les effets de lisière sur les attributs structuraux entre les peuplements provenant d'îlots de rétention post-coupe et les peuplements issus d'îlots résiduels post-feu (Chapitre 4). L'objectif de ce chapitre était de déterminer si l'effet de lisière sur les attributs structuraux apparaissait similaire entre les îlots générés par le feu et les rétentions de coupe, et de savoir si les rétentions de coupe étaient plus vulnérables à la perte de leur habitat intérieure à cause de leur lisière franche ou de leur petite taille. De plus, nous avons testé si l'effet de lisière s'affaiblissait avec le temps d'exposition à la matrice perturbée.

1.8 Territoire à l'étude

L'aire d'étude se situe à l'est de la forêt boréale canadienne, occupant un territoire de 412 400 km^2 situé entre le 49^e et le 51^e parallèles de latitude nord, soit dans le sous-domaine bioclimatique de la pessière à mousses de l'ouest du Québec. Le feu y constitue la principale perturbation naturelle qui façonne le paysage forestier (Payette, 1992). Historiquement, le feu se caractérisait par un cycle relativement court, de l'ordre de 100 à 200 ans (Bergeron *et al.*, 2001) et actuellement, il s'est allongé et il est estimé à plus de 400 ans. À ceci se rajoutent, depuis plusieurs décennies, les effets de la coupe forestière comme principale source de perturbation anthropique (DeLong et Tanner, 1996; Noss *et al.*, 2006; Cyr *et al.*, 2009; Imbeau et al., 2015).

Les paysages y sont assez uniformes, puisque le couvert forestier est nettement dominé par l'épinette noire (*Picea mariana* Mill., BSP), qui y forme un nombre non négligeable de peuplements monospécifiques, à laquelle s'ajoutent différentes espèces compagnes, soit le pin gris (*Pinus banksiana* Lamb), le sapin baumier *(Abies balsamea* [L.] Mill), le bouleau à papier (*Betula papyrifera* Marsh) et le peuplier faux-tremble (*Populus tremuloides* Michx.). Les températures annuelles moyennes varient de -2.5 à 0°C, les précipitations annuelles moyennes allant de 700 à 900 mm, le climat est subpolaire, subhumide continental (Bergeron *et al.*, 1999a; Blouin et Berger, 2005). La topographie de cette région forme une plaine légèrement ondulée et les sols minéraux sont généralement composés d'argile glaciolacustre à l'ouest, de type till argileux vers l'est (Robitaille et Saucier, 1998).

Les peuplements étudiés proviennent de trois types de milieux d'origine : soit d'îlots après feu, de rétentions après coupe et de forêts continues non perturbées. Les données concernant les peuplements d'îlots résiduels post-feu sont issues de six feux sévères, soit trois jeunes feux (0-19 ans) et trois feux âgés (20-40 ans). Les données sur les peuplements d'îlots de rétention post-coupe sont issues de treize parterres de coupes, à raison de sept jeunes coupes de 0 à 19 ans de deux types (CPRS à rétention de bouquets ou d'îlots) et de six vieilles coupes totales de 20 à 40 ans avec des séparateurs secs et d'îlots à orignaux. Enfin, les données concernant la forêt continue (témoin) sont issues d'un précédent projet centré sur le même territoire à l'étude et ayant utilisé des méthodes d'échantillonnage similaires aux nôtres (Chaieb *et al.*, 2015).

CHAPITRE II

DEADWOOD ABUNDANCE IN POST-HARVEST AND POST-FIRE RESIDUAL PATCHES: AN EVALUATION OF PATCH TEMPORAL DYNAMICS IN BLACK SPRUCE BOREAL FOREST

Louiza Moussaoui, Nicole J. Fenton, Alain Leduc, Yves Bergeron

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2.1 Abstract

In managed boreal forests, variable retention harvest is considered by forest managers as a means of mitigating harvest impacts on biodiversity. Variable retention harvest consists of maintaining within a cutblock structural attributes of the original forest stand in intact forest patches that could provide quality habitat (i.e., with large trees and deadwood) for many forest species during forest regeneration. However, retention patch modalities (size, shape, age of the forest) allowing both persistence and sustainable recruitment of deadwood over time remains unknown. The objective of this study is to evaluate the abundance of recent deadwood in post-harvest and post-fire residual patches and to compare their temporal dynamics in black spruce dominated stands located in northwestern Quebec. Abundance of the recent deadwood, estimated as the sum of recent standing deadwood volume and recently fallen deadwood volume was analyzed in 41 post-fire residual patches, and in 45 post-harvest retention patches of varying ages (i.e. exposure time to the disturbed matrix) and in 37 continuous black spruce forest stands (controls). This study shows that post-fire residual patches appear in general more durable than post-harvest retention patches after disturbance. In a management context, our results indicate that: (1) large island patches and large linear separators oriented to escape windthrow usually have deadwood recruitment dynamics similar to that of post-fire patches; (2) retention patches with an initial stand volume greater than 60 m^3ha^{-1}will generate more deadwood volume over time. This suggests that the selection of large retention patches in the shape of an island or a separator, with high volume (between 60 and 300 m^3ha^{-1}) should help increase the persistence of post-harvest retention patches in black spruce forest, and simultaneously ensure quality habitat for several forest species while the adjacent managed forest regenerates.

Additional Keywords: Disturbance, Forest retention harvesting, Mortality dynamics, Black spruce-feathermoss forests, Ecosystem based management.

2.2 Résumé

En forêt boréale aménagée, la rétention variable est considérée par plusieurs forestiers comme le moyen de mitigation des effets de la coupe sur la biodiversité. La rétention variable consiste à maintenir dans un secteur coupé des îlots de forêt appelés îlots de rétention post-coupe, qui pourraient offrir un habitat de qualité (i.e., avec des gros arbres et du bois mort) pour de nombreuses espèces forestières le temps que la forêt prélevée adjacente se reconstitue. Or, on en connait peu sur les modalités de rétention (taille, forme, âge de la forêt) permettant à la fois leur persistance et un rendement soutenu en bois mort dans le temps. L'objectif principal de cette étude est d'évaluer l'abondance du bois mort récent des îlots résiduels post-feu et de rétentions post-coupe et de comparer leur dynamique temporelle en pessière à mousses de l'ouest du Québec. L'abondance du bois mort récent, estimée comme le volume de bois mort debout et au sol peu décomposé, a été analysée dans 41 îlots post-feu et 45 îlots post-coupe d'âges (temps d'exposition à la matrice perturbée) variables et dans 37 peuplements de forêt continue (contrôles). Cette étude montre que les îlots résiduels post-feu apparaissent, généralement, plus durables que les îlots de rétentions post-coupe. En contexte aménagé, nos résultats indiquent que : (1) les grands îlots de rétention à orignaux et les grands séparateurs secs orientés pour échapper au chablis ont, généralement, une dynamique de recrutement de bois mort semblable à celle d'îlot post-feu ; (2) les îlots de rétention ayant un volume de bois initial supérieur à 60 m^3ha^{-1} génèrent plus de volumes de bois mort au fil du temps. Ceci suggère que la sélection de parcelles de forêts à fort volume de bois (entre 60 et 300 m^3ha^{-1}) et de grandes superficies, sous la forme d'îlot ou de séparateur, lors de la création d'îlots de rétention devrait augmenter la durée de vie post-coupe des îlots de rétention en pessière à mousses, et d'assurer simultanément un habitat de qualité pour plusieurs espèces le temps que la forêt prélevée adjacente se régénère.

Mots clés additionnels : Perturbation, Rétention variable, Dynamique de mortalité, Pessière à mousses, Aménagement écosystémique.

2.3 Introduction

In recent decades the progressive loss of old-growth forests has been of particular interest because of the potential impacts on biodiversity (Bergeron et al., 2002; Perron et al., 2008). In boreal ecosystems, the predominance of clearcutting and the absence of consideration of the cumulative landscape scale effects in planning results in the rejuvenation and simplification of forest structure across the landscape (Harper et al., 2004; Bergeron et al., 2007; Kuuluvainen et al., 2015). In a forest landscape subject to relatively short harvest rotations, the old-growth forest matrix is gradually replaced by smaller residual forests, dispersed in a matrix dominated by post-harvest regenerating stands (Gauthier et al., 1996; Bergeron et al., 2002). In managed landscapes, these residual forests are likely to be the only structural legacies of the original forest. As several species are partially or entirely dependent on old-growth forests (Drapeau et al., 2000), their decline is likely to influence both fauna and flora (Franklin et al., 1997). To limit the impact of forest harvest on biodiversity, variable retention harvesting is a frequently proposed technique (Gustafsson et al., 2012; Lindenmayer et al., 2012). Variable retention harvesting consists of maintaining structural attributes (live and dead trees, woody debris), of the original forest stand in intact forest patches dispersed across the cutblock (Gauthier et al., 2001, 2008; Beese et al., 2003). In freshly disturbed areas, variable retention can be considered ecosystem based management if its modalities are inspired by patterns generated by natural disturbances (Payette, 1992; Franklin, 1993; Gauthier et al., 1996; Harvey et al., 2002).

In boreal forests, fire shapes the structure of forest mosaics (Kafka et al., 2001). However, fire does not generally burn all trees within its boundaries, and intact patches, here called “post-fire residual patches” of varying size and age remain (Gasaway and DuBois, 1985; DeLong and Kessler, 2000; Bergeron and Fenton, 2012). Several studies suggest that post-fire residual patches could represent significant and unique refuge habitats for many plant (Ferron and St-Laurent, 2005; Perhans et al., 2009; Hylander and Johnson, 2010), or animal species (Gandhi et al., 2001; Pearce et al., 2005; Schmiegelow et al., 2006). Over time, these post-fire residual patches could also constitute seed banks providing propagules for recolonization of the burned surrounding areas (DeLong and Kessler, 2000; Madoui et al., 2011). In contrast, the selection of retention patches during variable retention harvesting is generally based on operational criteria, such as proximity to water bodies, tree age and species, and accessibility. Therefore, these post-harvest retention patches could present different habitat conditions and different forest dynamics than those that characterize post-fire residual patches (Harper et al., 2004; Work et al., 2004).

The tree mortality dynamics, i.e., the recruitment of snags or fallen deadwood and their eventual decomposition, has been little studied in post-harvest residual patches. In addition, most of the research conducted to date has taken place in the boreal mixed forest (Bose et al., 2013). Forest retention patches, as currently established, are often small in size (clumps) or linear (cuts separators) and subject to significant windthrow events (Ruel et al., 2001; Dragotescu and Kneeshaw, 2012; Lavoie et al., 2012), especially during the first years after establishment (Scott and Mitchell, 2005; Hautala and Vanha-Majamaa, 2006; Lavoie et al., 2012; Urgenson et al., 2013). Although mortality observed in the first years after harvest can be a significant source of deadwood (Mitchell and Beese, 2002; Beese et al., 2003; Thorpe and Thomas, 2007), this contribution could be short-lived if the rate of mortality of large trees exceeds their rate of recruitment in the canopy (Thorpe and Thomas, 2007). In other words, these post-harvest retention patches could open up over time, thereby eroding their ecological value. In managed areas, these retention patches need to remain for at least 100 years, a period necessary for the surrounding black spruce regenerated forests to become a mature forest (Burns and Honkala, 1990). Therefore, it is important to document the durability of these post-harvest retention patches. In boreal forests, tree mortality dynamics observed in retention patches have been found to be influenced by many local factors (Dragotescu and Kneeshaw, 2012; Lavoie et al., 2012), including characteristics of the trees (height and average diameter), of the stands (size, shape, age) (DeWalle, 1983; Cyr et al., 2009), of the soil (type and depth), of the surrounding context (time since last disturbance) as well as of forest harvesting techniques (Ruel, 1995; Jönsson et al., 2007; Lavoie et al., 2012).

The main objective of this study is to evaluate the abundance of recent deadwood in post-harvest and post-fire residual patches and to compare their durability over time, considering continuous black spruce forest as a control. The first specific objective is to compare recent deadwood volumes between post-harvest retention patches and post-fire residual patches of varying ages (i.e. exposure time to the disturbed matrix). In this case, we anticipate that due to their greater vulnerability to wind, there will be greater volumes of recent deadwood in the post-harvest retention patches than in the post-fire patches and this especially during the first years of exposure to the disturbed matrix. The second specific objective is to evaluate the effect of stand volume of the pre-disturbance forest on the volume of recent deadwood in post-harvest and post-fire patches of different ages. We estimate that regardless of their age and their original disturbance i.e. harvest or fire, pre-disturbance volume of the patches will be positively correlated with recent deadwood volume. The third specific objective is to determine which explanatory factors explain recent deadwood volume in residual patches. The potential explanatory factors are: time since the last fire, which corresponds to the age of the original forest from which the patch was formed; patch area and shape; tree anchoring substrate, estimated by the thickness of the organic layer; and mean diameter and height of living trees. Finally, these results are integrated to generate a predictive model that will allow us to make recommendations in terms of size, shape and type of forest stand that should be targeted for post-harvest retention in order to increase persistence of patches and ensure the expected ecosystemic services are provided.

2.4 Material and methods

2.4.1 Study area

This study was conducted in eastern Canada's boreal forest, between 74–80°W and 49–51°N; in the black spruce-feathermoss bioclimatic subdomain (Figure 2.1). The topography of this area forms an undulating plain. The mineral soil type is composed primarily of glaciolacustrine clay in the west, and clay till in the east (Robitaille and Saucier, 1998). The mean annual temperature varies between −2.5 and 0.0 °C, and the mean annual precipitation varies between 700 and 900 mm and the climate is subpolar, continental sub-humid (J.-F. Bergeron et al., 1999; Blouin and Berger, 2005). Forest stands are dense (canopy cover 40–80%) and dominated by black spruce (*Picea mariana* Mill., BSP) with jack pine (*Pinus banksiana* Lamb), balsam fir (Abies balsamea [L.] Mill), birch (*Betula papyrifera* Marsh) and trembling aspen (*Populus tremuloides* Michx.).

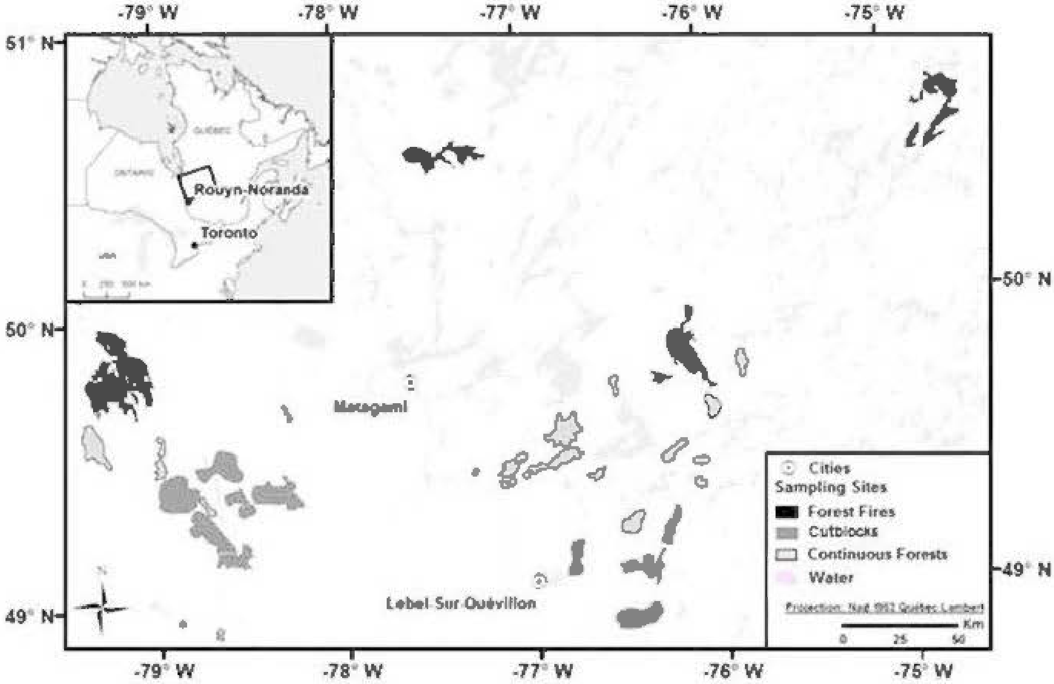

Figure 2.1 Location of the study sites in the black spruce boreal forest. Post-fire residual patches located in forest fires (black); post-harvest residual patches located in cutblocks (dark gray) and the continuous forest stands are represented in pale gray surrounded in black.

Fire is the main natural disturbance that shapes the forest landscape in the study area (Payette, 1992), with historically a relatively short fire cycle, on the order of 100–200 years (Bergeron et al., 2001). Currently this fire cycle is lengthening and is now over 400 years. As the fire cycle has lengthened, the effects of forest harvest have become the main source of disturbance on the landscape (Bergeron et al., 2004; Cyr et al., 2009). Since the late 1980s, the harvesting method commonly used has been harvest with protection of regeneration and soils (CPRS in French), which consists of harvesting all merchantable stems (DBH > 9 cm) in cutblocks with a maximum size of 250 hectares. Retention patches were placed linearly between these cutblocks (separators) with a width of 60 to 100 m and in the form of large patches (3–10 ha) within the cutblocks for moose (*Alces americanus*) (Gouvernement du Québec, 1988). In the ten last years, two new retention types have been used: small clumps and large intact forest patches, which are supposed to maintain structural attributes similar to those created by fires (Y. Bergeron et al., 1999; Harvey et al., 2002).

2.4.2 Location of the study sites

We used three types of study sites: post-fire residual patches, post-harvest retention patches and undisturbed continuous forest stands (Table 2.1). Six fires, i.e., three young fires (0–19 years old) and three old fires (20–40 years) were selected using the fire maps of the Ministère des Ressources Naturelles et de la Faune du Québec (MRNF). Thereafter, we selected between five to eight residual patches by fire for a total of 41 post-fire residual patches (Figure 2.1). The selection of cutblocks was undertaken using eco- forestry maps and recent harvest GIS layers of three forestry companies and harvest licenses (TEMBEC UAF 085-51, and EACOM UAF 086-64 and PF Résolu PRAN 087-62). Thirteen cutblocks were studied: seven young cutblocks (0 –19 years) with retention in clumps and large islands, and six old cutblocks (20–40 years) with linear separators and large islands. Three to five retention patches were selected per cutblock for a total of 47 post-harvest retention patches (Figure 2.1). The residual patches were: (1) randomly selected from accessible patches (<1 km from a road) using ArcGis® mapping software based on the fire and eco-forestry maps, and recent harvest GIS layers and harvest licenses; then (2) validated in the field according to the criteria of representativeness, accessibility, presence of late successional species (*P. mariana* Mill., BSP) and absence of salvage logging in the case of fires. 37 old-growth forest stands (control), aged between 74 and 1320 years were selected (Chaieb et al., 2015) from the same landscape.

Table 2.1 Characteristics of the sampled residual patches and the continuous forest stands. All factors considered are given as mean (range): EXT, exposure time since the last disturbance (year); TSF, time since the last fire (year); MSI, mean shape index; ARP, area of residual patch (ha); TOL, thickness of the organic layer (cm); MHT, mean height of living trees (m); DBH, mean diameter at breast height (cm); ISV, initial stand volume (m^3ha^{-1}); LSV, living stand volume (m^3ha^{-1}); %RDV, proportion of the recent deadwood volume (%). The residual patch types ST are: OF, old fire; YF, young fire; OCs, old cut separator; OCi, old cut island; YCc, young cut clump; YCi, young cut island. C, continuous forest. CPRS: harvesting with the protection of regeneration and soils.

Disturbance type	**Site name**	**EXT (ys)**	**ST (n)**	**TSF (ys)**	**MSI**	**ARP (ha)**	**TOL (cm)**	**MHT (m)**	**DBH (cm)**	**ISV (m^3ha^{-1})**	***ln* (ISV)**	**LSV (m^3ha^{-1})**	**%RDV**
Fire	Casa Chapais Lebel	36 37 30 27	OF (23)	138.1 (80-216)	1.3 (0.9-1.6)	2.78 (0.06-12.11)	61.39 (19-169)	14.36 (10-17.8)	14.86 (11-18.9)	211.6 (32.66-370.8)	5.24 (3.49-5.92)	34.2 (1.6-107.8)	0.11 (0.01-0.31)
	Matagami Selbaie Lebel	15 16 17 16	YF (18)	152.2 (70-240)	1.37 (1.1-2)	2.55 (0.2-11.13)	54.39 (23-130)	13.23 (7.6-19.3)	13.49 (10.6-18.7)	131.62 (19.6-310.2)	4.54 (2.98-5.74)	50.07 (0-164.32)	0.17 (0-0.38)
Harvest	Separator 1 Separator 2 Separator 3	24 21 23	OCs (9)	124.6 (84-199)	1.61 (1.3-1.9)	5.59 (0.31-13.44)	41.22 (21-73)	15.48 (13.1-18.4)	15.26 (13.3-17.5)	240.8 (146.3-338.7)	5.44 (4.99-5.83)	79.66 (10.4-198.6)	0.14 (0.02-0.3)
	Island 1 Island 2 Island 3	21 21 24	OCi (9)	134.3 (97-222)	1.17 (1.1-1.3)	5.29 (3.57-7.32)	56.22 (36-75)	14.83 (9.6-18.4)	15.47 (12.7-17.8)	188.2 (106.9-382.8)	5.15 (4.67-5.95)	90.89 (10.7-245.8)	0.31 (0.05-0.9)
	CPRS-Clump 1 CPRS-Clump 2 CPRS-Clump 3 CPRS-Clump 4	5 3 7 4	YCc (20)	91.2 (71-134)	1.1 (1-1.4)	0.04 (0.2-0.7)	37.85 (18-65)	11.91 (8.7-18.2)	13.75 (10.4-23.4)	247.9 (122.1-439.8)	4.6 (3.1-6.08)	38.57 (0.7-173.1)	0.22 (0.01-0.52)
	CPRS-Island 1 CPRS-Island 2 CPRS-Island 3	1 2 1	YCi (9)	104.7 (81-147)	1.08 (0.9-1.1)	1.21 (0.5-1.74)	40 (26-50)	15.83 (10.3-20.6)	15.17 (11.6-18.9)	246.6 (48.3-474.2)	5.35 (3.87-6.16)	50.45 (3.7-119.1)	0.14 (0.06-0.4)
Continuous forest	Control	-	C (37)	151.2 (74-1320)	1	31.98 (10.14-360.62)	22.16 (10-60)	15.25 (11.3-18.8)	14.57 (11.1-19.8)	177.26 (89.4-292.3)	5.13 (4.49-5.68)	50.16 (1.5-190.2)	0.23 (0.02-0.64)

Six residual patch types were considered in the analyses based on their origin (fire or cut), their age (exposure time (EXT) to the matrix) and the retention types: (1) young clump retention patches, (2) young island retention patches, (3) old island retention patches, (4) old separator retention patches, (5) old fire residual patches, and (6) young fire residual patches (Table 2.1).

2.4.3 Data collection

Field data were collected in post-fire residual patches during the summers of 2012 and 2013 and in post-harvest retention patches during the summer of 2014. At the core of each retention or residual patch, one representative circular plot with a radius of 11.28 m (400 m^2) was established. In the young clump retentions with an area less than 400 m^2, a circular 200 m^2 plot was used to avoid edge effects. In each circular plot, diameter at breast height (DBH) of all commercial stems of all tree species (DBH $\geqslant$ 9 cm) was measured, their species were noted, and their average height was measured with a clinometer. The DBH and the decomposition class of all snags was also measured (Figure 2.2). The volume of living trees and snags (per hectare) was calculated following Fortin et al. (2007). The line intersect method was used to sample fallen deadwood (logs) $\geqslant$5 cm in diameter by decay classes (Figure 2.2) and their volume per hectare was calculated as in Van Wagner (1968).

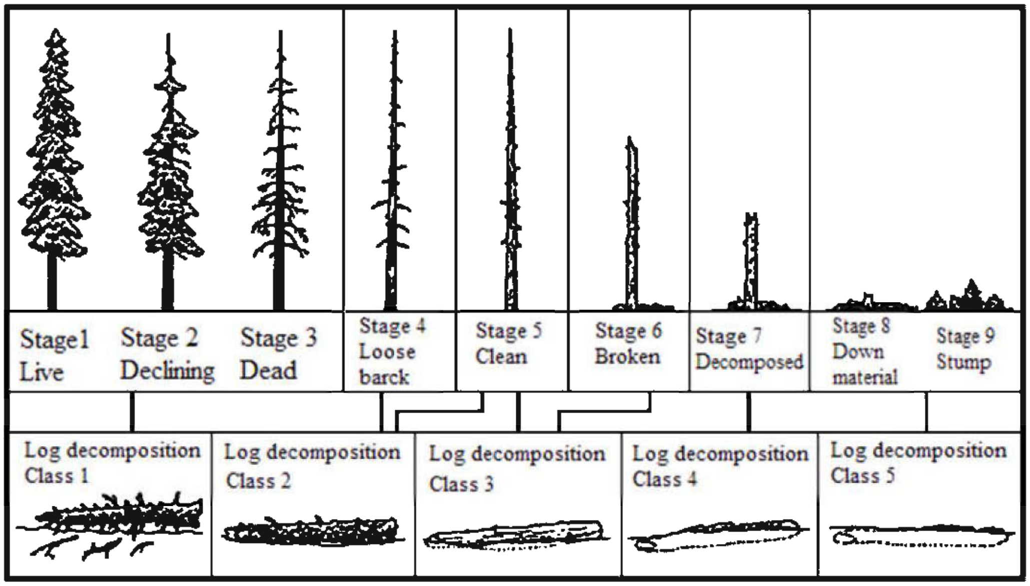

Figure 2.2 Visual representation of Thomas et al.'s (1979) decay classification system for snags and logs.

Other factors that could affect the volume of recent deadwood in residual patches were measured in each plot (Table 2.1). The thickness of the organic layer of each patch representing the tree anchoring substrate was determined in a soil pit dug in the center of each sample plot. Time since last fire, i.e., the age of the original forest from which the patch was formed, was estimated by coring and counting growth rings in ten individuals of the tallest cohort (Wagner, 1978), and it was determined as the maximum of the ages of the ten trees. The average shape index was calculated from the perimeter and the area of each residual patch according to McGarigal and Marks (1995). The perimeter and the area of each residual patch were measured by (1) tracing the exterior of the patches on foot with a handheld GPS, then (2) generating polygons from the lines generated by the GPS and (3) calculating the perimeter and area of the polygons using ARCGIs mapping software.

2.5 Data analyses

2.5.2 Estimation of deadwood abundance in residual patches

Deadwood abundance in post-fire residual patches, and post-harvest retention patches and in the continuous forest stands was characterized by recent deadwood volume (m^3ha^{-1}), the proportion of recent deadwood (ratio of the recent deadwood volume on the initial stand volume) and old deadwood volume.

Angers et al. (2012) found that the first stages of black spruce decomposition persist typically between 5 and 15 years, i.e., the persistence of recent deadwood of black spruce can range from 5 to 15 years. In this study, recent deadwood volume of post-fire patches, post-harvest retention patches and continuous forest stands was estimated as the sum of recent standing deadwood volume (classes 3 and 4; Figure 2.2), and the recent fallen deadwood volume (classes 1 and 2; Figure 2.2) based on Thomas et al.'s (1979) decay classification system for snags and logs. Class 1 corresponds to fallen dead trees with bark still intact and having all the branches without moss or lichen, and Class 2 fallen trees with intact bark and having only a few branches (Thomas et al., 1979). Assuming an average mortality rate of 1 –2% per year in the black spruce forest (Lussier et al., 2002; Bouchard et al., 2005; Aakala et al., 2006) and a potential residence time of 5–15 years for recent deadwood, we expect that a proportion of recent deadwood exceeding 5–30% of canopy volume could be indicative of loss of durability. We retain the maximum limit of 30% as a threshold over which sustainability in deadwood production is compromised or unlikely. Under this level of 30%, patch durability is not completely guaranteed but is less at risk.

The initial stand volume (ISV) at the time of the formation of each residual patch is estimated as the sum of current living volume and recent deadwood volume. The proportion of recent deadwood is estimated as the ratio of the recent deadwood volume on the initial stand volume. The old deadwood volume is the sum of standing deadwood volumes (snags) in classes 5, 6 and 7 (Figure 2.2) (Thomas et al., 1979) and fallen deadwood (logs) in the last three classes of decaying woody debris on the ground (Figure 2.2).

2.5.2 Comparison of post-fire residual patches versus post-harvest retention patches

Differences in recent and old deadwood volume among patches of different ages and origins (i.e., the six types of residual patches) and continuous forest stands (control) were tested using single factor linear mixed model (Pinheiro and Bates, 2000), using the software package nlme R (Pinheiro et al., 2007; RDevelopment-Core-Team, 2011). The differences in proportion of recent deadwood (ratio of the recent deadwood volume on the initial volume inherited from the original forest) between the six types of residual patches and continuous forest were tested in the same way but using logistic regression. In both cases, the location of a residual patch in a particular cutblock or fire event is considered as a random effect. The assumptions of homogeneity of variances and normality of residues were verified graphically in R.

2.5.3 Relationship between recent deadwood and initial stand volume

To take into account the effect of the initial stand volume on the recent deadwood volume, the recent deadwood volume in the six types of residual patches (classified according to their origin and age) and continuous forest was analyzed using a mixed linear model (Pinheiro and Bates, 2000), using the software package nlme R (Pinheiro et al., 2007; RDevelopment-Core-Team, 2011). The initial stand volume (cofactor) and the interaction between initial volume and residual patch type were included in the model, and the location was considered as a random effect. The assumptions of homogeneity of variances and normality of residues were verified graphically. As these assumptions were not respected in the variable recent deadwood, it was transformed with the logarithmic transformation.

2.5.4 Factors influencing the abundance of recent deadwood in residual patches

In order to explain variations in recent deadwood volume observed between the residual patches (origin and age) using explanatory factors documented in the literature, eight variables (k = 8) were considered (Table 2.1). Model choice was performed using an approach based on Akaike's information criterion, corrected for small samples (Burnham and Anderson, 2002; Mazerolle, 2006). We started by checking the potential effect of each explanatory variable individually using mixed linear models (Table 2.1). Based on univariate models with the smallest AIC values, we subsequently built models with two variables. The best two variable models were then selected and nested in models with three variables. We repeated this procedure several times until the variables or the interactions did not improve the models, based on Akaike's information criterion (AIC) (Burnham and Anderson, 2004). It should be noted that the explanatory variables were considered independent and were only used in models when the Pearson correlation coefficient was less than 0.5. This procedure permitted us to screen twelve applicant models to identify potential factors that could affect the volumes of recent deadwood in residual patches after fire and harvest (Table 2.2).

In the models considered, location was treated as a random effect. We verified the assumptions of normality of the residuals and homogeneity of the variances using the most complex model. We log-transformed the variable recent deadwood to normalize residuals and homogenize variances. Multiple regression models were used to estimate the statistical parameters using the maximum likelihood method (Aitchison and Silvey, 1957) with R (RDevelopment-Core-Team, 2011).

Table 2.2 Model selection results of the factors influencing recent deadwood volume in different residual patch types (YCc: reference category, YCi, YF, OCi, OCs, OF) and the continuous forest C, based on Akaike's information criterion (AIC). ST, residual patch type; TSF, time since the last fire (year); MSI, mean shape index; ARP, area of residual patch (ha); TOL, thickness of the organic layer (cm); MHT, mean height of living trees (m); DBH, mean diameter at breast height (cm); ISV, initial stand volume (m^3ha^{-1}). Elements in bold indicate the best models (ΔAICc<1). K: number of parameters, AIC_c: Akaike's information criterion corrected for small sample sizes, ΔAIC_c: AIC_c relative to the most parsimonious model, w_i: AIC_c model weight.

	Models tested	*Log-likelihood*	*K*	*AICc*	*ΔAICc*	*W_i*
1	MHT	-117.25	4	242.93	6.74	0.01
2	ISV	-118.94	4	246.30	10.11	0.00
3	ISV+TSF	-114.84	5	240.32	4.13	0.03
4	ISV+ST	-111.62	10	245.74	9.55	0.00
5	**ISV+TSF+ST**	**-105.58**	**11**	**236.19**	**0.00**	**0.25**
6	**ISV+TSF+ST+ARP**	**-104.49**	**12**	**236.62**	**0.43**	**0.20**
7	**MHT+TSF+ST+ISV**	**-104.62**	**12**	**236.87**	**0.68**	**0.18**
8	**MHT+TSF+ST+ISV+MSI**	**-103.38**	**13**	**237.05**	**0.86**	**0.16**
9	MHT+TSF+ST+ISV+DBH	-104.18	13	238.64	2.45	0.07
10	MHT+TSF+ST+ISV+DBH+MSI	-102.95	14	238.89	2.70	0.07
11	ISV+TSF+ST+MHT+MSI+ISV:ST	-97.02	19	241.66	5.47	0.02
12	ISV+TSF+ST+MHT+MSI+DBH+ARP+TOL+ISV:ST	-96.41	22	250.14	13.95	0.00

Model selection and multimodel inference were implemented in R using the AICcmodavg package (Mazerolle, 2011). Akaike weights were computed to evaluate the support of each model. When the top-ranked model had an Akaike weight < 1, we used multimodel inference to compute the model-averaged estimates of the explanatory variables and 95 % confidence intervals (Burnham and Anderson, 2002). Confidence intervals that excluded 0 indicated that the response variable varied with the explanatory variable of interest (Burnham and Anderson, 2002; Mazerolle, 2006).

Finally, the results of the preceding sections are integrated to generate a predictive model by projecting recent deadwood proportion on current living volume in order to make recommendations in terms of size, shape and type of forest stand that should be targeted for post-harvest retention in order to increase patch lifespan.

2.6 Results

2.6.1 Abundance of deadwood after harvest and after fire

Recent deadwood volume was ordered by origin in the six types of residual patch and continuous forest (Figure 2.3a) with greater volumes in harvested patches and continuous forest compared to fire patches. However, only the volumes in old fire patches and continuous forest were significantly different. Continuous forest was also characterized by less variability (Figure 2.3a).

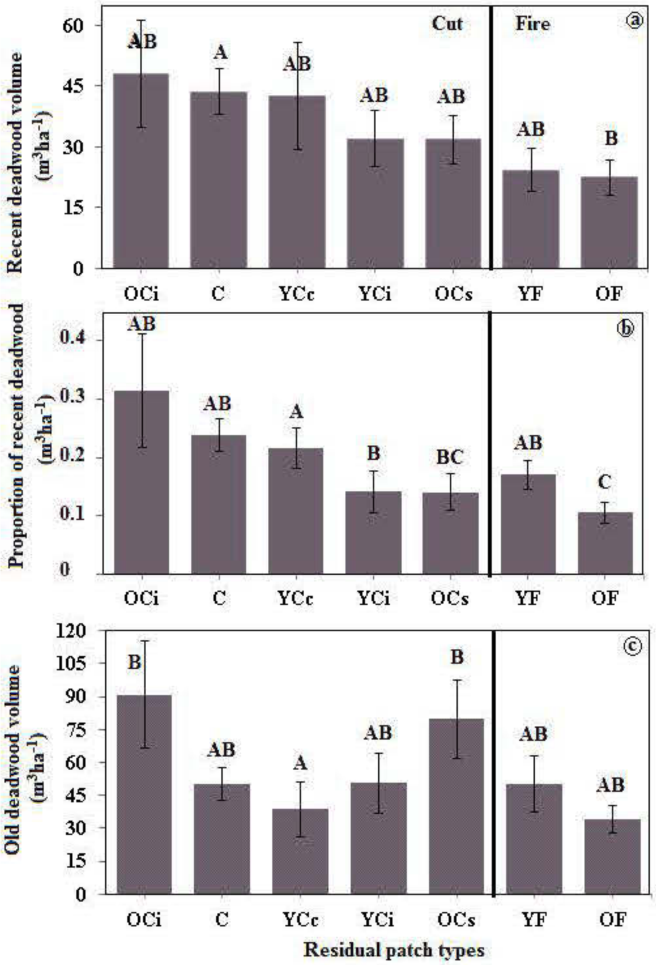

Figure 2.3 Bar charts showing recent deadwood volume m^{3}ha^{-1} (a), and its proportion (ratio of the recent deadwood volume on initial volume) in (b) and old deadwood volume (m^{3}ha^{-1}) (c) in six residual patches types and in continuous forest stands. Bar error represents the standard error. Young cut clump (YCc); young cut island (YCi) and young fire (YF): EXT: 0-19 years; old cut island (OCi), old cut separator (OCs), and old fire (OF): EXT $\geq$ 20 years and continuous forest (C): control. The proportion of recent deadwood volume is the ratio of the recent deadwood volume on the initial stand volume before disturbance. EXT, exposure time since the last disturbance. Letters illustrate the significantly different values among residual patches, following ANOVA and Tukey's HSD post hoc tests ($p<0.05$).

The proportion of recent deadwood (ratio of the recent deadwood volume on the initial volume) generally followed the same pattern, with a higher proportion of the recent deadwood in harvested patches, particularly old islands and young clumps (OCi; 31.4 ± 10%, YCc; 21.6 ± 3%), and continuous forest (C, 23.8 ± 3%), and a significantly lower average proportion in old fire patches (OF; 10.5 ± 2%; Figure 2.3b). Young post-harvest clump patches (YCc) were also significantly different from young post-harvest island patches and old post-harvest separators. With the exception of OCi and YCi, residual patches were organized by their ages (exposure time) in terms of the proportion of recent deadwood (Figure 2.3b). Young patches (YCc and YF) had a higher proportion of the recent deadwood with averages ranging from 14% to 22% while old patches (OCs and OF) had averages from 10% to 14.1% (Figure 2.3b). The volume of old deadwood was greater in old harvested island patches and old separators compared to young clump patches, and all other retention types and continuous forest stand had variable and comparable volumes of old deadwood (Figure 2.3c).

2.6.2 Effect of initial stand volume on recent deadwoodafter harvest and after fire

The recent deadwood was highly positively influenced by the initial stand volume at the time of patch formation (*t-value* (113) = 3.19 ± 0.24; *p*-value = 0.002). Furthermore, the results of the ANCOVA of the recent deadwood volume based on both initial stand volume and patch type (origin and age class) illustrated that, regardless of origin (fire or cut) and time of exposure to a disturbed matrix (age of the patch), recent deadwood volume remained low when the initial volume of the original forest was less than 60 m^3ha^{-1} (Figure 2.4). Thereafter, the recent deadwood volume increased linearly with increasing initial volume. Finally, except in case of old island retention patches (OCi), we generally observed a positive effect of initial volume on recent deadwood volume (Figure 2.4). Once the effect of initial stand volume is taken into account, more recent deadwood was observed in the younger patches (YF, YCi, and YCc) than in the old patches (OCs and OF). Continuous forest (C) was found between the YCc and OCi, and was characterized by a lot of variability. Moreover, except for the youngest retentions (YCi), the relationship between recent deadwood volume and initial volume was significant in young patches with a determination coefficient R^2 of 0.85 (*p-value* = 0.001) in YCc and of 0.47 (*p-value* = 0.01) in YF but not in old patches (OF, OCi, OCs), which had with determination coefficient of R^2 below 0.06.

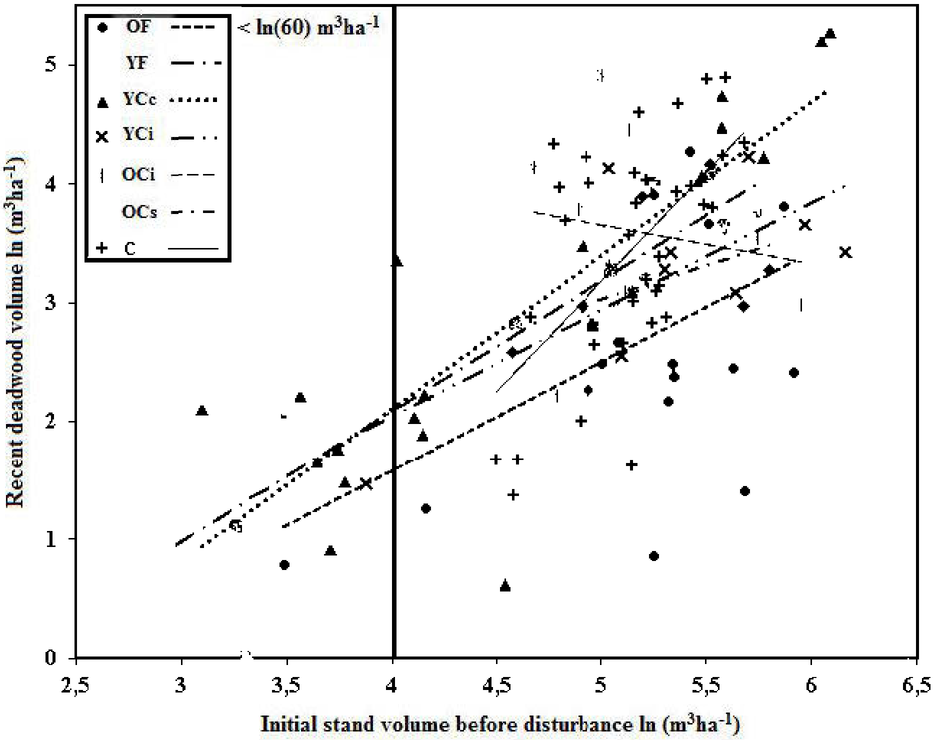

Figure 2.4 Recent deadwood volume ln (m^3ha^{-1}) in relation to initial stand volume before disturbance ln (m^3ha^{-1}) on the six residual patches types and the continuous forest stands and their interaction: The seven residual patches types considered are: young cut clump (YCc); young cut island (YCi) and young fire (YF): EXT: 0–19 years; old cut island (OCi), old cut separator (OCs), and old fire (OF): EXTP 20 years and continuous forest (C): control. EXT, exposure time since last disturbance.

2.6.3 Factors influencing the abundance of recent deadwood in residual patches

Model selection to determine which factors explained variations in recent deadwood volume indicated that four of the twelve models (5, 6, 7 and 8) had delta AIC_c less than 2 and comparable AIC_c weights. Model 5, which included the additive effects of initial stand volume, time since the last fire and type of residual patch (ST), had the highest AICc weight (Table 2.2; $AIC_c = 236.19$, $w_{ic} = 0.25$), followed by model 6, which included the additional effect of area of residual patch ($AIC_c = 236.62$; $w_{ic} = 0.20$), then by model 7, which included the additive effect of mean height of living trees ($AIC_c = 236.87$; $w_{ic} = 0.18$), and finally by model 8, which included the additive effects of mean height of living trees and mean shape index of the patch ($AIC_c = 237.05$; $w_{ic} = 0.16$). As no single candidate model dominated ($w_{ic} \geq 0.9$; Table 2.2), we used multi-model inference to compute the model-averaged estimates of the explanatory variables and their 95 % confidence intervals (Table 2.3). Multi-model inferences indicated that type of residual patch (origin and age) influenced the recent abundance of deadwood after disturbance (fire or cut) with additional positive effects of initial stand volume and age of the original forest (Table 2.3). Generally, greater recent deadwood volume was associated with strong initial volumes ($\beta = 0.79$, $p < 0.05$, Table 2.3) and with the older stands ($\beta = 0.05$, $p < 0.05$; Table 2.3).

Table 2.3 Model-averaged estimates (β) of explanatory variables influencing recent deadwood volume in different residual patch types and continuous forest stands with their respective 95% unconditional confidence intervals. Elements in bold indicate that the effect of the explanatory variable on the response variable excludes 0. For acronyms see Table 2.1.

Parameter	*Estimate(β)*	*lower CI at 95%*	*upper CI at 95%*
Initial stand volume (ISV, m^3ha^{-1}) (+)	**0.79**	**0.24**	**1.34**
Mean diameter at breast height (DBH, cm) (+)	0.04	-0.04	0.11
Mean Shape Index (MSI)	-0.91	-2.03	0.2
Area of residual patch (ARP, ha)	-0.18	-0.42	0.16
Mean height of living trees (MHT, m)	0.07	-0.02	0.16
Time since the last fire (TSF) (+)	**0.05**	**0.02**	**0.09**
Residual patch type (ST)			
OF – Ycc	**-1.38**	**-1.99**	**-0.76**
OCi – Ycc	-0.43	-1.22	0.35
OCs – Ycc	**-0.86**	**-1.68**	**-0.04**
YF – YCc	**-0.82**	**-1.53**	**-0.11**
YCi – Ycc	**-0.82**	**-1.56**	**-0.08**
C – Ycc	-0.39	-1.29	0.5
OCi – OF	**0.94**	**0.33**	**1.56**
OCs – OF	0.51	-0.11	1.14
YCi – OF	0.56	-0.08	1.19
YF – OF	**0.55**	**0.03**	**1.08**
C – OF	**0.98**	**0.27**	**1.7**
OCi – YF	0.39	-0.28	1.06
OCs – YF	-0.04	-0.73	0.65
YCi – YF	0	-0.71	0.71
C – YF	0.43	-0.33	1.19
OCs – Oci	-0.43	-1.22	0.36
YCi – Oci	-0.39	-1.1	0.32
C – Oci	0.04	-0.57	0.66
YCi – Ocs	0.04	-0.8	0.88
C – Ocs	0.04	-0.65	0.73
C – Yci	0.43	-0.29	1.15

2.6.4 Recent deadwood recruitment versus temporal dynamics of residual patches

The relationship between the proportion of recent deadwood volume and current living volume in each patch was used to show two important properties of residual patches, their deadwood productivity versus their durability after fire or harvest (Figure 2.3). The recent deadwood proportion in the canopy, i.e., the ratio of recent deadwood volume over initial stand volume was considered to reflect the durability of the patch (Figure 2.5, Y axis) and the current living volume of wood was considered as the recent deadwood recruitment (Figure 2.5, X axis). This graphic can be divided into four quadrants, formed by the 30% maximum sustainable limit of recent deadwood in canopy, and a current living volume threshold of 60 m^3ha^{-1} suggested by the results of section 2, which corresponds to the threshold for open black spruce stands (and for commercial volume), which are unlikely to generate significant deadwood volume. In the lower left quadrant, residual patches were stable because of their low living volume but they produced relatively little deadwood. The residual patches in the lower right quadrant appear stable as the recent deadwood proportion compared to the living volume is low, however these patches also produce significant quantities of recent deadwood. Residual patches in the upper left quadrant have a high proportion of recent deadwood compared to their living volume and they consequently are probably unsustainable. These residual patches are likely to open up and join the low living volumes patches. Finally, the residual patches occupying the upper right quadrant were likely in transition phase towards the upper left quadrant as evidenced by the large amount of deadwood on the ground (Figure 2.3c).

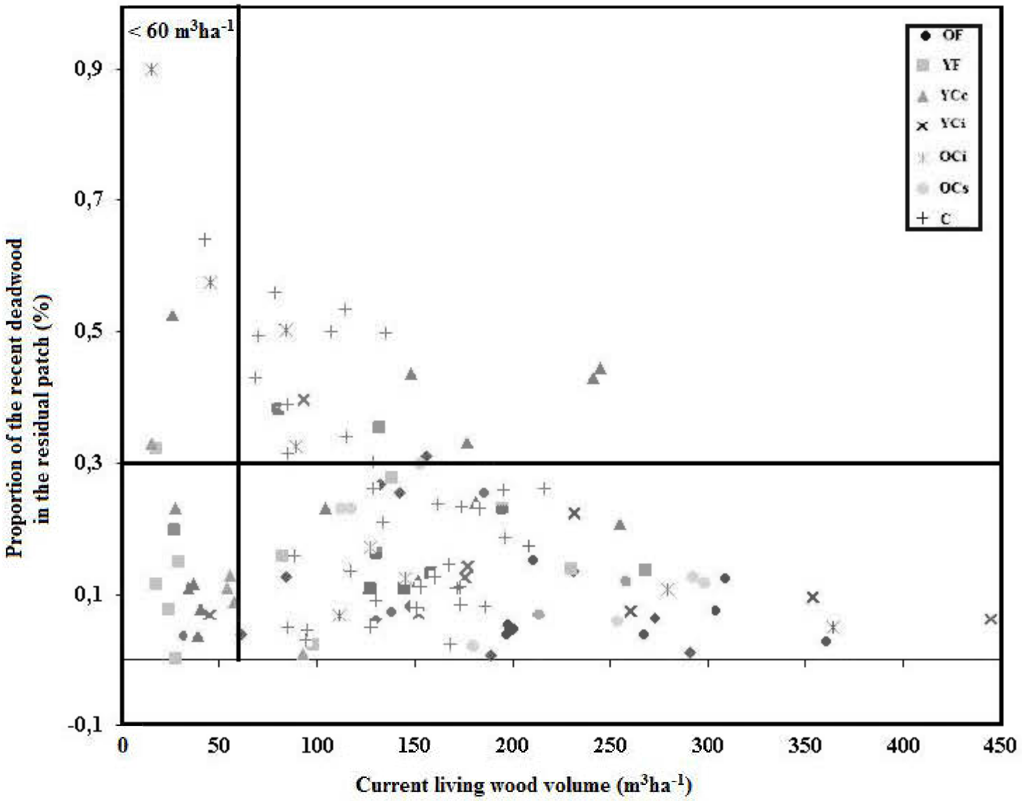

Figure 2.5 Relation between the proportion of the recent deadwood volume m^3ha^{-1} and the current living wood volume (m^3ha^{-1}) in six residual patch types and continuous forest stands. The proportion of the recent deadwood volume is the ratio of the recent deadwood volume on the initial stand volume before disturbance. Young cut clump (YCc); young cut island (YCi), and young fire (YF): EXT: 0-19 years; old cut island (OCi), old cut separator (OCs), and old fire (OF): EXT ≥ 20 years and continuous forest (C): control.

This model illustrates that most of residual patches (post-fire and post-harvest) appear sustainable with a proportion of recent deadwood lower than the maximum 30 % of the current living volume (Figure 2.5). Moreover, some continuous forest stands (7 of 37) showed signs of collapse with recent deadwood proportions exceeding the 30 % threshold. However, 30 of 37 continuous forests were characterized by proportion of recent deadwood lower than 30 % of the living volume. Some old island retention patches OCi (3 of 9) showed general signs of collapse with recent deadwood proportions beyond 30 % (Figure 2.5). Six of the nine old islands, however, had survived and had a similar dynamic to that of the old post-fire residual patches. Furthermore, half of young clump retention patches YCc (10 of 20) produced relatively little deadwood and characterized by low living volume, and the rest of YCc showed generally signs of collapse with recent deadwood proportion exceeding 30 %.

2.7 Discussion

Our results support our first hypothesis that in black spruce boreal forests, post-fire residual patches have less recent deadwood than post-harvest retentions. However, this study emphasizes that regardless of the origin of the residual patch (fire or cut), the abundance of the recent deadwood in residual patches was strongly controled by the initial characteristics of the patch, i.e., that of the forest they originated from. First, we discuss the factors of the original forest that explained the variations in post-fire and post-harvest deadwood abundance observed in the studied residual patches. Secondly, we attempt to discuss the possibility of using the relative abundance of deadwood to evaluate the durability of post- disturbance patches in the black spruce boreal forest in western of Quebec.

2.7.3 Factors responsible of variations of abundance of post-disturbance deadwood

This study, as with others in the boreal forest, indicates that the initial conditions of forest stands influence the evolution of residual patches (Cyr et al., 2009; Smith et al., 2009; Ouarmim et al., 2014; Bolton et al., 2015). We found that regardless of their origin and age, residual patches with a high initial stand volume generated more deadwood over time. This result supports our second hypothesis that in the black spruce boreal forests of north-western Quebec, forests with greater living volume result in residual patches with a greater volume of deadwood than stands that were initially open (Ruel, 1995; Harper et al., 2005). Moreover, when the original volume is less than 60 m^3ha^{-1} (open stands) the abundance of recent deadwood in the residual patches remains low regardless of exposure time. Nevertheless, this result is not surprising knowing that black spruce grown in open areas are generally pre-adapted to an open environment and are thus more resistant to post-disturbance mortality (Gardiner et al., 1997; Rich et al., 2007). However, a closed stand generates more recent deadwood after its unexpected exposure to the new open environment (Ruel, 1995). Having never previously been exposed to the wind, dense stands are more vulnerable to windthrow, especially in a forestry context where tree retention patches are generally characterized by abrupt edges surrounded by a completely open environment (Ruel, 1995; Lecomte et al., 2006). In addition, this can be due to the structural type of residual patches or continuous forest. Small trees in irregular stands that grow in more open conditions can reduce the wind weight applied on dominant trees by dissipating part of the wind energy (Gardiner et al., 2005).

Our analyzes also confirm the hypothesis anticipating the positive effect of age of the original forest (TSF) on the abundance of recent deadwood (Bouchard et al., 2009; Cyr et al., 2009). This is in contrast with other studies that revealed the opposite relationship, i.e., a greater susceptibility of younger regular stands to windthrow compared with older irregular forest stands, which are generally characterized by a more open structure (Ruel, 1995; Rich et al., 2007; Lavoie et al., 2012). Deadwood recruitment dynamics are generally believed to follow the form of a U (Harmon et al., 1986) with greater recruitment of deadwood immediately after fire, which then decreases over time until it increases again in old forests. In our case, the low and positive effect of TSF on the abundance of deadwood in the studied residual patches may simply be due to the gradual opening of the original forest over time due to secondary disturbances (Kneeshaw, 2001; McCarthy, 2001; Kneeshaw et al., 2011).

Mean diameter at breast height and mean height of living trees were not significant factors explaining the abundance of recent deadwood in the residual patches even though these two variables are often identified as important factors for explaining mortality at the tree scale (Jönsson et al., 2007; Rich et al., 2007). This inconsistency in our results with previous studies is probably due to the low range of variation in the mean diameter and height of living trees measured in this study (Table 2.1).

At the residual patch scale, although models that integrate the variables residual patch area and mean shape index (Table 2.2) were selected by the model comparison procedure, these two factors did not have effects when the confidence intervals were examined (Table 2.3). The absence of effect of area and shape may result from an interaction with the exposure time. For instance, linear separators that accumulate less recent deadwood are old (EXP > 20 years) and clump retentions that accumulate high proportion of deadwood are young. Moreover, among the smaller post-harvest retention patches included, those in the clump retention patches YCc (EXT between 3 and 7 years) were older than the island retention patches YCi (EXT $\leqslant$ 2 years). Therefore, the young island patches could not accumulate as much deadwood as the clump retention patches because they have had almost no exposure time since the last disturbance.

2.7.2 Recruitment dynamics of deadwood and patch temporal dynamics

This study shows that post-fire residual patches appear in general more durable than post-harvest retention patches after disturbance. This could be related to the type of buffer zone surrounding the residual patches left after the passage of fire. Post-fire residual patches are usually surrounded by a buffer zone in which the fire severity is slowed, because of the site characteristics including fuel quality, topography and soil moisture (Hély et al., 2000; Cyr et al., 2007). Post-fire patches can be preserved for millennia, burning only during particularly severe fires (Ouarmim et al., 2015). In contrast, as harvest is systematic it often creates sharp edges between open and closed areas, potentially explaining the higher abundance of deadwood in post-harvest retentions compared to post-fire patches. In addition, as the post-fire residual patches and post-harvest retention patches were sampled in consecutive years, a windthrow event occurring during the sampling period could have influenced the results. So, the retention patches sampled more recently would have been affected and not the residual post-fire patches that were sampled one or two years before.

As in this study, high residual tree mortality in the first years after disturbance has been documented elsewhere in similar stand types in both managed (Hautala and Vanha-Majamaa, 2006; Lavoie et al., 2012; Urgenson et al., 2013) and natural contexts (Heikkala et al., 2014). Initial high mortality may be due to both the active recruitment of dead stems in the first five years after disturbance (Mascarúa López et al., 2006), and the fact that the remaining trees in the older patches were probably more resistant to wind (Busby et al., 2006). Moreover, given that the recent deadwood compartment has a lifespan of five to fifteen years (Angers et al., 2012), deadwood that fell immediately after the disturbance is probably no longer in the “recent” decomposition stage.

Nevertheless, in a management context, initial high mortality may be also due to the retention type, i.e., small clump, big island, and large linear separator. Old island retention patches OCi seem to continue to accumulate mortality and deadwood over time, particularly compared to old separator patches OCs that accumulate less recent deadwood. This higher recent deadwood accumulation of OCi can be due to a severe wind event occurring during the sampling period in some island patches. However, the lower proportion of recent deadwood observed in older linear retentions OCs, and the fact that they tend to have a high volume of old deadwood can be explained by both the active recruitment of deadwood during the first five years following their creation (Scott and Mitchell, 2005; Hautala and Vanha-Majamaa, 2006; Lavoie et al., 2012; Urgenson et al., 2013), and their spatial orientation (DeWalle, 1983; Ruel, 1995). The east–west orientation of the old separator patches in the cutblocks studied likely ensured that the dominant western winds did not strike the edge.

2.8 Conclusions and implications for forestry and conservation biology

This study displays that most post-fire residual patches produce deadwood in significant quantity and without jeopardizing their existence until the surrounding disturbed forest regenerates. In a management context, the deadwood dynamics of post-harvest remnant patches is a key element that could determine the success or failure of forestry retentions (Thorpe et al., 2008). Our results show that in managed black spruce forest, large island patches and large linear separators oriented to escape windthrow usually have a deadwood recruitment dynamics similar to those of post-fire residual patches, and when their initial stand volume is more important than the merchant commercial volume (> 60 m^3ha^{-1}) they engender a significant but sustainable deadwood supply. This suggests that the selection of large retention patches in the shape of an island or a separator, with high (between 60 and 300 m^3ha^{-1}) volume should help increase the post-harvest lifespan of retention patches in black spruce forest, and simultaneously ensure quality habitat (deadwood, large trees) for several forest species while the adjacent harvested forest regenerates. The implementation of this recommendation by forest managers will allow a more sustainable management in the boreal black spruce forest. The value of this study is based partly on the fact that we evaluated and compared abundance of deadwood in post-harvest retentions with that in post-fire patches and continuous forests, and also on the presence of replicates. However, it will be important to also determine if post-harvest retention patches have structural characteristics similar to that of post-fire residual patches both in their core and edge in order to support the present results.

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CHAPITRE III

CAN RETENTION HARVEST MAINTAIN NATURAL STRUCTURAL COMPLEXITY? A COMPARISON OF POST-HARVEST AND POST-FIRE RESIDUAL PATCHES IN THE BOREAL FOREST

Louiza Moussaoui, Nicole J. Fenton, Alain Leduc, Yves Bergeron

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3.1 Abstract

Variable retention harvest promotes biodiversity conservation in managed boreal forests by ensuring forest continuity and structural complexity. However, do post-harvest and post-fire patches maintain the same structural complexity? This study compares post-harvest and post-fire residual patches and proposes retention modalities that can maintain the same structural complexity as in natural forests, here considering both continuous forest stands and post-fire residual patches. In boreal black spruce forests, 41 post-fire residual patches, and 45 post-harvest retention patches of varying size and ages (exposure time to disturbed matrix) and 37 continuous forest stands were classified into six diameter structure types. Types 1 (inverted-J) and 2 (trunked-unimodal) characterized stands dominated by small trees. The abundance of small trees decreased and the abundance of large trees increased from Type 1 to Type 6. Type 6 had the most irregular structure with a wide range of diameters. This study indicates that: (1) old post-harvest residual retentions maintained the range of structural complexity found in natural stands; (2) Types 1 and 2 were generally associated with young post-fire patches and post-harvest retention clumps; (3) the structure of residual patches containing only small trees was usually younger (in terms of the age of the original forest from which residual patches were formed) than those with larger trees. To avoid the risk of simplifying the structure, retention patches should be intentionally oriented towards Types 3–6, dominated by intermediate and large trees.

Additional Keywords: Diameter structure; Structural attributes; Ecosystem based management; Disturbance; Black spruce-feathermoss forest; Continuous forest.

3.2 Résumé

En forêt boréale aménagée, la stratégie de rétention variable pourrait favoriser la conservation de la biodiversité par le maintien de la complexité structurale des forêts. Toutefois, est-ce que les îlots de rétention post-coupe maintiennent une compléxité structurelle naturelle? Cette étude compare les îlots résiduels post-feu et de rétention post-coupe et propose des modalités de rétention qui pourraient maintenir la complexité structurelle des forêts naturelles. En forêt boréale caractérisée par la pessière à mousses, 41 îlots résiduels post-feu, 45 îlots de rétention post-coupe de taille et âges (temps d'exposition à la matrice perturbée) variables et 37 peuplements de forêt continue ont été classés en six types de structure diamètrale. Type 1 (J-inversé) et type 2 (unimodale tronquée) caractérisaient les peuplements dominés par de petits arbres, alors que le type 6 avait une structure plus irrégulière avec une large gamme de diamètres. Cette étude indique que: (1) les vieilles rétentions post-coupe ont maintenu la complexité structurelle retrouvée dans les peuplements naturels; (2) les types 1 et 2 étaient généralement associés aux jeunes îlots résiduels post-feu et post-coupe sous la forme de bouquet; (3) la structure des îlots résiduels ne contenant que des petits arbres étaient généralement plus jeunes (en termes de l’âge de la forêt d’origine de l’îlot) que ceux qui ont des grands arbres. Pour éviter le risque de simplifier la structure, les îlots de rétention doivent être intentionnellement orientés vers les types 3 et 6, dominés par des arbres intermédiaires et grands.

Mots clés additionnels : Structure diamétrale, Aménagement écosystémique, Perturbation, Pessière noire, Forêt continue

3.3 Introduction

In boreal forests, landscape mosaics are now as likely to have been shaped by harvest as by fire [1]. At the landscape scale, fire severity is spatially heterogeneous, with partially or entirely intact tree patches in the burned matrix, here called post-fire residual patches. These residual patches are believed to preserve pre-fire continuous forest structure, including old growth structure. By preserving the structural attributes of old-growth forests, post-fire residual patches could represent a refuge habitat for many forest species [2–4], and could also constitute a source of propagules for recolonization of the burned matrix [5,6]. However, in managed landscapes, harvesting, including large-scale clearcuts practiced in the last half century, progressively homogenizes the forest mosaic and simultaneously reduces the proportion of old-growth forests [7,8]. Consequently, the simplification of internal structure of forest stands could cause a loss of habitat for species that require structures associated with irregular old-growth forests [9,10]. It is increasingly recognized that increasing the structural complexity in managed forests by mimicking natural disturbance patterns can promote biodiversity [11]. Therefore, it is necessary to develop forest practices that maintain the structural complexity of natural forest stands [12], such as that observed within unburned continuous forests or post-fire residual patches [13,14].

The internal structure of forest stands, i.e., the vertical and horizontal arrangement of trees, is a key attribute in maintaining forest productivity and biodiversity of old-growth forests [15,16]. Forest stand dynamics are usually evaluated by observing the changes in structure and composition over time [17]. Forest stand dynamics are marked by several stages ranging from establishment, structural maturity, canopy closure and finally by reopening of the stand during the breakup phase [17]. Consequently, the structural changes induced by the closure and reopening of the canopy can affect several species, particularly plants and mosses occupying the forest floor [18,19] or birds and insects associated with internal stand structure [20,21]. In the boreal forest, an unimodal regular diameter structure is often associated with a juvenile stand, while mature stands often have an irregular diameter structure with stem density in all sizes and a reopening of the canopy [22]. Many factors may influence both forest stand dynamics and structure after fire or after harvest, including the type of original disturbance [15], the magnitude of past human impact [23,24], the initial local conditions before disturbance [25–28], time since last fire and soil characteristics [29].

In managed boreal forests, variable retention harvesting is the most frequently suggested technique to retain the structural attributes of original continuous forest stands within a cutblock. Variable retention harvesting leaves living and dead trees and woody debris of the original forest stand in unharvested forest patches, called "post-harvest retention patches" [30,31]. However, it is currently unknown whether the selection of post-harvest residual patches in cutblocks, which is generally based on operational criteria such as the market value of the residual patch, proximity to water bodies, field accessibility and tree age, permits post-harvest residual patches to preserve a variety of structural types similar to those characterizing post-fire residual patches or continuous forest stands [32,33]. In addition, it is also unknown whether the structural characteristics of retention patches are maintained throughout time after harvest, because of their susceptibility to windthrow [34,35]. A comparison of forest structure of post-harvest and post-fire residual patches is required for developing forestry strategies that can maintain biological diversity after harvest.

This study aims to compare the structural complexity of current post-harvest and post-fire residual patches and unburned continuous forest stands (as controls) in black spruce dominated stands located in northwestern Quebec, Canada. More specifically, we wish (1) to develop a classification of post-fire and post-harvest residual patch structural types and continuous forest stands based on their diameter distribution; (2) to describe the internal structural complexity and forest canopy closure of the generated structural types; (3) to identify factors that may explain the differences between structural types; (4) to determine if stands of post-harvest residual patches maintain the variety of structural types observed in post-fire residual patches and continuous forest stands. Finally, in order to evaluate the link between patch structural complexity and their temporal dynamics in black spruce boreal forests, we have characterized the structural types in terms of their deadwood dynamics on a deadwood diagram developed by Moussaoui et al. [28] (Chapitre 2).

3.4 Materials and methods

3.4.1 Study area

The study area is located between 74–80° W and 49–51° N (Figure 3.1) in the eastern Canadian boreal black spruce-feathermoss forest which is characterized by dense stands (canopy cover 40%–80%) and dominated by black spruce (*Picea mariana* Mill., BSP) with jack pine (*Pinus banksiana* Lamb), balsam fir (*Abies balsamea* [L.] Mill), birch (*Betula papyrifera* Marsh) and trembling aspen (*Populus tremuloides* Michx.). The topography of this area forms an undulating plain. The mineral soil type is composed primarily of glaciolacustrine clay in the west, and clay till in the east [36]. The mean annual temperature varies between −2.5 and 0.0 °C, and the mean annual precipitation varies between 700 and 900 mm and the climate is subpolar, continental sub-humid [37,38].

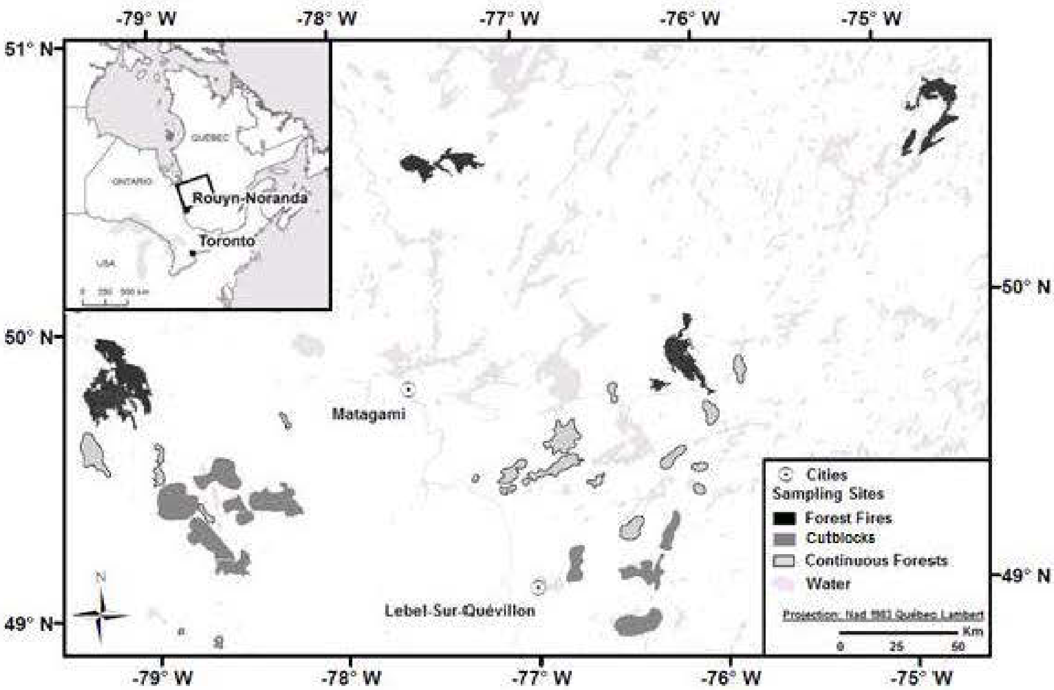

Figure 3.1 Location of 125 study sites in the black spruce boreal forest. 41 post-fire residual patches located in forest fires (black); 47 post-harvest residual patches located in cutblocks (dark gray) and 37 continuous forest stands are represented in pale gray surrounded in black.

Fire is the main natural disturbance that shapes the forest landscape in the study area [39]. The fire cycle was historically relatively short, in the order of 100–200 years [40] and currently it is lengthening and is estimated at over 400 years. Accordingly, the effects of forest harvest have become the main source of disturbance to the landscape [8,41]. Since the late 1980s, the harvesting method commonly used has been harvest with protection of regeneration and soils (CPRS in French), which consists of harvesting all merchantable stems (DBH > 9 cm) in cutblocks with a maximum size of 250 hectares. Retention patches were placed linearly between these cutblocks (separators) with a width of 60–100 m and in the form of large patches (3–10 ha) within the cutblocks for moose [42]. In the last decade, small forest clumps and large intact forest patches are two new retention types that have been used in order to maintain structural attributes similar to those created by fires [43,44].

3.4.2 Location of the study stands

Three stand origins were studied: Post-fire residual patches, post-harvest retention patches and undisturbed continuous forests. Six fires, including three young fires (0–19 years old) and three old fires (20–40 years), were selected using the fire maps of the Ministère des Ressources Naturelles et de la Faune du Québec (MRNF). Then, five to eight residual patches were selected per fire for a total of 41 post-fire residual patches (Figure 3.1). The selection of cutblocks was undertaken using eco-forestry maps and recent harvest GIS layers of three forestry companies and harvest licenses (TEMBEC UAF 085-51, and EACOM UAF 086-64 and PF Résolu PRAN 087-62). Thirteen cutblocks were studied: Seven young cutblocks (0–19 years) with retention in clumps and large islands, and six old cutblocks (20–40 years) with linear separators and large islands. Three to five retention patches were selected per cutblock for a total of 47 post-harvest retention patches (Figure 3.1). The residual patches were: (1) randomly selected from accessible patches (<1 km from a road) using ArcGis 10.2 mapping software (ESRI, Redlands, CA, USA, 2013) based on the fire and eco-forestry maps, and recent harvest GIS layers and harvest licenses; then (2) validated in the field according to the criteria of representativeness of size and position, accessibility, presence of late successional species (*Picea mariana* Mill., BSP) and absence of salvage logging in the case of fires. A total of 37 continuous forest stands (controls, C), aged between 74 and 1320 years were selected from the same landscape [45].

Six residual patch types of varying size [28] were considered in some analyses based on their origin (fire or cut), their age (exposure time (EXT) to disturbed matrix) and the retention type: (1) young clump retention patches YCc (3–7 years old); (2) young island retention patches YCi (1–2 years old); (3) old island retention patches OCi (21–24 years old); (4) old separator retention patches OCs (21–24 years old); (5) old fire residual patches OF (27–37 years old); and (6) young fire residual patches YF (15–17 years old) [28] (p. 20).

3.4.3 Data collection

Stand structure and local factors characterizing the study sites were measured in post-fire residual patches during the summers of 2012 and 2013 and in post-harvest retention patches during the summer of 2014. At the core of each retention or residual patch, one representative circular plot with a radius of 11.28 m (400 m^2) was established. Because edge influence is believed to extend approximately 5 m into the forest from the disturbed matrix in boreal forest as Harper et al. [46], in the young clump retentions with an area less than 400 m^2, a circular 200 m^2 plot was used to avoid edge effects.

In each circular plot, diameter at breast height (DBH) of all commercial stems of all trees (DBH $\geq$ 9 cm) and saplings (DBH $<$ 9 cm) was measured, their species was noted, and their average height was measured with a clinometer. The DBH and the decomposition class of all snags were also measured. The volume of living trees and snags (per hectare) was calculated following Fortin et al. [47]. The line intersect method was used to sample fallen deadwood (logs) $\geq$5 cm in diameter by decay class, and their volume per hectare was calculated as in Van Wagner [48]. Proportion and volume of recent deadwood and old deadwood in post-fire residual patches, and post-harvest retention patches and in the continuous forest stands were evaluated as in Moussaoui et al. [28] (Chapitre 2). Following Moussaoui et al. [28], recent deadwood volume of post-fire patches, post-harvest retention patches and continuous forest stands was estimated as the sum of recent snag volumes (Classes 3 and 4), and the recent log volumes (Classes 1 and 2). Decomposition stage was based on Thomas et al.'s [49] decay classification system for snags and logs, and their old deadwood volume was the sum of snag volumes in Classes 5, 6 and 7 and log volumes in the last three classes of decaying woody debris on the ground based on Thomas et al. [49].

The average shape index (MSI) was calculated from the perimeter and the area of each residual patch according to McGarigal and Marks [50]. The perimeter and the area of each residual patch were measured by (1) tracing the exterior of the patches on foot with a handheld GPS; then (2) generating polygons from the lines generated by the GPS and (3) calculating the perimeter and area of the polygons using ArcGis® mapping software. The thickness of the organic layer (TOL) of each site representing the tree anchoring substrate, was determined in a soil pit dug in the center of each sample plot. The time since last fire (TSF), i.e., the age of the original forest from which the patch was formed, was estimated using one of two methods. Time since last fire was estimated in most stands by coring and counting growth rings in 10 individuals of the tallest cohort [51]. However, in some natural stands where the TOL was around 1 m and TSF approached the average maximum age of black spruce (i.e., 200 years) [52], radiocarbon dating (^{14}C) by accelerator mass spectrometry (AMS) was used to date the most recent local fire event based on the methodology of Chaieb et al. [45]. AMS was conducted on charcoal samples by the radiochronology laboratory C.E.N. (Centre d'Étude Nordique, Laval, QC, Canada) and the earth System Science Department (Irvine, California, CA, USA).

In the data analyses, we started by classifying the post-fire and post-harvest residual patches and continuous forest stands based on diameter structure. Secondly, we described the internal structural complexity and forest canopy closure of the six structural types found in residual patches and continuous forest stands. Thirdly, environmental factors influencing stand structural types were identified and the structural types found in post-harvest and post-fire and continuous forest were compared. Then, we tested if Types 1 and 2 without large timber were associated with particular residual patch types. Finally, the link between patch structural complexity and the temporal dynamics of their deadwood was evaluated.

3.4.4 Structural classification of stands

A structural classification of 125 residual patches and continuous forest stands (C, OF, YF, OCi, OCs, YCc, YCi) was developed based on DBH class data, following a method developed by Moss [53]. More specifically: (1) determine from the DBH data of each site diametric classes of 2 cm, and to determine the class with the highest DBH; (2) build a matrix that contains the density (number of trees/ha) and the basal area of living trees per DBH class for each site; (3) transform the absolute data into the inverse cumulative data for each DBH class. Trees were cumulated to reduce the number of zeros and make distributions insensitive to the width of classes starting from the largest class (30 cm) to the smallest (10 cm). Then, in order to control for variations in density and basal area, the cumulative data was transformed to a percentage (relative scale). In this way, the structural types were only based on the shape of diameter class distributions.

Subsequently, using the two inverse cumulative matrices of density and basal area of residual post fire and harvest patches and continuous forest stands, structural types were determined using a clustering algorithm k-means [54]. K-means clustering is a heuristic technique used to partition observations into a limited number of groups in order to minimize intra-group distance [54–56]. The optimal number of clusters was evaluated following exploratory tests using the clValid function in R. The clValid function integrates three validation criteria, the connectivity, width and Silhouette Dunn index, which measure the compactness, connection and separation of different numbers of clusters. The classification was validated by visually comparing the diameter distributions of the different structural types.

Finally, the structural classification of stands was plotted in a triangle of structures in R, which is a structural representation method that has been used for over a century in Europe [57] and more than a decade in Quebec [58]. A triangle of structures is a ternary graph with three inputs for the proportion of three size classes of timber determined by the user, small timber (ST), medium timber (MT) and large timber (LT), which can be estimated using density, basal area or volume of trees [58]. In this study, the three timber size classes, ST (9 cm > DBH > 13 cm), MT (13 cm > DBH > 17 cm) and LT (DBH >17 cm), were based on natural breaks in the diameter distribution of black spruce (data not shown). So, based on these three size classes, we illustrated the relative contribution of small, medium and large stems within each structural type.

3.4.5 Description of structural types

3.4.5.1 Internal structure complexity

Our classification method was based on only the shape of the diameter class distribution. Therefore, to determine whether the structural stand types also differed in living tree density, basal area and volume, we used one factor linear mixed models, followed by a Tukey multiple mean comparison, by the means of a mixed linear model [59], using the package nlme in R [60]. The geographic location (cutblock, or fire or continuous forest) was considered as a random effect. The assumptions of homogeneity of variances and normality of residues were verified graphically in R. The analyzed stand characteristics are presented in Table 3.1.

Table 3.1 Mean and standard error of stand characteristics and environmental factors of the structural types. Letters illustrate the significantly different values among structural types following ANOVA and Tukey's HSD post hoc tests ($p < 0.05$). ST (9 cm > DBH > 13 cm), MT (13 cm > DBH > 17 cm) and LT (DBH > 17 cm).

Variable	**T1 (n=14)**	**T2 (n=14)**	**T3 (n=22)**	**T4 (n=29)**	**T5 (n=30)**	**T6 (n=16)**
Living wood						
Mean height of living trees (m)	9.8 ± 0.3 a	12.5 ± 0.5 b	13.7 ± 0.4 bc	14.8 ± 0.3 c	16.1 ± 0.4 e	16.3 ± 0.6 e
Mean tree diameter at breast height (cm)	11.1 ± 0.2 a	12.9 ± 0.4 ab	13.7 ± 0.3 bc	14.7 ± 0.3 ce	15.4 ± 0.3 e	17.7 ± 0.8 d
Mean total tree density (trees/ha)	1153.6 ± 105.2 b	1712.5 ± 182.1 ab	2114.8 ± 174.6 a	1881.9 ± 108.5 a	1449.1 ± 109.6 b	1139.1 ± 85.8 b
Mean tree basal area (m^2h^{-1})	11 ± 1.1 a	20.5 ± 2.3 a	30.6 ± 2.5 b	33.1 ± 1.9 b	31.2 ± 2.4 b	34 ± 2.4 b
Mean total tree volume (m^3h^{-1})	40.82 ± 7 a	98.1 ± 14.7 ac	146.2 ± 13.1 bc	173.8 ± 12.8 bc	173.3 ± 17.2 b	188.4 ± 22.5 b
Mean sapling density (saplings/ha)	4941.7 ± 771.4 a	4177.8 ± 867.75 a	2081.3 ± 486.7 b	1356.3 ± 419.4 b	1718.2 ± 346.5 b	1353.8 ± 352.9 b
Mean sapling basal area (m^2h^{-1})	7.2 ± 1.2 a	5.4 ± 0.6 ac	3.9 ± 0.9 bc	2.1 ± 0.5 b	3.1 ± 0.7 bc	1.7 ± 0.5 b
Mean small timber basal area (m2h-1)	9.5 ± 0.9 ab	11.5 ± 1.2 a	10.6 ± 1 a	7.2 ± 0.4 b	4.4 ± 0.4 c	2.2 ± 0.4 c
Mean medium timber basal area (m2h-1)	1.5 ± 0.3 a	7.6 ± 1 c	12.8 ± 1.2 b	13.6 ± 1.1 b	9.1 ± 1 c	4.8 ± 0.7 ac
Mean large timber basal area (m2h-1)	0.2 ± 0.1 a	1.6 ± 0.3 a	7.3 ± 0.8 b	12.4 ± 0.9 c	17.2 ± 1.3 d	26.8 ± 2.1 e
Deadwood						
Mean diameter of snags (cm)	11.1 ± 0.4 a	12.1 ± 0.4 ab	12.8 ± 0.4 ab	13.6 ± 0.5 bc	15.6 ± 0.5 c	18.5 ± 1.1 d
Mean total volume of snags (m3h-1)	2.2 ± 0.6 a	5.5 ± 1.1 a	11.6 ± 1.7 ab	19.3 ± 2.7 b	31.3 ± 3.5 bc	36.3 ± 5.5 c
Mean total volume of logs (m3h-1)	7.9 ± 1.6 a	19.22 ± 4.2 a	53.1 ± 12.5 ab	75.5 ± 11.8 b	85.6 ± 9.1 bc	123.7 ± 19.5 c
Recent deadwood volume (m3h-1)	4.6 ± 0.7 a	10.5 ± 1.8 a	26.6 ± 6.1 ab	41.5 ± 5.3 bc	47.7 ± 5.9 bc	62.1 ± 13.6 c

Old deadwood volume (m3h-1)	5.4 ± 1.6 a	14.2 ± 2.8 a	38.1 ± 10.8 ab	53.3 ± 10.1 b	69.1 ± 7.1 bc	98.1 ± 12.5 c
Environmental Factors						
Thickness of the organic layer (cm)	43.4 ± 6.4 a	38.6 ± 4.8 a	44.7 ± 9.1 a	35.8 ± 4 a	41.6 ± 4.5 a	49.2 ± 9.1 a
Mean shape index	1.2 ± 0.07 a	1.1 ± 0.02 a	1.2 ± 0.05 a	1.1 ± 0.03 a	1.3 ± 0.05 a	1.2 ± 0.03 a
Area of residual patch (ha)	4.5 ± 2.4 a	10.6 ± 4.9 a	8.4 ± 2.3 a	11.7 ± 2.4 a	7.4 ± 1.3 a	9.3 ± 4.2 a
Time since the last fire (year)	97 ± 7.3 a	115.2 ± 13.6 ab	120 ± 12.1 ab	126.7 ± 12.7 ab	149.2 ± 11.2 b	143.6 ± 11.7 b

3.4.5.1 Forest canopy closure

Because our classification method was performed on the relative abundance of trees to emphasize differences in shape of the diameter class distribution, it does not indicate whether a particular structural type was mainly dominated by a closed canopy. Canopy closure results from a particular combination of living tree size and density. In order to illustrate the relationship between forest canopy closure and structural types, the canopy closure threshold was assessed for each site by using modular-based structural stand density management (SDMMD) developed by Newton [61], for stands of pure black spruce. This is to show graphically, in each forest stand, the relationships between the average volume of living trees (dm^3) and their total density (stems/ha) on a base 10 logarithmic scale. This graphic is then divided into two parts, formed by a theoretical line suggested by Newton [61], which corresponds to the minimum threshold for natural black-spruce forest canopy closure. Forest stands to the right are considered as closed stands, while stands to the left are considered as open stands [61] (p. 181).

3.4.6 Factors influencing stand structure

In order to examine the local environmental factors that may explain the differences among structural types, we considered four factors: Time since last fire, which corresponds to the age of the original forest from which the patch was formed; tree anchoring substrate, estimated by the thickness of the organic layer; and site area and shape. First, we hypothesize that the structure of stands without large stems and with an inverted-J diameter structure would be juvenile stands, and the structure stands with stems in all sizes would be older stands [58–60]. Moreover, as site productivity (soil richness) can influence the rate of maturation of forest stands [62,63], we anticipate that structural types including large trees appear sooner on rich soils than on poor soils. Finally, we anticipate that due to their high susceptibility to windthrow, small stands will have collapsed structures without larger stems. The four factors were examined used one factor linear mixed models [59], followed by a Tukey multiple mean comparison, using the package nlme in R [60]. The assumptions of homogeneity of variance and normality of residues were verified graphically in R. The location of a stand in a particular cutblock, or fire or continuous forest was considered a random effect.

3.4.7 Structural types in post-harvest residual patches versus natural stands

Comparison of structural types encountered in post-harvest retention patch stands to those observed in naturel stands (post-fire residual patches and continuous forests) was realized by comparing the frequency of structural types present per type of residual patch or continuous forest stand (C, OF, YF, OCi, OCs, YCc, YCi) in a 2×2 contingency table. The relationship between the two categorical variables, residual patch type and structural type, was analyzed in R, with the Fisher-exact test (for small theoretical values <5). We tested the null hypothesis that each structure type could be in any residual patch type or continuous forest stand, i.e., the structure was independent of the disturbance (fire, cut). If the p-value was less than the critical value of 0.05, the null hypothesis was rejected, i.e., residual patch types and structural types were associated.

In order to determine whether inverted-J structure and truncated unimodal structures without large trees (structure of Types 1 and 2) were more abundant within certain residual patches, we generated two contrasts, first between Type 1 and other structural types (Type 2 to Type 6) and second between Types 1 and 2 and others (Type 3 to Type 6). We tested in this way if Types 1 and 2 could be associated to particular residual patch types. The null hypothesis for each contrast was that each structure was equally likely to be found in each residual patch type. The association was tested statistically with the Fisher-exact test (p-value = 0.05) in R. Then, to determine whether there were differences between fire and harvest origin patches of Types 1 and 2, we determined the age of the original forest from which the patch was formed (TSF) and thickness of the organic layer (TOL) for each origin and compared them with ANOVA.

Deadwood is an important functional and structural component of forest stands and it is related to the initial forest structure and dynamics [17,28]. So, in order to evaluate the link between the patch structural complexity and their temporal dynamics in black spruce boreal forests, we have characterized structural types in terms of their deadwood dynamics on a deadwood diagram suggested by Moussaoui et al. [28] (Chapitre 2).

3.5 Results

3.5.1 Structural classification of residual patch stands

K-means classified the 125 residual patches and continuous forest stands into six stand structural types (14 as Type 1; 14 as Type 2; 22 as Type 3; 29 as Type 4; 30 as Type 5 and 16 as Type 6). Average absolute basal area and stem density by DBH class of the six structural types generated by k-means clustering are presented in Figure 2. Type 1 had an inverted-J structure, dominated by saplings (DBH < 9 cm; Table 3.1) and trees of small DBH classes varying between 9.1 and 14 cm. Types 2–4 had a truncated unimodal structure with regular diameter structures, dominated by trees of small and intermediate DBH classes (10–18 cm). In the case of Type 2, the stands had practically no large trees. Type 5 had an intermediate bimodal irregular structure, dominated by trees of intermediate and relatively large DBH classes. Finally, Type 6 had an irregular structure, with a wide range of diameters, with higher abundance of the largest DBH class (Figure 3.2a,b).

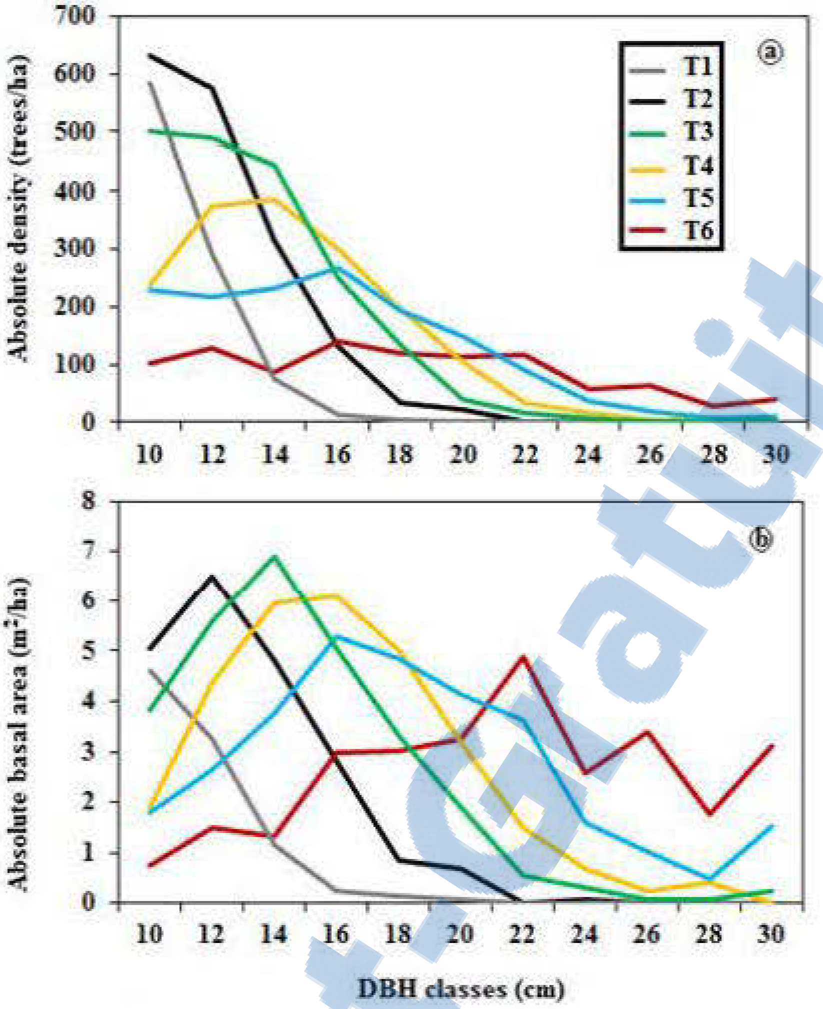

Figure 3.2 Representation of the six structural types (T1 to T6) present in residual patches and continuous forest stands (k-means structural types) with the distribution of the absolute average tree (a) density and (b) basal area plotted by DBH class. T: structural type.

The variation in the proportion of tree size classes among the six structural types is illustrated in Figure 3.3. Structural Types 1 and 2 (1, 2 in Figure 3.3) were dominated by small timber with 85.1% and 55.4%, respectively, while the structural Type 6 (6), which seemed to have a more irregular structure, had an average of 79.9% of large timber. The proportion of medium timber was highest in the three structural Types 3–

5. There is a structural evolution from Type 1 to Type 6 with a decrease in the proportion of ST and an increase in the proportion of LT (Figure 3.3).

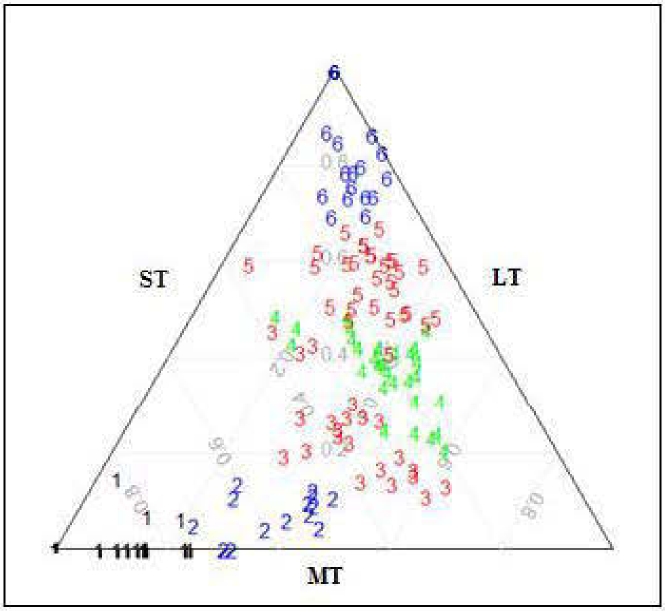

Figure 3.3 Ternary diagram (ternary plot) representing structural variability within and among structural types (from 1 to 6) by timber size (small timber ST (9 cm > DBH > 13 cm): left oblique axis; medium timber MT (13 cm > DBH > 17 cm): horizontal axis, and large timber LT (DBH > 17 cm): right oblique axis).

3.5.2 Complexity of structural stand types

Structural characteristics differed among the six structural types (T1–T6; Table 3.1). For almost all characteristics, the inverted-J structure (Type 1) was characterized by minimum values, while maximum values were typical of the stands of irregular structure (Type 6), except in the case of small and medium timber (ST, MT), where, the maximum values were recorded in the trunked-unimodal structure Types 2 and 4, respectively (Table 3.1). The characteristics of the residual patches and continuous forest stands with an inverted-J structure (T1) differed significantly ($p < 0.05$) from Types 4, 5 and 6 (Table 1). In addition, the analyses showed that generally Types 2 and 3 (trunked-unimodal structure) differed significantly ($p < 0.05$) from Type 6, which had an irregular structure characterizing stands dominated by a wide range of diameters (Table 3.1). The intermediate structure type (T5) and irregular structure type (T6) were not significantly different in terms of the average DBH of living and dead trees.

In terms of forest canopy closure, stands with an inverted-J structure or a truncated unimodal structure without relatively large trees (Types 1 and 2) had generally an open forest canopy (Figure 3.4). The structural Types 3–6, however, tended to have relatively closed structures.

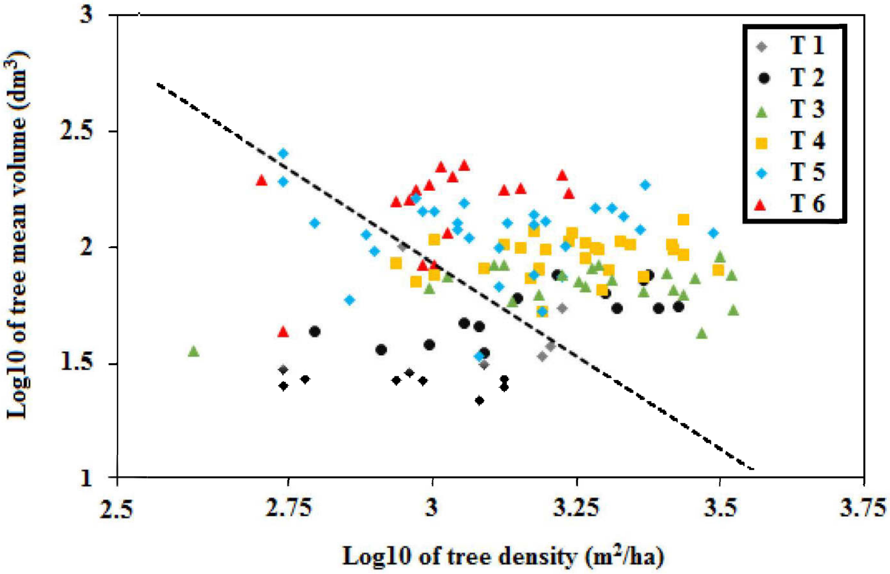

Figure 3.4 Average volume of trees (Log10 dm^3) based on their total density (Log10 m^2/ha) in the six structural types (from T1 to T6). The dotted line represents the minimum threshold for natural black-spruce forest canopy closure suggested by Newton [61]. Forest stands to the right are considered as closed stands, while stands to the left are considered as open stands.

3.5.3 Influence of TSF on structure

Organic layer thickness, stand size and shape did not vary among the structural types (Table 3.1). The results indicated that the time since the last fire (TSF), i.e., minimum age of original forest from which the patch was formed, varied among the structural types. Structural Type 1, characterized by trees of small DBH classes, showed an average TSF lower than structural Types 5 (intermediate) and 6 (irregular structure), which had higher TSF mean values (Table 3.1).

3.5.4 Structural types: post-harvest versus post-fire residual patches

The analysis of the relationship between structural types (T1, T2, T3, T4, T5, T6) present in natural stands (post-fire residual patches and continuous forest) and post-harvest retention patches showed that generally the structural variety observed in natural stands was maintained in post-harvest stands (Fisher's exact test, *p*-value = 0.257; Figure 3.5). We observed that over 60% of the old post-harvest retentions (EXT $\geq$ 20 years) had an intermediate or irregular diametric structure (Types 5 and 6). In fires, residual patches seemed to be characterized by variable structures similar to those characterizing the continuous forest stands (Figure 3.5). Stands with an inverted-J structure or a truncated unimodal structure without relatively large trees (Types 1 and 2) were primarily young residual patches (EXT: 0–19 years), particularly, post-harvest retention in the shape of clumps (YCc) and post-fire residual patches (YF; Figure 3.5; Fisher exact test, $p = 0.01$).

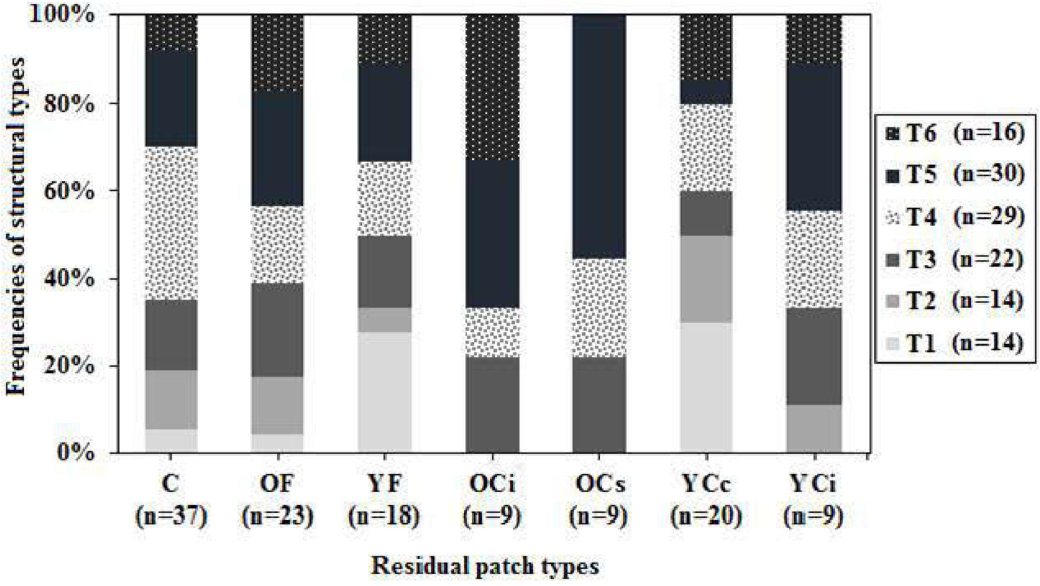

Figure 3.5 Stacked bars representing the frequencies of structural types (T1-T6) in each residual patch type and continuous forest stand. Young cut clump (YCc); young cut island (YCi), and young fire (YF): EXT: 0–19 years; old cut island (OCi), old cut separator (OCs), and old fire (OF): EXT ≥ 20 years and continuous forest (C): control.

The results indicated that organic layer thickness did not differ significantly ($F_{1,14}$ = 0.55, p = 0.47) between young post-fire residual patches (YF) and young retention in the shape of clumps YCc dominated by structure of Types 1 and 2. The time since the last fire (TSF), i.e., minimum age of the original forest from which the patch was formed, differed significantly between YF (138.8 years) and YCc (82.1 years; $F_{1,14}$ = 18.42, p = 0.0007).

The relationship between the density of trees and their volume indicated that based on the threshold suggested by Newton [61], that all stands of Type 1 were open and characterized as young post-disturbance patches (YF, YCc; Figures 3.4 and 3.5) with the exception of a single continuous forest stand. Four of the six open stands of Type 2 were young post-harvest retentions. In Types 3–6, the majority of stands were closed and were composed of continuous forest stands and old post-disturbance residual patches (OF, OCs, OCi and C; Figures 3.4 and 3.5).

When we plotted structural types on the deadwood diagram suggested by Moussaoui et al. [28] (Chapitre 2), we observed in terms of deadwood dynamics, that some structural types, especially, Types 1 and 2 characterizing some of young fire (YF) and half of young harvest (clump; YCc) patches are characterized by low living volumes and also by low volumes of deadwood (Figure 3.6). The occurrence of open canopy in others structural types (Types 3–6) appeared to be associated with a high relative volume of deadwood (Figure 3.6).

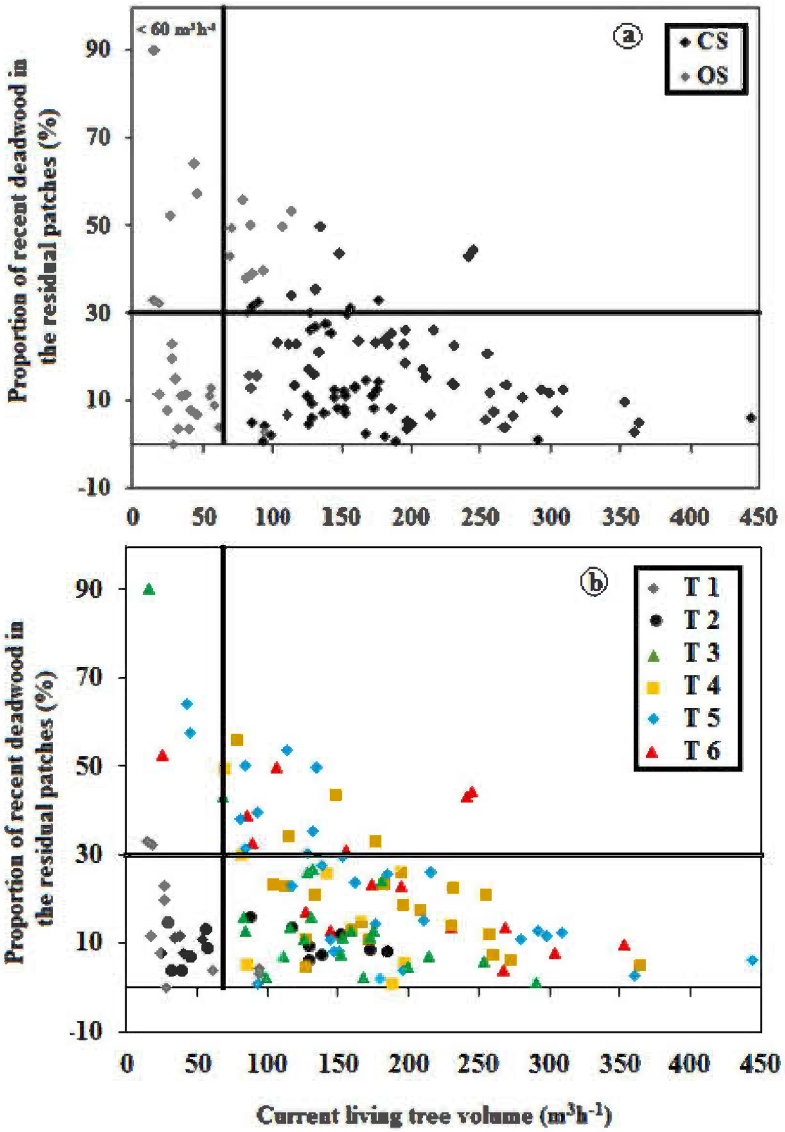

Figure 3.6 Relationship between the proportion of recent deadwood volume (%) and the current living wood volume (m^3ha^{-1}) in the residual patches and continuous forest stands in terms of (a) canopy closure and (b) structural diameter types. The proportion of the recent deadwood volume is the ratio of the recent deadwood volume on the initial stand volume before disturbance. The initial stand volume (ISV) at the time of the formation of each residual patch is estimated as the sum of current living volume and recent deadwood volume.

3.6 Discussion

The results of this study show that the structural complexity in post-harvest retention patches is generally similar to that characterizing natural stands of post-fire residual patches and continuous forests as previously suggested by Gandhi et al. [20] and Heikkala et al. [64]. Furthermore, our results also indicate that post-fire residual patches generally fall within the natural variability present in continuous forest stands. Our structural classification approach, based on the analysis of the size distribution of the merchantable trees, suggested that there are six distinct structural types characterizing residual patches (post-fire or post-harvest) and continuous forest stands in black spruce boreal forests. Type 1 (inverted-J diameter structure) and trunked-unimodal structure (type 2) characterize stands dominated by trees in small DBH classes, while, Type 6 had a more irregular structure with a wide range of diameters. In stands ranging from Type 1 to Type 6, the merchantable volume and basal area, and degree of the canopy closure could be influenced over time by of the development of large trees [65,66].

Our results indicate that the residual patches containing only small timber were generally younger (in terms of the age of the forest stand) than those with timber in all size classes. This supports studies that suggest that stand structural complexity in boreal forests increases with the time since fire [67–69]. This is not surprising because the time since last fire, i.e., the age of a forest stand, describes the natural structural maturation of trees. Initially, the young forest develops significant merchantable volume until the age of collapse, followed by a stage of transition to uneven structures [69,70], then the merchantable volume will be again reduced with forest age [71]. However, although the structure of residual patches and continuous forest stands is influenced by time since last fire, this influence is highly variable (Table 3.1), probably due to the interaction with site productivity, as a higher growth rate in productive stands is likely to induce earlier senescence and thus an earlier passage to an uneven-sized structure [69]. Otherwise, some residual patches may have simply preserved the original structures of unproductive sites, which typically have an uneven-sized structure.

In fact, in addition to time since fire, site productivity has often been cited as an important factor influencing the structure of the coniferous boreal forest [72,73]. As site productivity (soil richness) can influence the rate of maturation of forest stands [62,63], structural types including large trees appear sooner on rich soils than on poor soils. In this study, no significant effect of tree anchoring substrate on the structure of residual patches and continuous forest stands was found. This inconsistency in our results with previous studies [62,74,75] could possibly be explained by the small range of variation in the mean thickness of the organic layer among our identified structural types (Table 3.1).

The hypothesis on the relationship between residual patch area and mean shape index on structural complexity in residual patches and continuous forest stands was also not supported. This may be due to an interaction with the exposure time of patches and their post-disturbance temporal dynamics. However, our results also show that regardless of the origin of the residual patch (fire or cut), in terms of exposure time (EXT) to the disturbance matrix, types 1 and 2 are generally associated with young post-disturbance residual patches (YCc, YF). Humidity, as indicated by a thick organic matter layer, could be a factor influencing the creation of some young post-fire residual patches as they had thick organic layers despite a relatively young forest age [76]. Fire escape stands of types 1 and 2 could maintain this structure for a long period of time as tree growth is relatively slow in these environments [73]. In these fires, our raw data show that the post-fire structure of the patches is usually aged of more than 120 years. In the case of cutblocks, these retentions have usually less than 95 years and may have resulted from a selection bias of the operator, who selected retention patches with a low market value.

Furthermore, when we plot structural types on the deadwood diagram suggested by Moussaoui et al. [28] (Chapitre 2), our results show that despite the fact that half of young clump retention patches YCc (10 of 20) and some of young post-fire YF residual patches are characterized by low living volumes, the low volume of deadwood in these retentions (Figure 3.6) suggests that their structures did not result from a collapse of more advanced structural types, but simply reflect a legacy of the original forests. In this case, the open, inverted-J structure of young fire and young harvest (clump) patches may have simply preserved their original open structures, which are more resistant to post-disturbance mortality [77]. However, the occurrence of open canopy in some other structural types (Types 3–6) appears to be associated with a high relative volume of deadwood (Figure 3.6). Thus, this suggests that this canopy openness could come from a collapse of the original forest structure. In this case, even if these residual patches have low living volumes, the high proportion of recent deadwood would not indicate stand collapse but rather a structural retrogression to intermediate stages or a truncated bell shape as they maintain some larger timber (Figure 3.6).

3.7 Conclusions and silvicultural implications

It is increasingly recognized that conservation of biodiversity requires the preservation of the structural attributes of natural forest stands in the context of forest management [11]. Consequently, foresters need to develop forestry practices that maintain key structural complexity similar to that found in natural forests [12]. This study indicates that current post-harvest residual retentions in black spruce forests maintain much of the natural range of structural complexity found in post-fire residual patches and also within continuous forest stands. In addition, although there is a high volume of deadwood especially in stands in structural Types 3–6, our result show that this mortality does not result in a significant loss of structural complexity. This suggests that despite the fact that some of stands in Types 3–6 are partially collapsed, as shown in the deadwood diagram, these structural types persist or retrogress to intermediate stages such as a truncated bell shape as they maintain some larger timber. In our study area, we suggest that operators chose retention patches with a low merchantable value. This bias appears only in the young retentions in the shape of clump YCc, but not in other types of old retention (separator OCs or island OCi) in which the operator had no choice in the type of forest retained. So, our results suggest that selection bias of the operator may simplify the structural diversity of retention patches favoring sectors devoid of large stems and with little merchantable volume.

As structural Types 1 or 2, which are devoid of large stems, are created naturally by fire as well as by harvest, we might be tempted to conclude that the retention of Types 1 and 2 are acceptable targets. However, only Types 3–6 generated by past practices retain intermediate and large trees over time. In harvest areas, retention of some large trees and of large closed patches in the shape of an island or separator (Types 3–6) can contribute both to the preservation of natural structural complexity and to the maintenance of natural dynamics of deadwood (similar to residual patch or continuous forest deadwood dynamics) [28] while the surrounding harvested forest regenerates. In addition, as structural attributes of natural forests are important for different forest dwelling species, these retention patches could represent a refuge habitat for many species. To support all of these results, it will be important to compare also edge effects on stand structure of post-fire residual patches versus of post-harvest residual retentions, that can vary depending on the type of edge (post-fire or post-harvest), edge age (exposure time to disturbed matrix) and forest structure and composition [78].

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3.9 Authors contributions

Louiza Moussaoui participated in this research as Ph.D. student researcher, carried out field and laboratory work, analyzed data, designed and drafted the manuscript. Nicole J. Fenton, and Alain Leduc and Yves Bergeron are scientist supervisors, supervised the research, read, commented and approved the final manuscript.

3.10 Conflits of interest

The authors declare that they have no competing interests.

3.11 References

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CHAPITRE IV

EDGE INFLUENCE ON STRUCTURAL ATTRIBUTES IN POST-FIRE VERSUS POST-HARVEST RESIDUAL PATCHES: IMPLICATION FOR ECOSYSTEM-BASED MANAGEMENT IN BOREAL FOREST

Louiza Moussaoui, Nicole J. Fenton, Alain Leduc, Karen A. Harper, Yves Bergeron

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4.1 Abstract

1. Variable retention aims to emulate fires by maintaining forest patches within a cutblock to provide quality habitat (i.e., with large trees and deadwood) for many forest species while the adjacent harvested forest regenerates. However, because of edge influence, these post-harvest retention patches could become edges devoid of interior habitat. The objective of our study was to determine whether, after harvest, retention patch edges are modified in the same way as the edges of post-fire residual patches in black spruce dominated stands in northwestern Quebec.

2. Edge influence, determined as the difference in structural characteristics between the inside border of the edge and interior forest, and edge contrast, determined as the difference between the outside and inside border of the edge, were analyzed in 41 post-fire residual patches and 45 post-harvest retention patches of varying size and age (representing exposure time to the disturbed matrix).

3. Edge influence on the structural attributes of post-harvest and post-fire residual patches appeared similar. These effects depended on the initial conditions of the residual patch before disturbance and on their exposure time to the surrounding disturbed matrix.

4. Low initial living tree volume could explain the weaker edge influence on structural attributes of residual patches observed at the time of sampling. Because of their small size and high initial tree volume, some post-harvest retentions are more vulnerable to collapse, and therefore to the loss of their interior habitat.

5. *Synthesis and applications.* To prevent edge influence from affecting their core and to ensure continued recruitment of deadwood and living trees, our results suggest that large closed forest blocks during harvesting.

Additional Keywords: black spruce, deadwood, edge contrast, edge effects, fire edges, forest structure, habitat, harvest edges, interior forest.

4.2 Résumé

1. La stratégie de rétention variable consiste à recréer dans le parterre de coupe comme après les feux des îlots de forêt appelés îlots de rétention post-coupe, susceptibles d'offrir un habitat de qualité (i.e., avec des gros arbres et du bois mort) pour de nombreuses espèces forestières le temps que la forêt prélevée adjacente se reconstitue. Toutefois, sous l'effet de lisière, ces îlots de rétention pourraient être amenés, précipitamment, à devenir des lisières dépourvues d'habitat d'intérieur. L'objectif de cette étude était de documenter si après coupe, les lisières d'îlots de rétention sont altérées ou non de la même façon que les lisières d'îlots résiduels issus de feu en pessière à mousses de l'ouest du Québec.

2. L'effet de lisière sur la structure de la forêt intérieure, estimée comme la différence entre le bord intérieur de la lisière et la forêt d'intérieure ainsi que l'érosion de la lisière telle que mesuré par la différence entre les bords intérieur et extérieur de la lisière, ont été analysés dans 41 îlots résiduels post-feu et 45 îlots de rétention post-coupe de taille et âges (temps d'exposition à la matrice perturbée) variables.

3. Les conditions initiales prévalant dans la forêt avant perturbation et le temps d'exposition au milieur ouvert environnant sont des facteurs qui contrôlent la vulnérabilité aux effets de lisière.

4. Un faible volume initial en bois marchand pourrait expliquer les faibles effets de lisières sur les attributs structuraux d'îlots résiduels observés au moment de l'échantillonnage. En raison de leur petite taille et de leur fort volume de bois initial, certaines rétentions de coupe sous la forme de bouquet sont plus vulnérables à l'écroulement, donc à la perte de leur habitat d'intérieur.

5. *Synthèse et applications.* Cette étude suggère qu'une rétention de grands îlots de forêt fermée dans le parterre de coupe permettrait aux effets de lisière à se stabiliser avant d'atteindre leur centre tout en continuant d'assurer, à moyen et long terme, le recrutement de bois mort et d'arbres vivants.

Mots clés additionnels : bois mort, contrast de bordure, forêt d'épinette noire, forêt intérieure, habitat, lisière anthropique, lisière naturelle, structure forestière.

4.3 Introduction

In forest mosaics subject to relatively short harvest rotations, the progressive opening of the forest landscape is reflected not only in an increase in fragmentation of the forest matrix (Gauthier *et al.*, 1996; Bergeron *et al.*, 2002) but also by an increase in the proportion of edges (Harper *et al.*, 2005b). In boreal forests, although they are often associated with the effects of anthropogenic fragmentation generated by forestry practices (Lindenmayer and Fischer, 2013), forest edges are also omnipresent in natural landscapes that have been shaped primarily by fires (Harper *et al.*, 2004) and numerous water bodies. The forest edge is an ecotone at the interface between a forest and an open area (van der Maarel, 1990; Forman, 1995; Fagan *et al.*, 2003; Harper *et al.*, 2005b) and is usually characterized by an abrupt change in forest structure (Didham and Lawton, 1999).

The forest edge is subject to edge influence, which can result in a continuous gradient from the open matrix to interior forest habitats (Watkins *et al.*, 2003; Harper *et al.*, 2005a; Harper *et al.*, 2005b; Harper *et al.*, 2015). By creating a discontinuity in the landscape, forest edges have different microclimate (humidity, temperature, light, wind exposure) and vegetation (composition, abundance, mortality) compared to relatively stable conditions in the undisturbed interior forest, which vary with distance to edge (Chen *et al.*, 1995; Didham and Lawton, 1999; Saunders *et al.*, 1999; Brosofske *et al.*, 2001). Different habitat conditions may extend, depending on the forest ecosystem, for a few meters in boreal forests, to over 100 meters in rainforests (Chen *et al.*, 1995; Laurance *et al.*, 2002; Harper *et al.*, 2005b, 2015; Mascarúa López *et al.*, 2006). Tree mortality and regeneration are key processes in the amplification or attenuation of edge influence over time (Harper and Macdonald, 2002; Dupuch and Fortin, 2013). Edge maintenance or changes in edge structure over time could extend or inhibit edge influence and consequently influence the structure and composition of interior forest habitats (Greene *et al.*, 1999; Herlin and Fry, 2000; Harper and Macdonald, 2002; Magura et al. 2017).

In boreal forests, edge influence may vary depending on the type of edge (post-fire or post-harvest), age (exposure time to disturbed matrix) and forest structure and composition before a disturbance event (Harper *et al.*, 2015). Because edge influence is affected by patch contrast (difference in the structure and composition between the interior forest and adjacent open areas), it may differ between post-fire and post-harvest residual patches (Harper *et al.*, 2005b). As fires create more gradual edges (Harper *et al.*, 2004; Larrivée *et al.*, 2008; Braithwaite and Mallik, 2012) compared to forest harvesting, edge influence could be less pronounced. Furthermore, some persistent residual patches in the boreal forest are sometimes linked with water bodies or peatlands (Kafka *et al.*, 2001; Cyr *et al.*, 2007) and therefore have permanent humid edges (Brandt, 2009). These patches may be more resistant to edge influence because trees at these edges may be more wind-resistant (Harper et al. 2007). In contrast, forest harvesting typically leaves small retention patches with relatively young trees of low market value (Rheault *et al.*, 2003; Mascarúa López *et al.*, 2006), few seedbeds and abundant pre-established regeneration. Consequently, these post-harvest retention patches could become all edge with relativelly no interior habitat (Mascarúa López *et* *al.*, 2006; Boudreault *et al.*, 2008). If alternatives to current forestry practices are to maintain forest characteristics within their natural range of variability, edge influence on post-harvest retention patches and post-fire residual patches should be comparable.

Our main objective was to determine whether structural attributes of post-harvest retention patches were more vulnerable to edge influence than those of post-fire residual patches in black spruce dominated stands in northwestern Quebec. We had two specific objectives: (1) to compare structural variables at different distances from the edge among residual patches of different origins (post-fire, post-harvest) and ages (exposure time to the disturbed matrix) and (2) to determine whether edge contrast, the difference in structural attributes between the outside and inside of the edge, (Dodonov et al. 2013), was similar in post-harvest and post-fire residual patches. Our structural variables included living tree, snag and deadwood volume, and sapling and regeneration density. We expected greater deadwood volume and less living tree volume at sharper edges of post-harvest retentions compared to post-fire residual patches, and that edge contrast would decrease with time since exposure to the disturbed matrix for both edge types because of tree mortality and eventual regeneration of adjacent disturbed areas.

4.4 Materials and methods

4.4.1 Study area

Our study was conducted in western Quebec, Canada, in the boreal black spruce-feathermoss forest, located from 74 to 80°W, and from 49 to 51°N (Figure 4.1). Stands generally have 40-80% canopy cover and are dominated by black spruce *Picea mariana* Mill., BSP. with jack pine *Pinus banksiana* Lamb., balsam fir *Abies balsamea* [L.]

Mill., paper birch *Betula papyrifera* Marsh. and trembling aspen *Populus tremuloides* Michx. The climate is subpolar, continental sub-humid; average annual temperature and precipitation vary respectively from -2.5 to 0.0°C, and from 700 to 900 mm (Bergeron *et al.*, 1999; Blouin and Berger, 2005). The topography of this area forms an undulating plain. The mineral soil type is composed primarily of glaciolacustrine clay in the west and clay till in the east (Robitaille and Saucier, 1998).

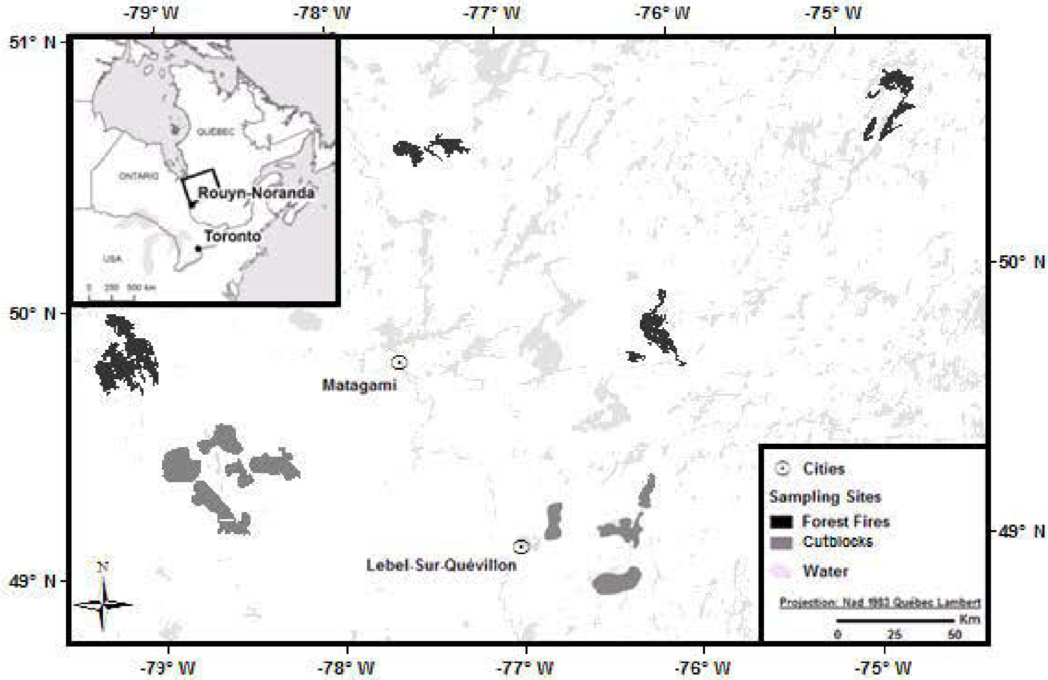

Figure 4.1 Location of 88 study residual patches in boreal black spruce-feather moss forests of western Québec, Canada. There are 41 post-fire residual patches located in forest fires (black) and 47 post-harvest residual patches located in cutblocks (grey).

Recently, landscape mosaics are as likely to have been shaped by harvest as by fire (Bergeron *et al.*, 1998; Imbeau et *al*. 2015). Fire severity is spatially heterogeneous as patches of intact forest are left within the burned matrix (Madoui *et al.*, 2011). Historically, the fire cycle was relatively short, on the order of 100-200 years (Bergeron *et al.*, 2001), but is currently lengthening to over 400 years. The harvesting method commonly used since the late 1980s has been harvest with protection of regeneration and soils (CPRS in French), which consists of harvesting all merchantable stems (diameter at breast height, DBH > 9 cm) in cutblocks with a maximum size of 250 hectares. Retention patches were placed linearly between these cutblocks (separators) with a width of 60 to 100 m and also as large islands (3-10 ha) for moose habitat (*Alces americanus*) within the cutblocks (Gouvernement du Québec, 1988). In order to maintain structural attributes similar to those created by fires, small forest clumps and large intact forest patches are two new retention types that have been used in the last decade (Bergeron *et al.*, 2002; Harvey *et al.*, 2002).

4.4.2 Location of the study sites

We studied post-harvest retention and post-fire residual patches (Figure 4.1). We located cutblocks using eco-forestry maps and recent harvest GIS layers from three forestry companies and harvest licenses (TEMBEC UAF 085-51, and EACOM UAF 086-64 and PF Résolu PRAN 087-62). We selected three to five retention patches per cutblock for a total of 47 post-harvest retention patches. Retention patchs were distributed in thirteen cutblocks: seven young (0 to 19 years) cutblocks, with retention in clumps and large islands, and six old (20 to 40 years) cutblocks, with linear separators and large islands. We located three young fires (0-19 years old) and three old fires (20-40 years) using the fire maps of the Ministère des Ressources Naturelles et de la Faune du Québec (MRNF). We selected five to eight residual patches per fire for a total of 41 post-fire residual patches. Residual patches were: (1) randomly selected from accessible patches (<1 km from a road) using ArcGis® mapping software based on the fire and eco-forestry maps and recent harvest GIS layers and harvest licenses; then (2) validated in the field according to the criteria of representativeness, accessibility, presence of late successional species (*Picea mariana* Mill., BSP) and absence of salvage logging in the case of fires.

Based on their origin (fire or cut), their age (time exposed to the disturbed matrix) and the retention type, we considered six types of residual patches: (1) young cut clump, YCc, (2) young cut island, YCi, (3) old cut island, OCi, (4) old cut separator, OCs, (5) old fire, OF, and (6) young fire, YF (Table 2.1 in Moussaoui *et al.* (2016b); Chapitre II).

4.4.3 Sampling design and data collection

We sampled post-fire residual patches during the summers of 2012 and 2013 and post-harvest retention patches during the summer of 2014. We established one representative circular plot with a radius of 11.28 m (400 m^2) at the core of each retention or residual patch (interior forest). In the young clump retentions with an area less than 400 m^2, a circular 200 m^2 plot was used to avoid edge influence. Generally, edge influence is believed to extend approximately 5 m into the forest from the disturbed matrix in boreal forests (Harper *et al.*, 2004, 2015). Therefore, to study edge influence, we placed three rectangular plots of 100 m^2 (5 x 20 m, length parallel to the edge) along a linear transect from the northwestern edge of each retention or residual patch at + 5 m into the patch (inner edge), - 5 m into the matrix (outer edge), and - 20 m into the matrix (matrix; Figure 4.2). We established five 2 x 2 m sapling subplots and ten 1 x 1 m regeneration subplots systematically along the major axis of the circular plots, and three 2 x 2 m sapling subplots and six 1 x 1 m regeneration subplots along the major axis of the rectangular plots. In each plot we used the line intersect method to sample fallen deadwood (logs).

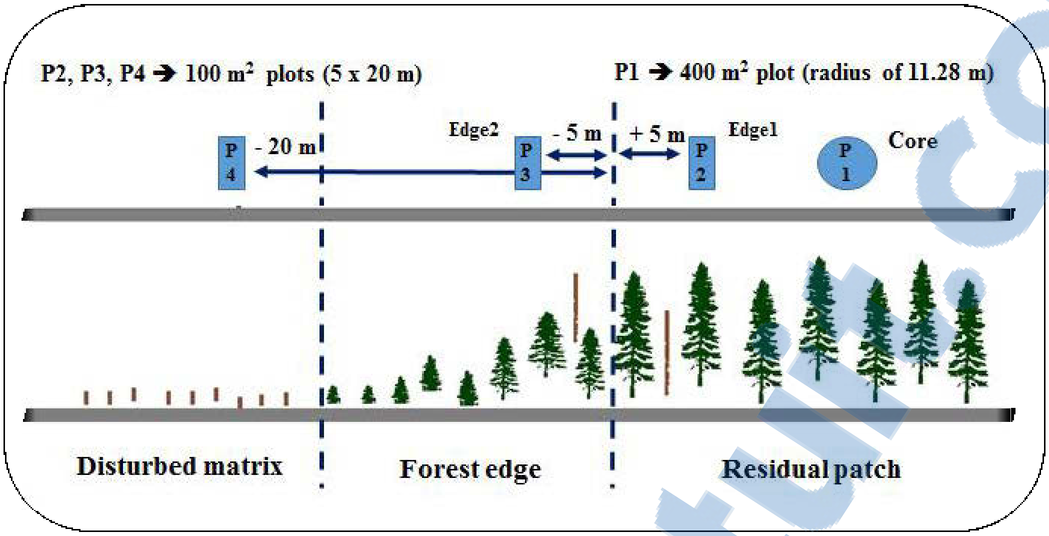

Figure 4.2 Sampling design used to evaluate edge influence in post-fire and post-harvest residual patches in boreal black spruce-feathermoss forest in northwestern Quebec, Canada. The line of outermost trees (DBH ≥ 9 cm) represents the forest edge.

In each plot, we noted the species, DBH and height of living trees and snags (standing dead trees) (DBH ≥ 9 cm). We calculated the average DBH and height of living trees, and also living tree and snag volumes following Fortin *et al.* (2007) (Table 4.A1). Within the 2 x 2 m subplots, we determined the species and densities of commercial and non-commercial saplings (1 < DBH < 9 cm). We measured the density, species and height of regeneration (size < 1.5 m) in the 1 x 1 m subplots (Table 4.A1). We evaluated initial stand volume before disturbance, and proportion and volume of recent deadwood at the core of residual patches as in Moussaoui *et al.* (2016b). For logs, we measured fallen deadwood ≥ 5 cm in diameter by decay classes (Thomas et al. 1979) and calculated their volume (Van Wagner 1968). Following Moussaoui et al. (2016b), recent deadwood volume of post-fire and post-harvest residual patches was estimated as the sum of recent snag volumes (Classes 3 and 4), and the recent log volumes (Classes 1 and 2). The initial stand volume (ISV) at the time of the formation of each residual patch was estimated as the sum of current living volume and recent deadwood volume. The proportion of the recent deadwood volume was the ratio of the recent deadwood volume on the initial stand volume before disturbance.

4.4.4 Data analyses

In our study, we define edge influence as the difference in the average of a response variable between the inside edge of the patch (inner edge) and the interior forest (core), and edge contrast as the difference between the outside (outer edge) and inside (inner edge) of the patch edge. We estimated edge influence and edge contrast for the volume of living trees, snags, logs and deadwood (snags and logs).

We graphiquelly described the general pattern of differences in living tree, snag and log volumes, and sapling and regeneration density at different distances from the edge among residual patches of different ages and origins (i.e., the six types of residual patches).

We used a LogLik test to determine whether the random location effect (i.e., belonging to a particular cutblock or fire event) has an influence on the models of edge influence and edge contrast (Pinheiro and Bates, 1995). When spatial location did not influence the model, a simpler model without random effects, i.e., linear model (lm), was used to analyse edge influence and edge contrast among residual patches of different ages and origins (i.e., the six types of residual patches), followed by a Tukey multiple mean comparison. Area of residual patch, initial tree volume before disturbance, and the proportion of deadwood at the core of residual patches were considered as co-variables. When one or more of these co-variables were significant ($p < 0.05$), adjusted edge infuence or edge contrast ($\hat{y}$) was calculated using a multiple regression equation ($\hat{y} = b_0 + b_1x_1 + b_2x_2 + b_3x_3 + b_4x_4$). Where x_1 is absolute edge influence or edge contrast (by type of residual patch), x_2 is area of residual patch, x_3 is initial tree volume before disturbance, x_4 is the proportion of recent deadwood at the core of each residual patch. $b1$, $b2$, $b3$, *and* $b4$ are the sample estimates of the co-variables and b_0 is the estimate of the reference group (YCc).

We performed all statistical analyses using R software 3.2.1 (Pinheiro *et al.*, 2007; RDevelopment-Core-Team, 2011) with a significance level of $\alpha = 0.05$.

4.5 Results

Structural attributes varied not only with distance from the edge but also among the six types of residual patches (Figure 4.3; Table 4.A1). Living tree volume was higher in older residual patches (OCs, OF, OCi) than in the young residual patches (YCc, YF) except for young cut island patches (YCi). However, edge influence on living tree volume was more pronounced (p-value < 0.05) in young post-fire residual patches and in the old residual patches (OCi, OCs, OF), than in young cut clumps and in the youngest cut islands (Figure 4.4a). The area of residual patch and proportion of recent deadwood at the core of post-fire residual patches were not significant (p-value < 0.05) explanatory factors (Table 4.B1). However, using adjusted differences for edge influence, we found that greater living tree volume in the patch core (as found in old residual patches) led to greater negative edge influence as compared to the young patches with the exception of the youngest cut islands (Figures 4.4a & 4.4b; Table 4.B1). Edge contrast for living tree volume was negatively (p-value < 0.05) affected by initial stand volume in the patch core and positively (p-value < 0.05) affected by the proportion of recent deadwood in the core (Table 4.B2). This edge contrast was greatest in the young cut island patches, followed by old residual patches (OCs, OF), young cut clump patches, then by old cut island patches and young fire residual patches, which had the lowest edge contrast for living tree volume (Figures 4.5a & 4.5b; Table 4.B2).

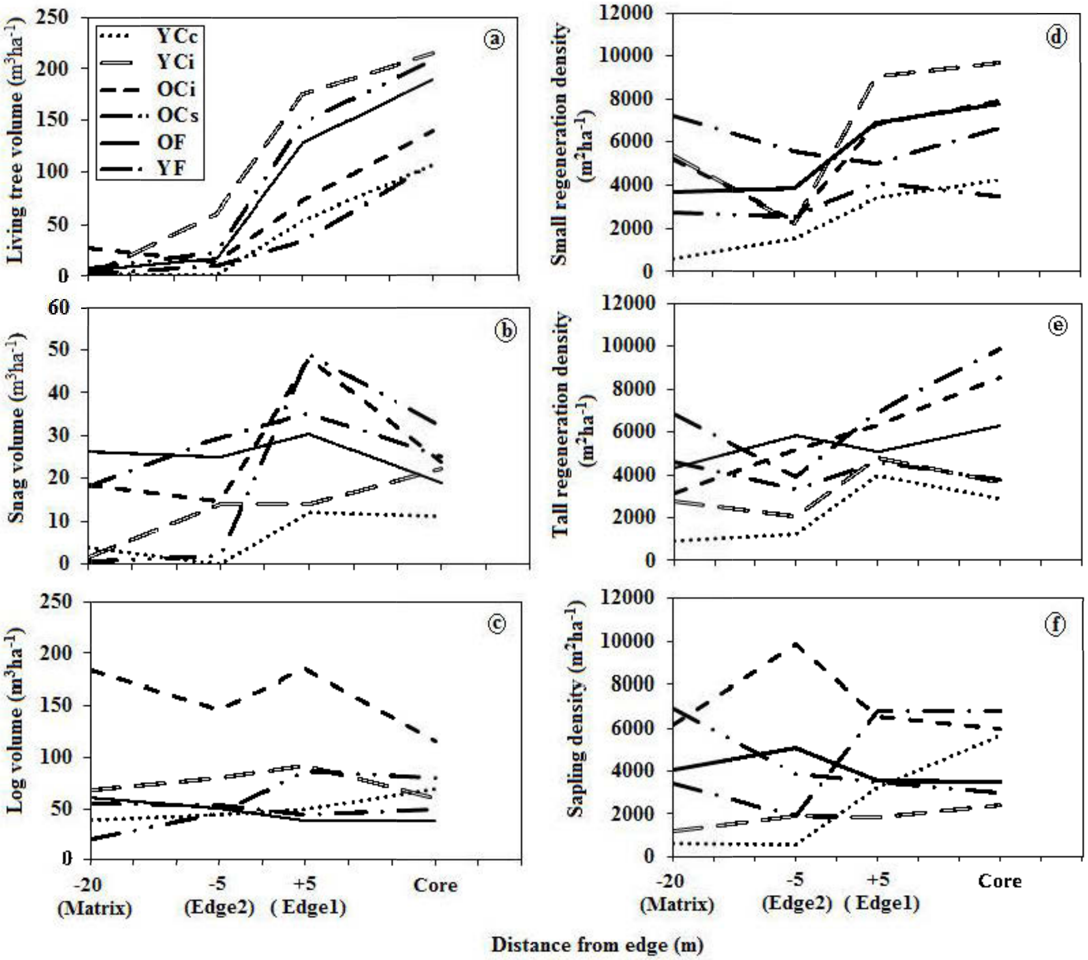

Figure 4.3 Average volume of living trees (a), snags (b), and logs (c); and average density of small regeneration (height ≤ 30 cm; d), tall regeneration (height > 30 cm; e), and saplings (f) in relation to distance from edge in the six residual patch types. The six residual patch types considered are: young cut clump (YCc); young cut island (YCi) and young fire (YF) exposed for less than 19 years; and old cut island (OCi), old cut separator (OCs), and old fire (OF) exposed for more than 20 years.

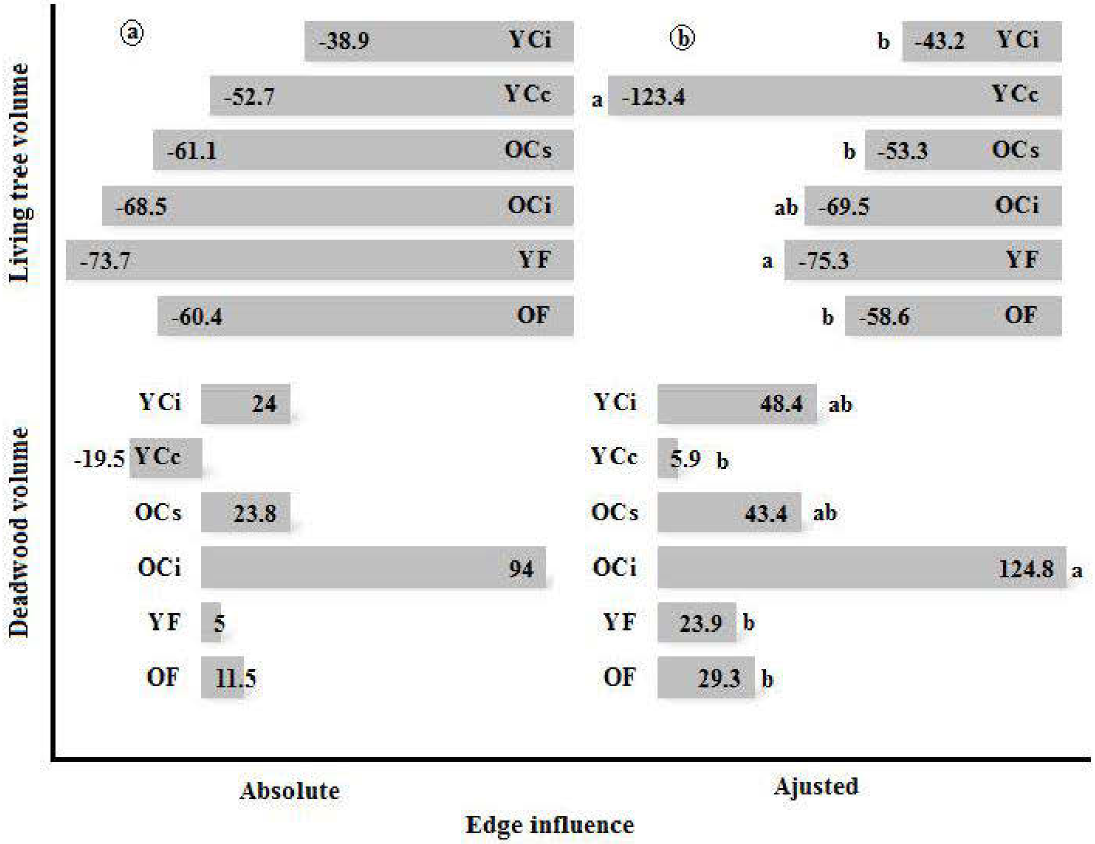

Figure 4.4 Edge influence determined as the absolute (a) and adjusted (b) differences between 5 m into the residual patch from the edge and the core of residual patches for living tree and deadwood volume for six residual patch types (see Fig. 3 for abbreviations). The adjusted difference accounted for initial stand volume (significant explanatory factor) at the core of each residual patch type as a co-variable in the linear model. In the case of absolute edge influence, negative and positive values indicate lower and greater values at the edge compared to the core, respectively. In the case of adjusted edge influence, the greater value (negative or positive) corresponding to greatest edge influence. Letters illustrate adjusted differences for residual patches that are not significantly different from each other following linear model (lm) and Tukey's HSD post hoc tests (p-value < 0.05).

Snag volume was generally higher at edge 1 than in other positions from the core, especially in old cut residual patches and post-fire residual patches (Figure 4.3b). Greater log volume was observed in old cut islands compared to other residual patch types, particularly at edge 1 (Figure 4.3c). Edge influence on deadwood (snags and logs) volume was usually positive (greater volume at inner edge than in the core), except for YCc, and was significantly greater in OCi than in post-fire residual patches and youg cut clump patches. Adding the proportion of deadwood in the core of residual patches and initial tree volume as co-variables did not affect these trends (Figures 4.4a & 4.4b; Table 4.B1). The greater amount of deadwood volume in the outer edge than in the inner edge of residual patches was largely offset by the negative and significant effect of the initial living tree volume and the proportion of recent deadwood in the core (Table 4.B2). Edge contrast was greater in the old retention patches (OCi, OCs) than in young residual patches, although not all differences were significant, and lowest in the old post-fire residual patches (Figures 4.5a & 4.5b; Table 4.B2).

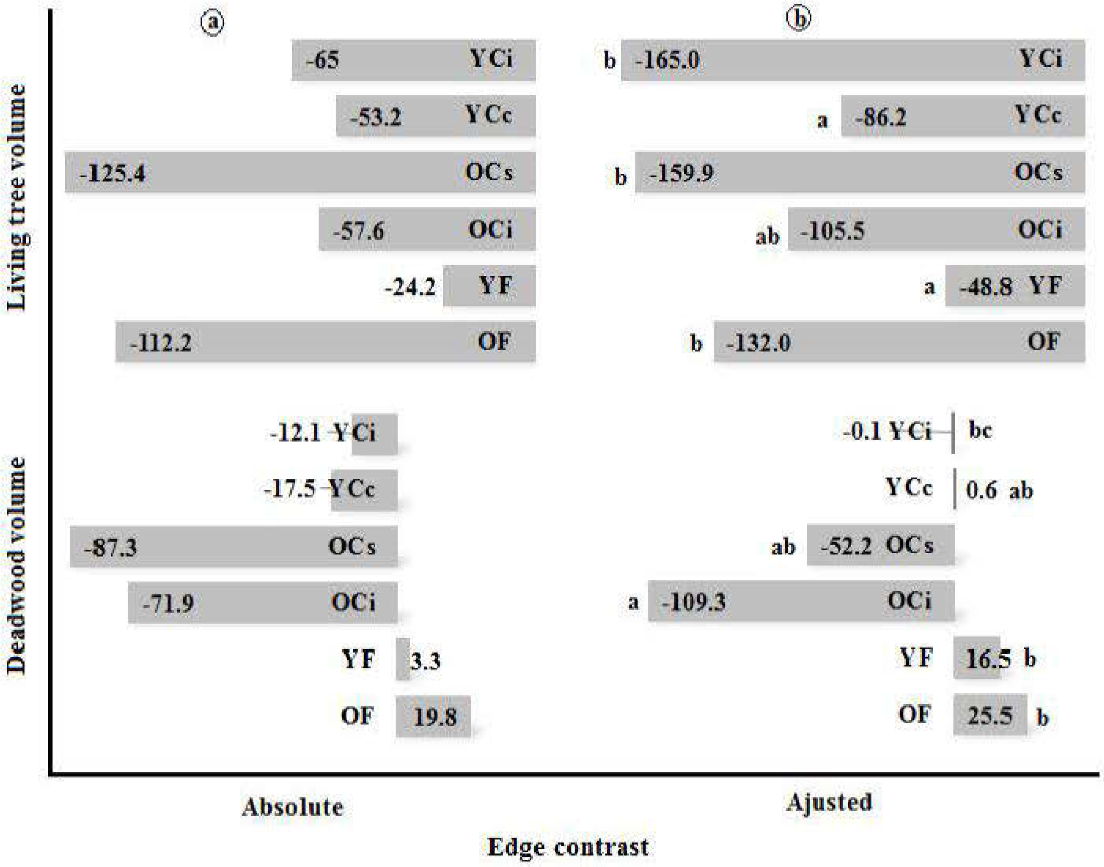

Figure 4.5 Edge contrast determined as the absolute (a) and adjusted (b) differences between outer and inner edge of residual patches for living tree and deadwood volume for six residual patch types (see Fig. 3 for abbreviations). The adjusted difference accounted for initial stand volume and the proportion of deadwood at the core of each residual patch type as a co-variable in the linear model. In the case of absolute edge influence, negative and positive values indicate greater and lower values at the inner edge compared to the outer edge, respectively. in the case of adjusted edge influence, negative and positive values indicate greater and lower edge contrast, respectively. Letters illustrate adjusted differences for residual patches that are not significantly different from each other following linear model and Tukey's HSD post hoc tests (p-value < 0.05).

Finally, there were generaly higher small and tall regeneration density in the core than in others positions regardless of residual patch type (Table 4.A1; Figures 4.3d & 4.3e). There were more saplings at the outer edge than at the inner edge and in the core, especialy at the outer edge of old cut island (Figure 4.3f; Table 4.A1).

4.6 Discussion

We found no evidence that post-fire residual patches are less vulnerable to edge influence than post-harvest retention patches as anticipated by our first hypothesis. Our results show that depending on the initial pre-disturbance conditions of the residual patch and on exposure time to the adjacent disturbed matrix, edge influence and edge contrast on structural attributes differ between post-harvest and post-fire residual patches.

The major structural changes at the edge in comparison to the interior of the patches included a reduction in living tree volume usually accompanied by an increase in snag and log volumes. This is not surprising because trees at the more open forest edges of residual patches experience windthrow due to their abrupt exposure to increased wind (Ruel, 1995; Ruel *et al.*, 2001, Watkins *et al.*, 2003; Harper *et al.*, 2005a, 2005b, 2015). These windthrow events could lead to the fall of neighbouring trees in the short or long term, and could ultimately cause the collapse of the entire residual patch with longer times since fire or harvest (Watkins *et al.*, 2003; Harper *et al.*, 2005a; Harper *et al.*, 2005b; Harper *et al.*, 2015). We found that edge influence on structural attributes of post-harvest and post-fire residual patches depended on exposure time to the disturbed surrounding-matrix and were generally greater in young patches similar to Harper *et al.* (2005b, 2014) who found that edge influence in black spruce boreal forests decreases with time due to edge regeneration. However, the youngest post-harvest retentions we sampled were probably too young to show edge influence.

In contrast, edge influence on the volume of snags and logs was greater in old residual patches than in young residual patches with the exception of young post-harvest retentions YCi, which is rather surprising. Weaker edge influence on deadwood on young residual patches was likely due to their low initial stand volumes of less than 60 m^3h^{-1}. At such low volumes, deadwood abundance in residual patches remains low regardless of exposure time to disturbed matrix (Moussaoui et al. 2016b), probably because open black spruce stands are generally pre-adapted to an open environment and are thus more resistant to post-disturbance mortality (Gardiner et al., 1997; Rich et al., 2007). Our results partially confirm our second hypothesis that edge influence decreases with time exposed to the disturbed matrix due to tree mortality and the eventual regeneration of adjacent disturbed areas.

The smaller young post-harvest clump retentions may be experiencing edge influence or fragmentation effects throughout their entire area. The low edge contrast we observed in these patches may be due, in certain cases, to the collapsed core (Moussaoui *et al.*, 2016b), because of their small size (Mascarúa López *et al.*, 2006; Rich *et al.*, 2007; Lavoie *et al.*, 2012). Also, the absence of edge influence on deadwood in clumps could be due to their high susceptibility to windthrow during storms (Esseen, 1994), especially during the first years following their creation (Lavoie *et al.*, 2012; Solarik *et al.*, 2012; Urgenson *et al.*, 2013; Hallinger *et al.*, 2016). Low edge contrast in old post-harvest retention island patches could be explained by more open interior forest within some retention patches that already had a lot of deadwood before becoming exposed to the disturbed matrix, likely due to a windthrow event because of their advanced age (Moussaoui *et al.*, 2016b; Moussaoui et al. 2016a). This suggests that the edge dynamics of residual patches is inherited from the initial forest stand and that once a residual patch collapses, it is no longer affected by edge influence that might have caused its collapse, as we found for clump retentions.

4.7 Synthesis and applications

Our results indicate that post-fire residual patches are not more vulnerable to edge influence than post-harvest retention patches, and that edge influence on structural attributes depends primarily on the pre-disturbance initial conditions of the residual patch and on the time exposed to the surrounding disturbed matrix. We suggest that three factors, low initial volume of the residual patch (YF, OCi), collapse of the edge (YCc) and regeneration in the cutblock (OCs) could explain weaker edge influence on deadwood in residual patches. We recommend that foresters keep large closed-canopy retentions rather than small clumps of trees within cutblocks so that edge influence does not affect their core; this will ensure the continued recruitment of deadwood and living trees in residual patches in the medium and long term (Work *et al.*, 2010). However, we argue that at landscap scale, edge influence is one issue, but the abundance and distribution of post-harvest retention should also be considred in forest management strategies for better conserving boreal forest interior and its biodiversity.

4.8 Acknowledgements

This study was part of a large project on post-harvest and post-fire residual patches in boreal forests. It was funded by the National Science and Engineering Research Council (NSERC) in partnership with Tembec, Eacom and Resolute Forest Products. The first author acknowledges funding received through the CRSNG-FQRNT-BMP scholarship program. We sincerely thank all of the people who helped us during fieldwork, especially Raynald Julien, Myriam Paquette, Pierre Crespin, Marion Barbé, Joëlle Castonguay, Marine Duguay Baril, Louis Dubois, Béatrice Perron, Philippe Heine and Anne-Laure De Vuillaume. Thanks also to Julie Filion at PFRésolu for her accommodation during fieldwork. We acknowledge Louis Imbeau and Francine Tremblay for their helpful comments on this paper during the evaluation of L.M. thesis.

4.9 Supporting information

Appendix 4.A. Supplementary material

Table 4.A1. Characteristics of the six sampled residual patch types at different distances from the edge (position), given as mean ± standard deviation. The residual patch types (ST) are: OF, old fire; YF, young fire; OCs, old cut separator; OCi, old cut island; YCc, young cut clump; YCi, young cut island. Characteristics include: V1, living tree volume; V2, snag volume; V3, log volume; V4, V5 and V6, log volume in different decay stages, respectively in c1 and c2 (recent log volume), c3 (intermediate log decomposition) and c4 and c5 (old log decomposition) following Thomas et al. (1979); V7, average height of regeneration; V8, small regeneration density (0 to 30 cm of height); V9, tall regeneration density (height > 30 cm); V10, sapling density; V11 to V17, sapling density for black spruce (Picea mariana Mill., BSP), jack pine (Pinus banksiana Lamb), trembling aspen (Populus tremuloides Michx.), balsam fir (Abies balsamea [L.] Mill), larch (Larix decidua), birch (Betula papyrifera Marsh) and non-commercial species, respectively. Density and volume are measured in m^{2}ha^{-1} and m^{3}ha^{-1}, respectively.

Edge type	**ST**	**Position**	**V1**	**V2**	**V3**	**V4**	**V5**	**V6**	**V7**	**V8**	**V9**	**V10**	**V11**	**V12**	**V13**	**V14**	**V15**	**V16**	**V17**
Fire edges	**OF**	**Core**	189.2 ± 83.8	18.9 ± 24.1	37.6 ± 29.3	12.6 ± 12.7	7 ± 8.5	17.9 ± 18.4	36.8 ± 18.9	7782.6 ± 6584.8	6304.3 ± 5972.9	3519.6 ± 4268.4	3223.9 ± 4039.9	0	0	104.3 ± 198.8	8.7 ± 41.7	156.5 ± 463	26.1 ± 68.9
		(+ 5 m)	128.8 ± 60	30.3 ± 45.8	37.7 ± 36	17.1 ± 28.3	8.2 ± 12.9	12.3 ± 15.3	37 ± 20.1	6884 ± 7373.6	5072.5 ± 4307.6	3579.9 ± 3199.9	2318.1 ± 1958.3	0	0	579.5 ± 1266.7	57.9 ± 198.5	189.8 ± 867.6	434.6 ± 1227.1
		(- 5 m)	16.6 ± 14.6	25 ± 45.1	50.2 ± 46.2	8.1 ± 13.1	10.7 ± 12.6	31.4 ± 32.3	44.7 ± 30.4	3840.6 ± 4335.5	5869.6 ± 6978.8	5075 ± 6979.8	4052.2 ± 5345.5	81.1 ± 240.9	0	108.6 ± 381.3	108.7± 367.9	615.7 ± 2291.2	108.6 ± 286.8
		(- 20 m)	5.4 ± 2.8	26.2 ± 39.6	61.2 ± 56.1	5.8 ± 10.8	19.6 ± 23.9	35.8 ± 36.7	42.6 ± 34.6	3623.2 ± 3782.3	4347.8 ± 4625.9	4039.4 ± 4169.2	2960 ± 3640.1	0	0	289.7 ± 926.5	210.1 ± 550.8	217.3± 719.9	362.2 ± 933.9
	YF	**Core**	107.3 ± 76.2	25.1 ± 24.3	49.3 ± 50.8	16.4 ± 18.4	5.6 ± 10.5	27.2 ± 33.4	45.6 ± 11.9	6611.1 ± 5370.3	9888.9 ± 5400.3	6820.6 ± 4871.6	5319.4 ± 5368.5	0	0	915.3 ± 1221.3	219.4 ± 740.8	66.7 ± 237.6	300 ± 767.7
		(+ 5 m)	33.6 ± 17.6	35.5 ± 53.4	43.9 ± 55.8	14.1 ± 13.1	12.5 ± 24.2	17.3 ± 31.1	46 ± 22.9	5000 ± 7754.4	6944.4 ± 6423.2	6766.2 ± 3918.2	4887.3 ± 3186.1	0	0	1110.7 ± 2618.6	120.3 ± 284.6	0	647.9 ± 1126.9
		(- 5 m)	9.4 ± 14.6	29.5 ± 40.1	53.2 ± 49.4	14.7 ± 17.1	14.8 ± 13.1	23.7 ± 28.7	34.1 ± 24	5555.6 ± 6617.5	3888.9 ± 4917.6	1906.8 ± 2801.3	1277.4 ± 1548.2	0	0	370.2 ± 1376.8	27.7 ± 117.8	46.3 ± 196.3	185.1 ± 609.8

		(- 20 m)	1.5 ± 2.8	18.3 ± 25.5	54.4 ± 50.7	10.6 ± 16.3	13.7 ± 14.8	30.2 ± 42.3	39.7 ± 25.8	7222.2 ± 8800.6	6851.8 ± 5109.5	3433.9 ± 5052.6	2138.1 ± 3311.9	46.2 ± 196.3	370.2 ± 1376.8	740.4 ± 2173.7	0	0	138.8 ± 428.6
Harvest edges	**OCi**	**Core**	140.2 ± 112.2	23.7 ± 16.1	115.1 ± 77.5	39.1 ± 40.4	21.6 ± 20.4	54.4 ± 47	49.2 ± 23.4	7888.9 ± 5325.5	8555.6 ± 6247.2	6000 ± 4023.7	2422.2 ± 1677.6	0	0	2555.6 ± 3463.8	0	133.3 ± 264.6	888.9 ± 975.2
		(+ 5 m)	71.7 ± 44.9	48.1 ± 44.2	184.7 ± 78.1	54.2 ± 74.3	36 ± 32.4	94.5 ± 72.3	54.2 ± 27.6	6851.8 ± 9662.5	6296.3 ± 4470.4	6555.6 ± 5598.2	2833.3 ± 2263.8	55.6 ± 1666.7	55.6 ± 166.7	2277.8 ± **3270.2**	55.6 ± 166.7	111.1 ± 333.3	1166.7 ± 1274.7
		(- 5 m)	14.1 ± 12.7	14.5 ± 18.5	146.4 ± 83.1	22.2 ± 31.2	31.5 ± 58.8	92.8 ± 62.1	59.4 ± 27	2407.4 ± 2060	5185.2 ± 4203.5	9833.3 ± 5809.5	3722.2 ± 3857.7	0	0	3111.1 ± 2803.8	0	55.5 ± 166.7	2944.4 ± 3669.5
		(- 20 m)	26.9 ± 24.9	18.5 ± 16.9	183.8 ± 78.4	21.9 ± 44.5	40.7 ± 76.9	121.3 ± 61.7	30.2 ± 35.8	5185.2 ± 7703	3148.1 ± 3674.6	6166.7 ± 4769.7	1722.2 ± 2152.2	0	0	1500 ± 2015.6	0	0	2944.4 ± 4267.9
	OCs	**Core**	209.1 ± 71.5	32.2 ± 18.9	79.2 ± 53.9	16.7 ± 13.6	5.3 ± 5.4	57.3 ± 52	37.9 ± 35.4	3444.4 ± 4798.7	3777.8 ± 3961.6	3000 ± 2529.8	1555.5 ± 1227.9	0	0	1066.7 ± 1910.5	0	0	377.8 ± 651.5
		(+ 5 m)	148 ± 72.2	49.1 ± 27.9	86.1 ± 44.6	21.4 ± 24.3	17.7 ± 21.1	47 ± 41.6	51.4 ± 33.8	4074.1 ± 4339	4629.6 ± 5053.7	3500 ± 4092.7	2222.2 ± 2751.3	0	111.1 ± 333.3	833.3 ± 2136	0	0	333.3 ± 500
		(- 5 m)	22.6 ± 17.9	2.1 ± 3.6	45.8 ± 25.1	2.7 ± 3.5	6.5 ± 11.9	36.6 ± 23.3	37.5 ± 32.8	2592.6 ± 4258.2	3333.3 ± 3435.9	3888.9 ± 1900.3	2777.8 ± 1371.8	0	166.7 ± 500	388.9 ± 546.4	0	222.2 ± 440.9	333.3 ± 559
		(- 20 m)	7.2 ± 4.5	0.8 ± 2.4	19.8 ± 30.6	0	8.9 ± 15.1	10.9 ± 16.5	41.3 ± 25.3	2777.8 ± 2500	4629.6 ± 6054	6944.4 ± 4706.7	4611.1 ± 4090.9	555.6 ± 1666.7	222.2 ± 506.9	166.7 ± 353.5	55.6 ± 166.7	333.3 ± 707.1	1000 ± 1520.7
	YCc	**Core**	105.9 ± 81.9	11.3 ± 15.8	69.9 ± 89.8	33.5 ± 46.1	9 ± 15.6	27.4 ± 49	42.8 ± 26.4	4250 ± 5097.7	2900 ± 2573.1	5670 ± 4514.4	4160 ± 3930.2	0	80 ± 219.1	530 ± 1639.3	0	0	900 ± 1065.2
		(+ 5 m)	53.2 ± 47.3	12 ± 12.2	49 ± 57.2	22.9 ± 32.2	10.1 ± 12.7	16.1 ± 28.6	41.9 ± 32.4	3416.7 ± 3764.8	4000 ± 3876.7	3225 ± 2494.6	2350 ± 2340.1	0	0	225 ± 785.9	0	0	650 ± 1136.7
		(- 5 m)	0	0	43.5 ± 28.8	9.3 ± 9.8	24.5 ± 19.7	9.7 ± 15	31.7 ± 34.4	1583.3 ± 2324.2	1250 ± 1699.2	550 ± 944.5	75 ± 183.2	25 ± 111.8	100 ± 447.2	0	0	0	350 ± 890
		(- 20 m)	1.4 ± 6.4	4 ± 14.9	39.2 ± 36.5	10.6 ± 18.1	20.6 ± 13.1	7.9 ± 19.2	12.4 ± 21.6	583.3 ± 1241.9	916.7 ± 1831.7	625 ± 1503.3	25 ± 111.8	75 ± 335.4	0	25 ± 111.8	0	0	500 ± 1395.5
	YCi	**Core**	214.7 ± 125.2	22.4 ± 13.4	60 ± 39.6	12.6 ± 11.8	10.9 ± 8.9	36.5 ± 37.1	29.6 ± 14.7	9666.7 ± 8972.2	3666.7 ± 3391.2	2377.8 ± 3672.1	2111.1 ± 3512.9	0	0	111.1 ± 226.1	0	0	155.6 ± 466.7
		(+ 5 m)	175.8 ±102.4	14.1 ± 13.4	92.3 ± 57.6	44.2 ± 27.6	16.2 ± 16.1	31.9 ± 32	24.3 ± 26	9074.1 ± 10836.9	4814.7 ± 6148.9	1833.3 ± 2091.6	1388.9 ± 2073.3	0	0	333.3 ± 559	0	0	111.1 ± 220.5
		(- 5 m)	60.2 ± 87.4	13.9 ± 18.5	80.4 ± 48.1	37.8 ± 44.8	22.3 ± 19.9	20.4 ± 22.6	28.5 ± 21.1	2222.2 ± 3435.9	2037 ± 2468.9	1888.9 ± 2619.4	555.6 ± 1210.5	0	333.3 ± 661.4	111.1 ± 333.3	0	0	888.9 ± 2666.7
		(- 20 m)	0	1.7 ± 5	67.6 ± 43.2	10.5 ± 11.8	25.1 ± 18.8	31.9 ± 53.3	29.2 ± 29.4	5185.2 ± 7010.8	2777.8 ± 3004.6	1166.7 ± 1561.2	722.2 ± 1502.3	0	55.5 ± 166.7	222.2 ± 506.9	0	0	166.7 ± 353.5

Appendix 4.B. Results of of edge influence and edge contrast models

Table 4.B1. Edge influence measured as the difference between inner edge (+ 5 from the edge) and the core of residual patches for different response variables at different exposure time to disturbed matrix and patch origins (six residual patch types). All values are given as estimate ± standard error. In all instances, negative and positive value indicate lower and greater values at inner edge compared to the core of residual patches, respectively. The six residual patch types (ST) are: young cut clump (YCc); young cut island (YCi) and young fire (YF), all with less than 20 years of exposure time; old cut island (OCi), old cut separator (OCs), and old fire (OF), with more than 20 years of exposure time since last disturbance. The same letters indicate values that are not significantly different among residual patches following linear model (lm) and Tukey's HSD post hoc tests (p-value < 0.05); ns, non-significant co-variables.

Edge effect	**ST**	Living tree volume (m^3ha^{-1})	Volume of deadwood (snags + logs) (m^3ha^{-1})	Snag volume (m^3ha^{-1})	Log volume (m^3ha^{-1})
Fire edge	OF	43.1 ± 17.4 **b**	23.4 ± 23.3 **b**	9.8 ± 11.8 **a**	13.6 ± 18.5 **b**
	YF	- 21.6 ± 17.3 **a**	18 ± 23.2 **b**	7.4 ± 11.7 **a**	10.6 ± 18.3 **b**
Harvest edge	OCi	18.1 ± 23.8 **ab**	118.9 ± 32 **a**	17.9 ± 16.2 **a**	100.9 ± 25.3 **a**
	OCs	65.9 ± 24.4 **b**	37.5 ± 32.7 **ab**	12.6 ± 16.6 **a**	24.8 ± 25.8 **ab**
	YCc	25.3 ± 15.72 **a**	5.9 ± 21.1 **b**	0.8 ± 10.7 **a**	5.1 ± 16.7 **b**
	YCi	79.5 ± 21.2 **b**	42.5 ± 38.4 **ab**	- 8.1 ± 14.4 **a**	50.6 ± 22.4 **ab**
Co-variable					
Initial stand volume at the core		- 0.6 ± 0.05	ns	ns	ns
Proportion of deadwood at the core		ns	ns	ns	- 0.9 ± 0.4
Area of residual patch		ns	ns	ns	ns

Table 4.B2. Edge contrast measured as the difference between outer edge (at distance – 5 from the edge into the matrix) and inner edge (at distance + 5 from the edge into the residual patch) for different response variables at different exposure time to disturbed matrix and patch origins (six residual patch types). All values are given as estimate ± standard error. In all instances, negative and positive value indicate lower and greater values at outer edge compared to inner edge of residual patches, respectively. The six residual patch types (ST) are: young cut clump (YCc); young cut island (YCi) and young fire (YF), all with less than 20 years of exposure time; old cut island (OCi), old cut separator (OCs), and old fire (OF), with more than 20 years of exposure time since last disturbance. The same letters indicate values that are not significantly different among residual patches following linear model (lm) and Tukey's HSD post hoc tests (p-value < 0.05); ns, non-significant co-variables.

Edge type	ST	Living tree volume (m^{3}h^{-1})	Volume of deadwood (snags + logs) (m^{3}h^{-1})	Snag volume (m^{3}h^{-1})	Log volume (m^{3}h^{-1})
Fire edges	OF	- 51.3 ± 17.3 **b**	24.9 ± 20.4 **b**	8.3 ± 10.8 **a**	- 16.6 ± 15.3 **b**
	YF	19.9 ± 22.7 a	15.9 ± 20.2 **b**	9.7 ± 10.8 **a**	6.2 ± 15.2 **b**
Harvest edges	OCi	- 28.3 ± 23.7 a**b**	-109.9 ± 27.9 **a**	- 10 ± 14.8 **a**	- 99.9 ± 20.9 **a**
	OCs	- 74.8 ± 24.3 **b**	- 52.8 ± 28.6 **ab**	- 27.8 ± 15.2 **a**	- 24.9 ± 21.4 **b**
	YCc	- 49 ± 15.7 **a**	0.6 ± 18.4 **ab**	- 8.5 ± 9.8 **a**	9.1 ± 13.8 **b**
	YCi	- 79 ± 21.1 **b**	- 0.7 ± 24.8 **bc**	8.3 ± 13.2 **a**	- 9 ± 18.6 **b**
Co-variable					
Initial stand volume		- 0.15 ± 0.4	- 0.2 ±0.06	ns	- 0.2 ± 0.04
Proportion of deadwood		0.8 ± 0.4	- 1.1 ± 0.4	ns	- 0.9 ± 0.3
Area of residual patch		ns	ns	ns	ns

4.10 References

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CHAPITRE V

CONCLUSION GÉNÉRALE

L'objectif général de cette thèse était de documenter les mécanismes ou les différences possibles de la dynamique post-perturbation de structure d'îlots résiduels laissés par le feu et d'îlots de rétention créés par la coupe sylvicole, dans un contexte d'aménagement forestier écosystémique.

Bien qu'en Fennoscandinavie et en Amérique du Nord, les études aient révélé la présence d'îlots résiduels ayant la capacité de se maintenir dans le territoire pendant plusieurs millénaires et pouvant être des refuges pour la biodiversité (Hemstrom et Franklin, 1982; Ouarmim *et al.*, 2014b), elles se sont rarement intéressées à leur structure ou dynamique. Les recherches se sont surtout penchées sur leurs caractéristiques spatiales (taille, forme, proportion) (Kafka *et al.*, 2001; Madoui *et al.*, 2011; Dragotescu et Kneeshaw, 2012). Afin de savoir en quoi les îlots de rétention post-coupe se comparent aux îlots résiduels post-feu en pessière à mousses de l'ouest du Québec, cette étude a comparé à l'échelle d'îlot la dynamique post-perturbation de leur structure tant au sein de leur forêt d'intérieure qu'en lisière. De plus, les conditions initiales des peuplements pouvant expliquer les différences entre eux ont été identifiées.

La thèse s'est premièrement penchée sur l'évaluation de l'abondance de bois mort récent dans les îlots résiduels après feu et après coupe et sur la comparaison de leur durabilité post-perturbation en considérant la forêt continue comme témoin (Chapitre

2). Deuxièmement, elle s'est intéressée à la comparaison de leur diversité structurale post-perturbation en faisant le lien avec la dynamique de leur bois mort (Chapitre 3). Enfin, cette thèse a évalué la vulnérabilité d'îlots résiduels post-feu et post-coupe à la perte de leurs habitats structuraux intérieurs sous l'effet de lisière (Chapitre 4).

Les analyses de l'abondance du bois mort des îlots résiduels étudiés nous ont permis de générer un modèle prédictif de la dynamique post-perturbation du bois mort des rétentions de coupe en vue d'augmenter leur durabilité. L'objectif était d'évaluer l'abondance du bois mort récent des îlots résiduels post-feu et des rétentions post-coupe, de taille et âges variables, afin d'en comparer leur durabilité post-perturbation. Les résultats ont montré que parfois, en raison de leurs conditions initiales (forêts peu volumétriques), bien que les îlots résiduels post-feu soient durables sur le moyen terme, étant peu volumétriques ils généraient très peu de bois mort. Toutefois, en raison de leur taille (≈ 400 m2), les bouquets figuraient parmi les îlots de rétention des plus vulnérables à l'écroulement (6 bouquets sur 20) même s'ils étaient peu volumétriques. En contexte aménagé, ceci suggère que même si l'on pouvait abaisser la vulnérabilité des rétentions sous la forme de bouquet, en sélectionnant des îlots dans de jeunes forêts ou dans des forêts ayant un faible volume sur pied, ceci limiterait sur le court ou moyen terme la production de gros bois mort à cause de l'absence de gros bois vivants et sénescents. Dans le meilleur scénario, à moyen ou long terme, le recrutement de nouvelles tiges marchandes se remettra en route et les tiges marchandes actuelles deviendront grosses dans ces bouquets. Sinon, si ces bouquets s'ouvrent davantage, leur écroulement va provoquer l'érosion de leur qualité d'habitat en raison de cette absence de gros bois vivants et sénescents. Du point de vue fonctionnel, ceci pourrait ainsi, mettre en péril la survie de plusieurs espèces. Par ailleurs, les résultats ont montré également que la dynamique de recrutement de bois mort dans les larges îlots à orignaux et les séparateurs secs orientés de manière à éviter le chablis était souvent similaire à celle d'îlots résiduels issus de feu, et que lorsque leur volume initial de bois était plus important que 60 m^3ha^{-1}, ils produisaient du bois mort, d'une façon soutenue.

Dans ce cas, le recrutement en petites tiges marchandes pourrait compenser pour la perte de grosses tiges. À la lumière de l'ensemble de ces résultats, afin de mieux assurer leur rôle potentiel de maintien des espèces dans la matrice coupée (Gustafsson *et al.*, 2012; Lindenmayer *et al.*, 2012), de larges parcelles de peuplements volumétriques (entre 60 à 300 m^3ha^{-1}) devraient être sélectionnées lors de la rétention de coupe. Ceci permettrait, ainsi, d'augmenter la durée de vie des rétentions et entre autres procurer un habitat de qualité (gros arbres et bois mort) pour de nombreuses espèces forestières le temps que la forêt coupée adjacente se reconstitue (Perhans *et al.*, 2009).

Notre approche de classification structurale, basée sur l'analyse de la distribution de la taille des arbres vivants marchands, a généré six types structuraux distincts. Le type 1 (structure diamétrale en j-inversé) et le type 2 (structure unimodale tronquée) caractérisaient les peuplements dominés par le petit bois. Le type 6 avait une structure irrégulière avec du bois de tous les diamètres. Un gradient d'apparition de larges tiges a été observé en allant du type 1 au type 6. Autrement dit, en termes de l'âge de la forêt d'origine, les îlots résiduels de feu ou de coupe de types 1 et 2 sont relativement jeunes, alors que les îlots résiduels de type 6 sont probablement issus de forêts matures voire vieilles. Les résultats ont montré que les îlots résiduels de feu en pessière à mousses sont représentatifs de la variabilité structurale rencontrée dans les peuplements de forêt continue. Ceci suggère que puisque les îlots résiduels constituent un échantillon non biaisé de la forêt continue, on pourrait dorénavant s'en inspirer pour établir notre référant dans la bonification des stratégies de rétention variable visant à protéger la variabilité de la matrice forestière et les espèces qui lui sont associées (Gauthier *et al.*, 2001; Beese *et al.*, 2003; Gauthier *et al.*, 2008a). La comparaison entre les types structuraux caractérisant les îlots résiduels post-feu et ceux de rétentions de coupe ont montré que, généralement, les rétentions de coupe maintiennent bien la variabilité structurale naturelle observée dans les îlots de feu et la forêt continue. Cependant, même si les types 1 et 2, structures jeunes et dépourvues de grosses tiges, étaient présents dans les peuplements naturels, seulement les peuplements de types 3 à 6 retenaient d'une part, du bois moyen et large longtemps après coupe et que d'autre part, ils assuraient le recrutement de nouvelles tiges marchandes. Ce chapitre nous mène aux mêmes conclusions que le chapitre 2. Spécifiquement, nos résultats suggèrent la rétention d'arbres dans des forêts à structure diamétrale de types 3 à 6 afin de procurer du bois moyen et gros, qui sont des attributs structuraux indispensables pour le maintien d'une dynamique de bois mort soutenable et la préservation des espèces dans la matrice aménagée.

Une autre façon de diagnostiquer la durabilité des îlots de rétention post-coupe était de déterminer si l'effet de lisière apparaissait similaire entre les îlots générés par le feu et les îlots de rétention de coupe et savoir à la même occasion, si les rétentions de coupe étaient plus vulnérables à la perte de leur habitat intérieur à cause de leur lisière franche ou de leur petite taille (Harper *et al.*, 2004; Fenton et Frego, 2005; Boudreault *et al.*, 2008). Pour ce faire, nous avons comparé les différences entre les attributs structuraux (arbres vivants, chicots, débris ligneux et régénération) de la lisière à ceux de la forêt intérieure dans des îlots résiduels d'âges variables issus de coupe et de feu. Les résultats de ce chapitre ont indiqué que les effets de lisières influençaient les attributs structuraux des îlots résiduels après feu et après coupe, généralement de manière similaire, et que dans les deux cas, ces effets dépendent, surtout des conditions initiales de l'îlot résiduel avant perturbation et de leur temps d'exposition à la matrice perturbée environnante. Ce chapitre suggère que les trois facteurs, volume initial en bois marchand faible, écroulement de la lisière et régénération du parterre de coupe, pourraient expliquer les faibles effets de lisières sur les attributs structuraux d'îlots résiduels présents au moment de l'échantillonnage. Autrement dit, dépendamment de ces trois facteurs, la dynamique spatiale d'effet de lisière est spécifique à chacun de ces types d'îlots résiduels (selon leur origine et leur âge). Précisément, les îlots résiduels post-feu présentaient déjà un volume initial faible avant feu et la matrice brûlée a eu le temps de se régénérer, ce qui a laissé le temps aux effets de lisière de s'atténuer. Les rétentions de coupe sous la forme de bouquet de petite taille étaient soit peu volumétriques ou, lorsque ayant un fort volume de bois initial, elles n'avaient plus d'habitats intérieurs au moment de l'échantillonnage. Ceci nous laisse croire que c'était l'effet de lisière qui a mené à l'écroulement de ces jeunes bouquets de petite taille. Les résultats suggèrent que lorsque les rétentions sous la forme de bouquet sont volumétriques, elles sont plus vulnérables aux effets de lisière. Cependant, bien que sur le court terme, les jeunes bouquets aient tendance à conserver quelques attributs structuraux (selon le Chapitre 3) lorsqu'ils sont peu volumétriques, ils ne permettraient pas le recrutement de bois mort grossier et de gros arbres vivants sur le court et moyen terme. Ainsi, retenir dans le parterre de coupe, dorénavant, des rétentions plus larges que les bouquets, dans des forêts fermées permettrait aux effets de lisière de se stabiliser avant d'atteindre leurs habitats intérieurs tout en continuant d'assurer, à moyen et long terme, le recrutement de bois mort et d'arbres vivants. Ceci permettrait ainsi, d'augmenter la durée de vie post-coupe des rétentions.

L'ensemble de ces résultats font écho aux travaux ultérieurs de même genre s'intéressant soit au territoire aménagé ou naturel (Mascarúa López *et al.*, 2006; Rich *et al.*, 2007; Work *et al.*, 2010; Lavoie *et al.*, 2012; Harper *et al.*, 2014; Heikkala *et al.*, 2014), qui suggèrent l'intérêt de retenir au sein des rétentions après coupe une importante structure du bois vivant et du bois mort, et surtout, de les maintenir dans le temps en vue de conserver un habitat de qualité pour les espèces forestières.

Les résultats de cette thèse contribuent à la connaissance scientifique visant à documenter les mécanismes responsables de la dynamique post-perturbation des structures d'îlots résiduels issus de feu et d'îlots de rétention créés par la coupe sylvicole, à l'échelle de l'îlot. Cette thèse a réussi à établir le lien entre la dynamique du bois mort, la complexité structurelle et l'influence des lisières afin d'évaluer le rôle de la structure, de l'âge des îlots résiduels et de son temps d'exposition depuis perturbation dans leur dynamique post-feu et post-coupe. Cette thèse met en évidence que les conditions actuelles qui prédominent dans les deux types d'îlots résiduels (post-feu et post-coupe) sont le résultat de la coexistence de deux processus dynamiques forestiers. Une dynamique de maturation et de succession forestière qui est présente en forêt continue à laquelle vient s'associer une dynamique d'effets de lisière qui découle de la mise en place de l'îlot résiduel. Une dynamique de maturation et de succession forestière est, généralement, contrôlée par l'état initial du peuplement (d'îlot résiduel) et une dynamique d'effets de lisière, surtout, conditionnée par la taille de l'îlot et le contraste à la lisière (cas des bouquets). La combinaison du degré de maturation structurale du couvert avec l'intensité de l'effet de lisière et du temps d'exposition à cet effet (effet lisière avancé se propageant au cœur de l'îlot) génère une multitude de structures (voir dans le Chapitre 3) au sein des îlots.

Spécifiquement, les résultats de cette thèse suggèrent plusieurs scénarios possibles de la dynamique post-perturbation des îlots résiduels après feu et après coupe en absence de nouveau feu ou coupe, en pessière à mousses de l'ouest du Québec. Ces scénarios peuvent être résumés ainsi :

1. Si la perturbation (feu ou coupe) survient lorsque la forêt est encore jeune, il n'y aurait ni d'effet de lisière sur l'îlot résiduel, ni de modification de sa dynamique de maturation naturelle (Figure 5.1). Donc la dynamique post-perturbation de l'îlot résiduel suivra le processus naturel de maturation et de succession des peuplements de pessière noire.

2. Si la perturbation survient dans de la forêt mature et fermée et que la lisière est moins franche en raison par exemple, d'une zone environnante partiellement perturbée, l'effet de lisière sur la dynamique de structure de l'îlot serait moindre et se stabilisera au fil du temps (Figure 5.1).

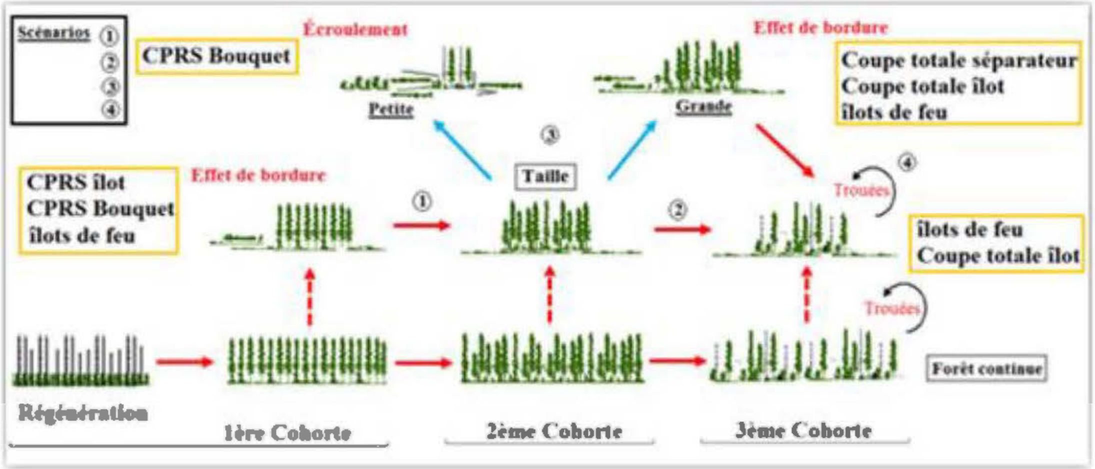

Figure 5.1 Les scénarios possibles de la dynamique post-perturbation de structure d'îlots résiduels de feu et de rétentions de coupe en absence de nouveau feu ou coupe en pessière à mousses perturbée de l'ouest du Québec. À partir des différentes forêts de maturation naturelle des peuplements proposée par Bergeron et Le Goff, (2005).

3. Si la perturbation survient dans de la forêt mature et fermée et que la lisière d'îlot résiduel est franche, l'effet de lisière sur l'îlot résiduel dépendra de sa taille. Si l'îlot est suffisamment grand, la dynamique spatiale se stabilisera au fil du temps, c.-à-d., l'effet de lisière sur l'îlot s'estompe avant d'atteindre sa forêt intérieure. Si en revanche l'îlot est petit, l'effet de lisière se propagera jusqu'au cœur de l'ilot, ce qui provoquera à court ou moyen terme, son écroulement (Figure 5.1).

4. Enfin, si la perturbation survient dans de la vieille forêt irrégulière et ouverte, l'îlot résiduel, qu'il soit issu de feu ou de coupe, aura peu d'effet de lisière et donc peu de modification de la dynamique naturelle de maturation des îlots résiduels post feu et post-coupe (Figure 5.1).

5.1 Implications pour la gestion de la conservation des forêts

Les connaissances qui ressortent des implications de résultats énoncées dans chaque chapitre et de la conclusion générale peuvent être résumées ainsi :

- Les trois chapitres de la présente thèse, mettent l'accent sur l'importance des conditions initiales de rétention sylvicole dans le maintien de sa dynamique de maturation et de succession forestière après coupe et dans l'atténuation de sa dynamique spatiale (effets lisières).

- Les rétentions sélectionnées dans de jeunes forêts peu volumétriques (ouvertes) et dépourvues de grosses tiges seront peu vulnérables aux effets de lisière et au chablis, mais, à court ou moyen terme, leur production de gros bois mort serait limitée à cause de l'absence de gros bois vivants et sénescents.

- Les rétentions sélectionnées dans des forêts volumétriques à structure diamétrale irrégulière (tiges de tous les diamètres) permettrait d'augmenter la durée de vie des rétentions (affaiblissant le risque de l'effet de lisière sur les habitats intérieurs) tout en continuant de produire du bois mort de façon soutenable.

- Du point de vue fonctionnel, si un habitat de qualité est une forêt fermée incluant de gros arbres vivants, sénescent et du bois mort récent, pour garantir cet approvisionnement, il faudrait d'une part, une bonne dynamique de recrutement qui soit en équilibre avec la dynamique de mortalité. D'autre part, il faudrait une parcelle de rétention suffisamment large permettant de réduire le risque d'effet de lisière sur la forêt d'intérieure.

En tenant compte de nos recommandations en matière de taille et de type de structure de peuplement à avantager lors de la rétention forestière, la gestion écosystémique de l'industrie forestière va se faire dans le respect de la certification *Forest Stewardship Council* (*FSC*), notamment, en matière de maintien du bois mort après coupe et de conservation de la variabilité d'habitats de qualité pour les espèces forestières. Finalement en documentant la dynamique des îlots résiduels laissés par le feu en foresterie boréale, cette thèse soutient qu'en plus d'avoir un impact positif sur la biodiversité, les recommandations contribueraient à l'industrie de manière à rester compétitive et viable surtout par l'acceptabilité sociale.

5.2 Limites et perspectives

Étant donné la grandeur de la forêt boréale et la diversité écologique et biologique qu'elle procure, les résultats de cette présente étude sont loin d'être suffisants. Bien qu'une placette d'échantillonnage de 400 m^2 soit jugée représentative pour l'étude d'un peuplement forestier au Canada, comparer un petit bouquet à un grand îlot d'un hectare ou plus en se basant seulement sur une seule placette d'échantillonnage reste une limite de la présente étude. Une autre limite de cette étude peut être le fait que les différents îlots résiduels et de rétention n'appartiennent pas au même massif forestier. Le cas idéal aurait été d'étudier dans un même massif forestier, des îlots de feu et de coupe et la forêt continue. Enfin, la dernière limite c'est le fait d'étudier juste des jeunes bouquets (moins de 10 ans) sans les vieux (de plus de 20 ans) ; ou alors des vieux îlots à orignaux sans les jeunes. Un suivi dans le temps des îlots résiduels post-perturbation échantillonnés permettrait de valider les présents résultats. Une étude de d'autres îlots résiduels de feu et de coupe ayant les mêmes conditions initiales permettrait aussi de valider les conclusions de ce thèse. D'autres recherches s'avèrent intéressantes également en vue d'étudier le rôle fonctionnel de cette variété de types structuraux après feu et après coupe dans la conservation des espèces, telles que les travaux actuels de mes collègues, Marion Barbé, Joëlle Castanguey et Émilie Chavel associés à ce même projet de thèse. Ces travaux de recherche complémentaires portent sur le rôle des îlots résiduels après feu et après coupe dans la dynamique des communautés bryophytiques et des petits mammifères en pessière noire à mousses du Québec.

Par ailleurs, bien qu'il soit utile de caractériser les structures des îlots résiduels issus de feux comme support essentiel à la biodiversité, l'objectif de la rétention verte vise surtout à minimiser le prélèvement fait dans la matrice aménagée. En ce sens, les caractéristiques des îlots résiduels post-feu répondent bien à un objectif de maintenir des refuges biologiques à l'échelle du paysage aménagé, mais, non pas à tous les objectifs visés par la rétention verte. Il serait donc interessant de faire le lien avec la configuration spatiale de ces îlots à savoir le nombre d'îlots par parterre de coupe et leur disposition, qui sont des aspects essentiels en aménagement forestier, mais qui ne sont pas directement pris en compte dans cette thèse.

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