

Intégration de la caractérisation de la sévérité du feu dans les outils d'aménagement écosystémique en forêt boréale

Thèse

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Intégration de la caractérisation de la sévérité du feu dans les outils d'aménagement écosystémique en forêt boréale

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Résumé

Chaque année en forêt boréale, les feux génèrent de grandes quantités d'arbres morts au Québec. Considérés comme une perte de revenu potentiel pour l'économie, le gouvernement demande qu'une partie de ces arbres soit récupérée. C'est d'ailleurs une pratique connaissant une tendance à la hausse au niveau mondial. Par contre, la récupération de ce bois est régie par diverses contraintes, dont la rentabilité des opérations et le respect des normes d'aménagement forestier écosystémique (AFE) visant la conservation de la biodiversité associée aux forêts brûlées. La mise en application de l'AFE nécessite de connaître l'impact du feu sur la forêt et ce de façon spatialement explicite. Dans cette optique, nous avons d'abord évalué la sévérité du feu sur le terrain dans 60 sites d'études répartis à travers cinq brûlis. Nous avons ensuite évalué le potentiel du « differenced Normalized Burn Ratio » (dNBR), une méthode de télédétection développée par des chercheurs américains pour estimer la sévérité du feu, à offrir une représentation fidèle des conditions de terrain. Les résultats positifs de cette étape nous ont permis de considérer le dNBR pour bonifier les outils d'aménagement utilisés en forêts brûlées. Du point de vue de la rentabilité de la récupération, nous avons utilisé le dNBR pour prédire la densité des attaques de Monochamus spp. (Coleoptera: Cerambycidae), qui constituent une source importante de dégradation de la qualité du bois et incidemment de sa valeur. Les connaissances acquises sur l'écologie des Monochamus spp. et les modèles établis permettent de prédire les niveaux d'attaques de ces insectes en fonction de l'essence, du diamètre des tiges et de la sévérité du feu (dNBR). Ensuite, suivant le cadre de l'AFE, nous avons cherché à identifier les forêts à haute valeur de conservation pour la biodiversité, en utilisant les coléoptères saproxyliques comme groupe indicateur, et les variables clés que sont l'essence, la dimension des arbres et la sévérité du feu (dNBR). Cela nous a permis d'identifier six groupes d'espèces écologiquement liées, desquels nous avons identifié trois groupes ayant un fort lien avec l'habitat brûlé. Puisque ces trois groupes contiennent des espèces associées aux brûlis et qu'elles sont liées à des habitats prisés par la récupération, comme le pin gris et les tiges de gros diamètres, ces espèces pourraient être négativement affectées par la récupération. Les résultats de nos travaux, grâce à l'utilisation d'un indicateur spectral de la sévérité du feu (dNBR) dans les outils d'aménagement, rendront possible l'optimisation de la récupération après feu, tant des points de vue économique que de la conservation, et ce dans le respect de l'AFE.

Abstract

Each year in the boreal forest, wildfires generate large amounts of dead trees in Quebec. Considered a potential loss of revenue for the economy, the government asks that a part of those trees is salvaged. This is also a practice experiencing a rising trend worldwide. On the other hand, post-fire salvage logging is governed by various constraints, concerning both the profitability of operations and compliance with the standards of the forest ecosystem management (FEM) aiming at conserving the biodiversity associated with burned forests. The implementation of FEM requires knowledge on the impact that fire has on the forest in a spatially explicit manner. In this light, we first evaluated on site burn severity for 60 study sites distributed accross 5 burns. We then assessed the ability of the differenced Normalized Burn Ratio (dNBR), a remote sensing method developed by US researchers to estimate burn severity, at providing an accurate representation of the terrain conditions. The positive results of this step allowed us to consider the dNBR improve management tools of burned forests. From the viewpoint of the profitability of salvage logging, we then evaluated the density of Monochamus spp. (Coleoptera: Cerambycidae) attacks, which constitute an important source of quality degradation of wood and incidentally their value. The knowledge acquired on the ecology of Monochamus spp. and established models predict the levels of these insects attacks based on tree species, stem diameter and burn severity (dNBR). Thirdly, following part of the FEM, we sought to identify high conservation value stands for biodiversity, using saproxylic beetles as an indicator group, and key variables that are tree species and diameter, as well as burn severity (dNBR). This allowed us to identify six groups of ecologically related species, of which, we identified three groups having a strong association with the burned habitat. Since these three groups contain species associated to burns, that are linked to habitats often salvaged such as jack pine and large diameters, they may be adversely affected by salvage logging. The results of our work, by using a spectral index of burn severity (dNBR) in management tools, make possible the optimization of post-fire salvage logging, from both the economic and conservation points of view, in compliance with the FEM.

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Liste des abréviations et des sigles

- AFE : Aménagement Forestier Écosystémique; FEM: Forest Ecosystem Management
- CBI : Composite Burn Index
- CFL : Centre de foresterie des Laurentides
- CIFQ : Conseil de l'Industrie Forestière du Québec
- DHP : Diamètre à Hauteur de Poitrine (1,3 m de la plus haute racine); DBH : Diameter at Breast Height
- dNBR : differenced Normalized Burn Ratio
- ÉcoDIF : Laboratoire de recherche sur l'Écologie et la Diversité des Insectes Forestiers
- EN: Épinette noire; BS: Black spruce
- FHVC: Forêts à Haute Valeur de Conservation; HCVFs: High Conservation Value Forests
- FQRNT : Fonds Québécois de la Recherche sur la Nature et les Technologies
- GAM : Generalized Additive Model
- GLMM : Generalized Linear Mixed Model
- iFor : Consortium de recherche sur les insectes forestiers
- MFFP : Ministère des Forêts, de la Faune et des Parcs du Québec
- NIR : Near Infrared
- NSERC-CRSNG : Conseil de recherches en sciences naturelles et en génie du Canada
- PAR : Programme des adjoints de recherche
- PG : Pin gris; JP : Jack pine
- RNCan : Ressources Naturelles Canada; NRCan : Natural Resources Canada
- RS : Remote Sensing
- SCF : Service canadien des forêts
- SOPFEU : Société de Protection des Forêts contre le Feu
- SOPFIM : Société de Protection des Forêts contre les Insectes et les Maladies du Québec
- SWIR : Shortwave Infrared
- UQAC : Université du Québec à Chicoutimi
- USGS-EROS : United States Geological Survey and The Earth Resources Observation Systems

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En 2011, en plus de me lancer dans l'aventure du doctorat, j'ai aussi entamé l'odyssée de la restauration d'une maison ancestrale à la campagne. Bien que passionnant et motivant, la route de ces aventures fut truffée de plusieurs embûches. Je garde donc une mention spéciale pour mes amis avec lesquels je peux m'évader à travers multiples activités sportives et soupers arrosés, et garder un bel équilibre entre travail et loisirs. Merci aussi à ma famille, ma sœur et mon beau-frère ainsi que leurs enfants qui sont une grande source de support et de bonheur, et bien sûr à mes parents qui sont toujours disponibles et que j'adore. Un merci spécial à mon père qui est toujours très motivé à embarquer dans tous mes projets! Finalement, merci à ma copine, Sonia, qui m'a supporté à travers toutes mes aventures depuis près de neuf ans, je t'aime!

Avant-propos

Le sujet, la structure et les objectifs de cette thèse proviennent directement du cru de l'étudiant, qui en a vendu l'idée premièrement à son co-directeur et ensuite à son directeur, qui ont accepté la proposition avec enthousiasme. Malgré tout, les idées menant à la réalisation de ce projet de doctorat ont découlées de nombreuses discussions avec Jacques Ibarzabal (directeur de maîtrise à l'UQAC), Christian Hébert et les membres du laboratoire d'ÉcoDIF, ainsi que des nombreuses lectures et rencontres que l'étudiant a fait lors de sa maîtrise. Cette thèse a comme objectif principal d'acquérir des nouvelles informations menant à la mise en place d'outils qui permettront d'améliorer l'aménagement des forêts brûlées selon une approche écosystémique. La thèse est constituée de trois chapitres tous rédigés sous la forme d'articles scientifiques en anglais, dans le but qu'ils soient soumis pour publication. Les chapitres retrouvés dans cet ouvrage sont :

Chapitre I – Boucher, J., Beaudoin, A., Hébert, C., Guindon, L., et E. Bauce. Assessing the potential of the differenced normalized burn ratio (dNBR) for estimating burn severity in eastern Canadian boreal forests. L'article a été soumis à International Journal of Wildland Fire.

Chapitre II – Boucher, J., Hébert, C., et E. Bauce. *Predicting post-fire* Monochamus *spp. attacks in black spruce and jack pine forests*. L'article a été soumis au *Canadian Journal of Forest Research*.

Chapitre III – Boucher, J., Hébert, C., Ibarzabal, J., et E. Bauce. *High conservation value forests for burn-associated saproxylic beetles: an approach for developing sustainable postfire salvage logging in boreal forest.* L'article a été soumis à *Insect Conservation and Diversity.*

Le design des dispositifs expérimentaux des chapitres et leur mise en place sur le terrain, ainsi que les diverses prises de mesures et inventaires terrains ont été entièrement dirigés et exécutés par l'étudiant, qui a bien sûr été aidé d'étudiants sur le terrain et au laboratoire. Cette thèse, dont ses trois chapitres, ont été rédigés en entier par le candidat au doctorat, qui a aussi fait les revues de littérature, les analyses statistiques et l'interprétation des résultats, ainsi que la mise en forme des tableaux et figures. Le directeur Éric Bauce s'est principalement impliqué au niveau de l'encadrement général du projet et à travers commentaires et critiques des chapitres, et en est ainsi co-auteur. Christian Hébert, codirecteur de recherche, a été très engagé dans plusieurs discussions entourant les objectifs et l'interprétation des résultats des trois chapitres, ainsi qu'au niveau de leurs révisions via commentaires et critiques. Il est donc aussi co-auteur des trois chapitres. André Beaudoin, chercheur scientifique en télédétection et modélisation spatiale au SCF-RNCan, s'est quant à lui impliqué au niveau des discussions entourant le Chapitre I et dans la révision de sa structure, et de ce fait en est second auteur. Luc Guindon, spécialiste en SIG, base de données et télédétection au SCF-RNCan, a contribué au Chapitre I par ses commentaires et critiques éclairantes, ainsi que par ses conseils judicieux en géomatique. Il est ainsi quatrième auteur de ce chapitre. Jacques Ibarzabal, professeur à l'UQAC et ancien directeur de maîtrise de l'étudiant, a été impliqué dans les premières discussions entourant le projet de doctorat, et a participé au troisième chapitre en apportant ses commentaires et critiques. Il est de ce fait troisième auteur du Chapitre III.

Les résultats des Chapitres II et III ont été présentés à l'occasion des congrès suivants :

Chapitre II :

- J. Boucher, É. Bauce, C. Hébert, J. Ibarzabal. *Predicting Longhorn beetle related postfire damage. Au Northeastern Forest Pest Council – 76th Annual Meeting: Promoting understanding and collaboration in forest health.* Québec, Québec, Canada. Mars 2014.
- J. Boucher, É. Bauce, C. Hébert, J. Ibarzabal. Où les longicornes font-ils le plus de dégâts après un feu? À la 140^e réunion annuelle de la Société d'entomologie du Québec (SEQ) ; Le langage intime des insectes. Ste-Adèle, Québec, Canada. Novembre 2013

Chapitre III :

 J. Boucher, É. Bauce, C. Hébert. Répartition de la diversité entomologique associée aux brûlis. À la 141^e réunion annuelle de la Société d'entomologie du Québec (SEQ) ; Les insectes dans le paysage. Wendake, Québec, Canada. Novembre 2014.

INTRODUCTION GÉNÉRALE

I. Impacts des feux et caractérisation de la sévérité

Certains indices géologiques, tels des fossiles de plantes carbonisées, montrent que le feu aurait rapidement suivi l'apparition des plantes au cours de l'histoire de la vie terrestre, ce qui suggère qu'il ait eu un impact important sur l'évolution des biomes (Bowman et al. 2009; Glasspool et al. 2004; Scott et Glasspool 2006). Au niveau mondial, le feu a donc joué un rôle majeur sur la biogéographie du paysage et sur les fonctions des écosystèmes (Pausas et Keeley 2009). Ce processus naturel influence toujours les patrons et processus globaux des écosystèmes, incluant les processus de restauration et de succession écologiques, la répartition et la structure de la végétation, la production de biomasse, les cycles géochimiques, le climat et la biodiversité (Bourgeau-Chavez et al. 2002; Bowman et al. 2009; Lentile et al. 2006; McCullough et al. 1998; Weber et Flannigan 1997). Le feu entraîne ainsi la formation de nouveaux habitats, allant de l'échelle du micro-habitat jusqu'à celle du paysage (Kennedy et Fontaine 2009). En milieu forestier, ces habitats sont principalement caractérisés par une grande quantité d'arbres morts sur pied produit en une courte période de temps, par des peuplements ouverts avec un sol plus chaud, par la présence de sol minéral exposé, et au fil du temps, par une augmentation du couvert arbustif (Nappi et al. 2004; Wikars 1992).

1. Terminologie reliée au feu

Le « **feu** » est la manifestation de la réaction chimique de combustion nécessitant trois éléments soient l'oxygène, une source de chaleur et un combustible. Le « **brûlis** » est quant à lui le terme utilisé afin de définir le milieu résultant du passage du feu en forêt. L'« **intensité du feu** » réfère à la vitesse à laquelle le feu produit de l'énergie thermique, ce concept est toujours exprimé en termes de chaleur (calories) ou de puissance (watts) (Chandler *et al.* 1983). La mesure la plus commune et la plus utile de l'intensité du feu est « **l'intensité à la ligne de feu** », qui est équivalente à la quantité de chaleur émise par unité de longueur de la ligne de feu et par unité de temps (Chandler *et al.* 1983). Elle est habituellement exprimée en kW/m à partir de la hauteur des flammes (Chandler *et al.* 1983). L'intensité du feu est essentiellement fonction des caractéristiques des combustibles

et des conditions topographiques et météorologiques (Hall *et al.* 1980). La « sévérité du feu » découle autant des caractéristiques du feu lors de son passage, que de ses effets immédiats sur l'environnement local après feu (Key et Benson 2002). Bien que la sévérité du feu découle souvent de l'intensité du feu (Key et Benson 2006; van Wagtendonk *et al.* 2004), il faut savoir qu'elle n'y est pas toujours corrélée (Miller et Yool 2002; Neary *et al.* 1999). Les caractéristiques du feu qui ont un effet sur la sévérité du feu sont par exemple le comportement du feu, qui joue un rôle important sur l'hétérogénéité verticale et horizontale de l'effet du feu, et la durée du feu, qui quant à elle détermine la quantité de chaleur transférée au sol (Lentile *et al.* 2006). Les effets immédiats du feu sont, par exemple, l'altération au niveau du sol comme l'épaisseur de matière organique brûlée, la quantité de végétation consumée, ainsi que la mortalité engendrée (Lentile *et al.* 2006). C'est l'ensemble des différents degrés de changements engendrés par le passage du feu, tant sur la couverture organique du sol que sur la végétation, qui définissent la sévérité du feu (Key et Benson 2006; Lentile *et al.* 2006). La sévérité du feu est un attribut qui doit être évalué après le passage du feu.

Dans la littérature, il existe beaucoup de confusion entre l'intensité du feu et la sévérité du feu, ces termes ont souvent été utilisés de manière interchangeable, et ce parfois dans un même document (Lentile *et al.* 2006). Il est donc important de garder en tête les définitions présentées ici. Une autre source de confusion dans la terminologie reliée au feu se retrouve au niveau des termes anglophones *« fire severity »* et *« burn severity »*. Ces deux termes se différencient, dans la littérature anglophone, du fait que la sévérité du feu réfère habituellement aux effets immédiats du feu, alors que *« burn severity »* se rapporte aux effets à court- et long-termes du feu sur l'écosystème (Lentile *et al.* 2006). Il est à noter qu'à notre connaissance, il n'existe pas de différenciation entre ces termes dans la littérature francophone. Dans le but de réduire toute confusion, nous utiliserons ici les termes *« sévérité du feu », et « burn severity »* dans la section anglaise, afin de référer à l'impact qu'a eu le feu sur le milieu, et ce pour toutes les strates verticales du milieu soit du sol à la cime des arbres. Cependant, nous préciserons à quel moment après feu notre évaluation de la sévérité a été faite.

2. Caractérisation de la sévérité du feu

Les divers types de végétations affectés par des sévérités de feu différentes suivent subséquemment des trajectoires de rétablissement écologiques diverses (Weber et Stocks 1998). Ces trajectoires se manifestent à travers des modifications dans la composition et dans la structure d'âge des espèces végétales, par des changements dans le recyclage des éléments nutritifs, dans la productivité de l'habitat et dans la biodiversité (Volney et Hirsch 2005). Puisque la sévérité est le reflet des changements physiques découlant de l'action du feu et qu'elle influence grandement les processus écologiques, les décisions d'aménagement forestier après feu devraient considérer la sévérité du feu comme une variable clé (Lentile et al. 2006). Pour les aménagistes forestiers, la quantification et la cartographie de la sévérité du feu sont d'ailleurs devenus des enjeux de premier plan, puisqu'elles permettent d'avoir une meilleure évaluation de la répartition spatiale des dommages causés par le feu à la végétation (Lindenmayer et al. 2008). Cela permet d'offrir un meilleur support à la planification des coupes de récupération et pour la remise en production des sites via le scarifiage et la plantation (Lindenmayer *et al.* 2008; Nappi *et al.* 2011). Certains auteurs (Kotliar et al. 2007; Smucker et al. 2005) ont d'ailleurs fortement argumenté sur l'importance d'inclure la sévérité du feu dans l'étude des réponses de la faune et de la flore au feu.

Pour des raisons pratiques, la sévérité du feu est souvent divisée en classes grossières allant de basse à élevée (Lentile *et al.* 2006; Miller et Thode 2007). La sévérité du feu a été par le passé une mesure plutôt subjective et sa classification a varié souvent en fonction des problématiques abordées, entre les diverses études ainsi qu'entre les organisations (Hutto 2006; Safford *et al.* 2008). Néanmoins, on sait que les symptômes biophysiques de la sévérité du feu varient de façon continue. Par exemple, pensons simplement au fait que l'on peut retrouver après feu toute une gamme de variabilité entre des peuplements d'arbres vivants contenant quelques arbres morts et des peuplements avec 100% de mortalité des arbres (Kennedy et Fontaine 2009). Cela a poussé Jain *et al.* (2004) à recommander que la quantification et la cartographie de la sévérité du feu soient faites en utilisant une variable continue plutôt que sous la forme de classes. Il a d'ailleurs été établi, lors du colloque « Les insectes et le feu » tenu en février 2010 au Centre de foresterie des Laurentides (CFL) du

Service canadien des forêts (SCF), qu'il y avait un besoin criant de définir une classification efficace et commune de la sévérité du feu au Canada, tant pour des besoins de recherche que de gestion.

Dans un contexte où l'on désire modéliser la sévérité du feu sur l'ensemble des territoires affectés par les incendies forestiers et que plusieurs brûlis sont à toutes fins pratiques inaccessibles, la télédétection s'avère un outil efficace (Wulder *et al.* 2009). Ainsi, depuis le milieu des années 80, plusieurs techniques de télédétection ont été développées afin d'évaluer le degré de changement écologique suite au feu (Lentile *et al.* 2006). Cet intérêt à cartographier et à quantifier la sévérité à l'aide de la télédétection est encore plus évident dans la littérature récente (Allen et Sorbel 2008; Cocke *et al.* 2005; De Santis et Chuvieco 2007; Epting *et al.* 2005; French *et al.* 2008; Hall *et al.* 2008; Key et Benson 2006; Lentile *et al.* 2011; Miller et Thode 2007; Miller et Yool 2002; Parks *et al.* 2014; Roy *et al.* 2006). Les changements dans la réflectance spectrale de la végétation suite au brûlage, qui sont captés par les différents satellites, ont permis l'établissement de divers indices (Lentile *et al.* 2006). Ainsi, des techniques de télédétection permettant d'évaluer et de suivre les changements reliés aux incendies forestiers dans le paysage, de façon rapide et rentable, sont maintenant disponibles (Lentile *et al.* 2006).

Parmi ceux-ci, le plus populaire est le « differenced Normalized Burn Ratio » (dNBR), qui est systématiquement utilisé aux États-Unis pour cartographier la sévérité des feux (Cocke *et al.* 2005; Eidenshink *et al.* 2007). Le dNBR est obtenu en calculant d'abord le « Normalized Burn Ratio » (NBR) avant et après feu à partir des portions NIR (« near infrared ») et SWIR (« shortwave infrared ») du spectre capté par les satellites Landsat (équation 1). Le dNBR est ensuite déterminé en faisant la différence entre le NBR provenant d'images avant et après feu (équation 2; pour détails voir: Key et Benson 2006). Après feu, la réflectance NIR diminue à cause des dommages causés au feuillage ou à sa consumation, tandis que la réflectance SWIR augmente en raison d'une réduction d'ombre et d'humidité dans la canopée (van Wagtendonk *et al.* 2004). Les valeurs de sévérité estimées par le dNBR résultent en un gradient numérique continu, facilitant la comparaison entre différents feux, mais pouvant aussi être potentiellement fractionné en « classes » de

sévérité (exemple : légère, modérée, élevée) selon les besoins de gestion (Lentile *et al.* 2006).

$$NBR = (NIR - SWIR) / (NIR + SWIR) \quad (1)$$

$$dNBR = NBR_{avant-feu} - NBR_{après-feu}$$
 (2)

L'efficacité d'une telle technique réside bien sûr dans sa capacité à représenter la réalité terrain de l'impact du feu sur le milieu. Ainsi, Key et Benson (2006) ont développé le « Composite Burn Index » (CBI), un index obtenu à partir d'une évaluation terrain de la sévérité du feu. Le CBI est établi en évaluant le taux de survie de la végétation et le pourcentage de consumation de celle-ci, des débris ligneux au sol, de l'humus et de la matière organique (Key et Benson 2006). Key et Benson (2006) ont choisi les attributs à évaluer en fonction des changements spectraux captés par les bandes NIR et SWIR des images Landsat. Une fois la grille d'évaluation terrain complétée, nous obtenons une valeur de CBI représentée de facon numérique continue et variant de 0 à 3. Les valeurs de CBI peuvent ensuite être mises en relation avec les valeurs de dNBR, afin de vérifier la capacité du dNBR à refléter la réalité terrain (Key et Benson 2006). Une fois la relation CBI-dNBR bien établie pour une région donnée, il est possible de l'utiliser pour réduire les investigations terrain lors de nouveaux incendies, et ainsi diminuer le temps d'élaboration de la cartographie de la sévérité pour les zones affectées par la perturbation. On peut ainsi diminuer les délais d'établissement des plans de récupération, un enjeu clé après un feu de forêt (Nappi et al. 2011).

Dans l'optique de définir une classification efficace et commune de la sévérité du feu au Canada, certains chercheurs (Hall *et al.* 2008; Soverel *et al.* 2010; Wulder *et al.* 2009) se sont penchés sur la relation CBI-dNBR dans les forêts de l'Ouest canadien. Ces travaux ont permis d'établir, pour les régions étudiées, que le dNBR offrait un reflet fidèle de la réalité terrain. Toutefois, aucune relation statistique n'a été investiguée jusqu'à présent dans les forêts de l'Est du Canada, où les feux sont pourtant relativement fréquents, particulièrement en régions boréales (Bergeron *et al.* 2004a; Bergeron *et al.* 2004b; Girardin *et al.* 2010).

3. Avantages et désavantages du « differenced normalized burn ratio »

Les satellites Landsat sont parmi les rares à offrir les longueurs d'ondes SWIR et ont l'avantage, contrairement à bien d'autres produits, d'être offerts gratuitement via le U.S. Geological Survey Earth Resources Observation and Science Center (USGS - EROS). De plus, le USGS-EROS rend maintenant disponible leurs images orthorectifiées en réflectance de surface à travers le Landsat Ecosystem Disturbance Adaptative Processing System (LEDAPS). Ces images ont l'avantage d'être directement utilisables et comparables entre elles, spatialement et temporellement. En plus, elles incluent un masque pour les nuages et leur ombre. Depuis une trentaine d'années, Landsat a mis en orbite plusieurs satellites offrant des bandes NIR et SWIR, soient : Landsat 4TM (opérationnel de juillet 1982 à décembre 1993), Landsat 5TM (opérationnel de mars 1984 à janvier 2013), Landsat 7ETM+ (opérationnel depuis avril 1999), et Landsat 8OLI (opérationnel depuis février 2013). Le large éventail d'images archivées facilite d'ailleurs l'utilisation d'un indice multi-temporel comme le dNBR. Malgré les aspects positifs du dNBR, il faut être conscient que son utilisation comporte aussi certains désavantages. En effet, les nouvelles générations de satellites offrent une meilleure résolution spatiale et temporelle, qui sont idéales pour la cartographie écologique fine (Arnett et al. 2015). En fait, la résolution de pixel de 30 m des satellites Landsat est maintenant surpassée par plusieurs autres satellites pouvant avoir une résolution de l'ordre de 5 m pour RapidEye, ou même de 2.4 m pour Quickbird par exemple. Par ailleurs, Landsat n'offre la couverture du territoire qu'une fois tous les huit jours. C'est-à-dire que lors de son passage, si les conditions atmosphériques ne permettent pas l'acquisition d'une image de qualité suffisante, on devra attendre au prochain cycle. Or, certains satellites peuvent maintenant offrir une nouvelle couverture d'un territoire donné chaque jour (Arnett et al. 2015). Ainsi, avec Landsat, il faut parfois patienter quelques semaines, voire des mois, avant de produire une cartographie de la sévérité du feu. Cette situation se produit d'ailleurs régulièrement en zone nordique où la couverture nuageuse en saison de feu est fréquente.

En revanche, une telle méthode a fait ses preuves au niveau mondial et peut s'avérer fort utile dans le cadre de comparaisons internationales et de suivis historiques des feux et de leur sévérité, ainsi que pour la production de bilans de carbone (Arnett *et al.* 2015; Sommers *et al.* 2014). De telles utilisations peuvent être possibles, puisque les archives Landsat utilisables pour le calcul du dNBR remontent à 1982. Le dNBR peut aussi être utile dans le cadre de travaux à moyen et long-terme, soit pour la planification de la remise en production des sites, mais aussi dans un contexte de récupération du bois à des fins de production de bioénergie (Lindenmayer *et al.* 2008; Nappi *et al.* 2011). Il est d'ailleurs maintenant connu que la sévérité du feu est une variable importante pour expliquer la répartition spatiale de certains insectes nuisibles ou même d'espèces menacées (Azeria *et al.* 2012; Azeria *et al.* 2011; Boulanger *et al.* 2010, 2013; Kotliar *et al.* 2007; Smucker *et al.* 2005).

II. Aménagement des forêts brûlées

1. Contexte boréal canadien

Au Canada, environ 4 millions ha de forêt ont brûlé en moyenne chaque année au cours des dix dernières années (RNCAN 2014). Les feux entrent souvent en conflit avec l'aménagement forestier, puisque ce dernier ne tient pas compte du risque d'incendie lors des calculs de possibilités forestières (Schmiegelow et al. 2006). Ainsi, lorsque du bois à valeur commerciale brûle, la coupe de récupération est généralement utilisée afin de réduire les pertes financières causées par la mort des arbres (Schroeder et al. 2012). Le bois récupéré est généralement destiné à produire du bois de charpente, du papier et de plus en plus considéré en tant que source de bioénergie (Nappi et al. 2011). La coupe de récupération après feu est facilitée par le développement du réseau routier forestier, qui améliore l'accessibilité aux brûlis (Nappi et al. 2004; Schmiegelow et al. 2006) et par les progrès technologiques dans les usines de transformation, permettant d'utiliser le bois brûlé de plus en plus efficacement (Saint-Germain et Greene 2009). Cependant, cette pratique soulève certaines inquiétudes au niveau de la conservation, car elle entraîne une diminution de la disponibilité en habitats brûlés (Dellasala et al. 2006; Lindenmayer et al. 2008). Elle soulève d'ailleurs certaines autres problématiques économiques en lien avec la dégradation du bois après feu (Saint-Germain et Greene 2009).

2. Cadre normatif de l'aménagement des forêts brûlées

Suite à l'adoption du concept d'aménagement durable des forêts par le gouvernement du Canada en 1992, le Conseil canadien des ministres des forêts (CCMF) a identifié l'aménagement écosystémique comme une approche pertinente afin de mettre en application ce concept (CCMF 2003). L'aménagement écosystémique suggère que le maintien des processus et interactions écologiques sont nécessaires pour conserver la composition, la structure et les fonctions de l'écosystème sous aménagement (Coulombe *et al.* 2004). Certaines provinces canadiennes, comme l'Alberta, l'Ontario et la Saskatchewan, ont inclus, dans leur loi sur les forêts, des directives d'aménagement quant à la récupération après feu, dans le but de minimiser les impacts de la coupe de récupération (Saint-Germain et Greene 2009).

En 2010, le Québec a emboîté le pas suite à la mise en application de la récente loi québécoise sur l'aménagement durable du territoire forestier. Cette loi prévoit que la forêt publique soit aménagée sur les bases de l'aménagement forestier écosystémique (AFE). L'AFE vise à diminuer les écarts entre la forêt aménagée et la forêt naturelle afin d'assurer le maintien de la biodiversité et des multiples fonctions des écosystèmes, ainsi que leurs bénéfices sociaux-économiques (Gauthier *et al.* 2008). Ce n'est qu'à l'été 2010 que les premiers plans de récupération à saveur écosystémique ont été mis en branle officiellement. Ceux-ci ont été établis à partir de l'expérience acquise lors d'un projet pilote dans le brûlis de l'Île René-Levasseur en 2006, ainsi qu'à partir des recommandations parues dans le document de Nappi *et al.* (2011) intitulé « La récolte dans les forêts brûlées : Enjeux et orientations pour un aménagement écosystémique ». Les grandes lignes de ces orientations sont : la conservation des îlots verts non-brûlés et la conservation de 30% de la variabilité des peuplements résultant de l'incendie, dans le but de préserver la variabilité naturelle des habitats créés par le feu, de la biodiversité et des processus écologiques associés à cette perturbation naturelle.

3. Problématiques associées à la récupération

3.1. Problématique économique

Comme dans toute opération de récolte de matière ligneuse, l'accessibilité (routes, topographie, etc.) aux peuplements à récolter est une contrainte majeure. Cependant, dans un contexte post-feu, d'autres problématiques s'ajoutent. En effet, les tiges récemment brûlées ont un taux de dessiccation élevé, faisant en sorte qu'une forte proportion (environ 66% chez l'épinette noire) de celles-ci peuvent présentées du fendillement après quelques mois seulement (Nakamura et al. 2003). De plus, certains champignons de coloration et de carie colonisent ces tiges, contribuant au même titre que le fendillement à réduire la valeur marchande du bois récupéré (Saint-Germain et Greene 2009). Cependant, la problématique économique se présentant le plus rapidement après feux et entraînant la majeure partie des pertes économiques est la présence d'insectes xylophages, plus particulièrement les longicornes (Coleoptera :Cerambycidae) (Lowell et al. 1992; Raske 1972; Saint-Germain et Greene 2009). Le longicorne noir (Monochamus scutellatus scutellatus (Say)) est reconnu comme le longicorne causant le plus de dommages aux tiges récemment brûlées au Canada (Gardiner 1957). Des travaux récents sur les insectes après feu dans les forêts boréales de l'Est du Canada ont rapporté un autre Monochamus causant des dommages, soit Monochamus mutator LeConte (Azeria et al. 2012; Boucher et al. 2012). Cette espèce n'est retrouvée que sur les pins (Yanega 1996) et semble favoriser le pin gris (Gardiner 1957). C'est deux espèces de Monochamus sont connues pour agir de façon similaire, toutefois la biologie de *M. mutator* est plutôt inconnue puisque ses larves sont indiscernables de celles de M. s. scutellatus (Gardiner 1957). En effet, ces insectes peuvent se rendre sur le territoire brûlé dans les premières heures suivant l'extinction de flammes, où les adultes se reproduisent et où la femelle pond ses œufs sur le bois récemment mort (Bélanger 2013). Les œufs éclosent 9-14 jours plus tard (Peddle et al. 2002; Rose 1957) et les larves passent à travers quatre stades durant leur cycle vital, qui lui varie en durée selon la location géographique et les conditions environnementales. Globalement, le cycle vital de 75-90% des individus s'étend sur deux ans, tandis qu'il ne prend qu'un an pour les autres (Bélanger et al. 2013; Cerezke 1977). Les deux premiers stades larvaires de l'insecte se développent dans la région cambiale de l'arbre, alors que les larves de troisième et quatrième stade se développent dans le xylème où elles creusent une galerie. À la fin du quatrième stade, elles excavent une chambre pour y devenir pupe. Ce sont les galeries faites dans le xylème, atteignant parfois le cœur de la tige, qui représentent une problématique économique importante (Raske 1972; Saint-Germain *et al.* 2004; Vallentgoed 1991). Certains ont évalué que les pertes économiques reliées aux galeries pouvaient représenter 30% de la valeur marchande du bois (Cerezke et Volney 1995; Raske 1972; Raske et Safranyik 1970). Cependant, ces évaluations ont été faites sur des empilements de bois de pin, où les niveaux d'attaques des longicornes sont généralement plus bas qu'en forêt brûlée (données non-publiées). Plus récemment, certains ont même rapporté que la présence des trous causés par les galeries larvaires, ou « trous de vers », pouvait réduire de 60% la valeur du bois d'œuvre (NLGA 2014). Dans le contexte d'une faible valeur marchande du bois, de telles pertes compromettent la rentabilité des opérations de récupération. La réduction des pertes reliées à ces insectes est donc un enjeu de premier plan lors de la planification des activités de récupération.

3.2. Problématique écologique

Du point de vue de la conservation, il y a déjà plusieurs indications que la récupération après feu interfère avec le rétablissement de certains processus écologiques naturels (Lindenmayer et Ough 2006), et qu'elle a plusieurs impacts négatifs sur la flore (Greene et al. 2006) et la faune (Nappi et al. 2004). Parmi ces impacts, l'extraction de chicots de dimensions commerciales réduit les sources in situ de semences pour la régénération des arbres. La coupe de récupération réduit la rémanence moyenne des chicots résiduels, dû à la création d'ouvertures en forêts et à une réduction généralisée du diamètre moyen et de la densité des chicots (Russell et al. 2006). De surcroît, les ouvertures résultantes mènent à une réduction des lits de germination adéquats et des conditions de croissance pour les semis et les plantes de sous-étage, causés par une augmentation de la température du sol et de la dessiccation (Purdon et al. 2002). Cela tend à homogénéiser et à réduire le couvert et la diversité en espèces végétales (Purdon et al. 2002). En outre, la complexité structurale des peuplements est altérée progressivement avec l'extraction des chicots et des tiges vivantes résiduelles (Lindenmayer et al. 2008). En termes d'assemblages de plantes et d'animaux, la composition des peuplements forestiers est simplifiée puisqu'elle est modifiée progressivement avec le déclin ou la perte de groupes fonctionnels (Lindenmayer et Ough 2006).

Un des impacts directs de la récupération est que le retrait des tiges récemment mortes diminue proportionnellement la quantité d'habitats pour les organismes saproxyliques. Ces derniers sont définis comme des organismes dépendants, durant une partie de leur cycle vital, 1) du bois mort ou moribond (debout ou au sol) ; 2) de champignons du bois ou 3) de la présence d'autres organismes saproxyliques (Speight 1989). Les insectes saproxyliques jouent un rôle important dans la décomposition du bois et du recyclage des éléments (Boulanger et Sirois 2007; Speight 1989). Ils représentent aussi une part non-négligeable de la diète de plusieurs espèces vertébrées (Kennedy et Fontaine 2009; Morissette et al. 2002; Nappi et al. 2004; Purdon et al. 2002). Certaines espèces de coléoptères saproxyliques ont d'ailleurs été récemment identifiées comme étant « associées aux brûlis », c'est-à-dire qu'elles se retrouvent en plus grande abondance/incidence dans le bois récemment brûlé, que dans le bois récemment mort provenant d'une autre perturbation (Boucher et al. 2012). De plus, dans l'éventualité où de telles espèces saproxyliques associées aux brûlis seraient bien adaptées à la récurrence des feux avec laquelle elles ont évoluées (Boucher et al. 2012; McPeek et Holt 1992), la récupération après feu pourrait excéder leur résilience (Le Goff et al. 2008). Il a d'ailleurs été démontré qu'une réduction de la surface terrière causée par la récupération a un effet négatif sur certaines espèces de coléoptères saproxyliques associées aux brûlis (Boucher 2010). Dans la foulée de l'AFE, il devient important d'établir certains critères et seuils encadrant la récupération, tels que ceux proposés par Nappi et al. (2011). Pour ce faire, il nous faut améliorer notre compréhension des facteurs influençant la répartition de la diversité des coléoptères saproxyliques colonisant les tiges brûlées.

III. Contexte de l'étude et objectifs

Au cours de l'été 2010, la région de la Haute-Mauricie, dans la province de Québec au Canada, a été le théâtre de plusieurs incendies forestiers majeurs. En effet, sept grands feux y ont fait rage, brûlant près de 200 000 ha de forêt mixte et coniférienne. C'est d'ailleurs à la suite de ces incendies que les premiers plans de récupération à saveur écosystémique ont été mis en œuvre à grande échelle. Lors des opérations de récupération, plusieurs questions ont d'ailleurs été soulevées en rapport avec la colonisation par les longicornes, particulièrement pour le pin gris (*Pinus banksiana* Lamb. ; PIG) et l'épinette noire (*Picea mariana* (Mill.) BSP ; EPN). De par leur proximité aux grands centres urbains et la

diversité de leur composition forestière, les brûlis de la Haute-Mauricie sont un territoire de prédilection pour l'acquisition de connaissances sur l'aménagement et l'écologie des brûlis.

La mise en œuvre de l'AFE dans les forêts brûlées nécessite l'utilisation d'outils permettant de cartographier des attributs clés afin d'établir spatialement les plans d'aménagement. Les principaux outils spatiaux d'aménagement disponibles après feux pour la mise en place des plans de récupération sont les cartes écoforestières (qu'on lie aux tables de stock) et les cartes de sévérité du feu produites par le Ministère des Forêts, de la Faune et des Parcs du Québec (MFFP). Ces outils procurent de l'information très utile concernant la forêt avant feu et sur l'état des dommages causés par le feu. La variabilité de la composition forestière avant la perturbation couplée à la non-uniformité de la propagation du feu à travers un paysage forestier sont responsables en grande partie de la diversité du bois mort et de l'habitat brûlé. Par contre, ces outils ne procurent pas forcément une finesse spatiale et une précision suffisamment élevées quant à la cartographie d'attributs clés, comme la sévérité, qui est définie sous forme de classes. De plus, ces outils ne donnent pas d'indications quant aux dommages reliées aux galeries de longicornes, ni quant à la conservation de la diversité des organismes saproxyliques associés aux brûlis.

Cette thèse vise à bonifier les outils d'aménagement disponibles en proposant une approche de caractérisation de la sévérité du feu par télédétection, sous la forme d'un indice spectral continu, pouvant être adapté aux différentes problématiques d'aménagement après-feu. Cette caractérisation de la sévérité du feu sera utile pour produire des modèles de prédiction des attaques de *Monochamus* spp. ainsi qu'à la caractérisation d'habitats à haute valeur de conservation pour les coléoptères saproxyliques associés aux brûlis. Les modèles développés et les connaissances acquises ont pour but d'améliorer la rapidité d'intervention et de définir des modalités optimales de récupération en intégrant les dimensions économiques et environnementales associées aux forêts brûlées, le tout dans un cadre d'aménagement écosystémique. Les travaux de cette thèse ont été concentrés sur des peuplements dominés par l'EPN et le PIG, car ce sont les essences boréales les plus touchées par les incendies (Doucet et Côté 2009) et par la récupération dans la forêt boréale de l'est du Canada (Annexe 1).

Les cartes de sévérité produites par le MFFP catégorisent le territoire brûlé en quatre classes de sévérité (non-brûlé, affecté, roussi, et carbonisé) à partir d'images RapidEye et d'outils automatisés de classification et de segmentation. Le produit cartographique résultant procure une bonne représentation des conditions de terrain. Par contre, le fait que cette caractérisation soit sous la forme de classes peut être contraignant dans le cadre d'études écologiques. De plus, cette cartographie n'est offerte que pour la zone commerciale de la forêt québécoise par le MFFP, et que depuis 2010. Dans l'optique des recommandations de Jain *et al.* (2004), concernant l'utilisation d'un indice continu de sévérité du feu, et afin répondre au besoin d'une méthode de caractérisation de la sévérité commune pour l'ensemble du Canada, soulevé en 2010 au SCF, nous utiliserons l'indice spectral du dNBR et la méthode proposé par Key et Benson (2006). De cette façon, nos résultats seront plus facilement comparables et transférables à d'autres régions que celle à l'étude. Néanmoins, pour le Québec, il sera possible de classifier les valeurs de dNBR afin de produire une cartographie similaire à celle faite par le MFFP.

La caractérisation de la sévérité du feu sera traitée au début de la thèse, puisque cet attribut sera par la suite utilisé comme variable clé dans l'étude de l'étendu des dommages reliés au *Monochamus* spp., ainsi que dans l'identification des forêts à haute valeur de conservation (FHVC) pour les coléoptères saproxyliques associés aux brûlis. En conséquence, la thèse se divise en trois chapitres dont les titres et les objectifs spécifiques sont les suivants :

Chapitre I

<u>*Titre:*</u> «Assessing the potential of the differenced normalized burn ratio (dNBR) for estimating burn severity in eastern Canadian boreal forests»

<u>Objectifs:</u> Le but de ce chapitre est d'analyser la force de la relation entre l'évaluation de la sévérité du feu par télédétection en utilisant le dNBR et celle obtenue *in situ* à partir du « composite burn index » (CBI) pour les forêts boréales de l'Est du Canada. Cet exercice contribue à généraliser un modèle qui pourrait être appliqué dans toutes les forêts boréales canadiennes. L'étude porte sur des peuplements dominés soit par l'épinette noire (EPN) ou le pin gris (PIG).

Nous avons établi deux objectifs:

- 1. Modéliser la sévérité du feu :
 - En analysant les différences entre les valeurs moyennes du NBR, dNBR et du CBI entre l'EPN et le PIG, ainsi que les différences de valeurs de NBR entre les périodes temporelles (avant-feu et après-feu).
 - En établissant les meilleurs modèles statistiques de la relation CBI-dNBR, pour une région représentative de la forêt boréale de l'Est, dans des peuplements dominés par l'EPN ou le PIG, et en déterminant si ces modèles sont significativement différents entre les deux essences étudiées.
 - iii) En comparant les cartographies de nos meilleurs modèles régionaux, représentant la relation CBI-dNBR, à la cartographie de la sévérité du feu produite par le MFFP. Depuis 2010, le MFFP utilise une méthode différente de cartographie de la sévérité du feu par télédétection à partir d'images RapideEye segmentées (communication personnelle avec Antoine Leboeuf, responsable de la section imagerie et télédétection à la direction des inventaires forestiers au MFFP). L'obtention de cartes dérivées des valeurs de dNBR seuillées, comparables à la carte du MFFP serait utile pour caractériser la sévérité en dehors du territoire de la forêt commerciale couverte par le MFFP et pour des feux s'étant produits avant 2010 et ailleurs au Canada.

Pour ce premier objectif, nous avons utilisé le « initial assessment strategy » proposé par Key et Benson (2006), produisant des images dNBR à partir d'images après feu prises la même année que le feu. Cette stratégie est reconnue pour être particulièrement utile pour répondre à des besoins de cartographie rapide (Key et Benson 2006), dans le cadre de récupération après feu par exemple.

2. Notre deuxième objectif est de tester l'application potentielle du modèle « Saturated growth », précédemment développé par Hall *et al.* (2008) pour les forêts boréales de l'Ouest Canadien, aux forêts boréales de l'Est du Canada. Les travaux faits par Hall *et al.*(2008) utilisent le « extended assessment strategy », c'est-à-dire que les images dNBR sont obtenues à partir d'images après feu prises durant la saison de croissance suivant le feu (Key et Benson 2006). Nous comparons donc nos modèles de type

« Saturated growth » obtenus en utilisant le « extended assessment strategy » ainsi que ceux obtenus avec le « initial assessment strategy » aux modèles de Hall *et al.* (2008), puisque chacune des stratégies ont leurs utilités. L'« initial assessment strategy » permet une évaluation de la sévérité à court-terme après le feu. Alors que l'« extended assessment strategy » est particulièrement utile pour évaluer l'effet à moyen et long-terme du feu, ainsi que pour pallier à l'absence potentielle d'image Landsat pour l'année du feu.

Chapitre II

Titre: «Predicting post-fire Monochamus spp. attacks in black spruce and jack pine forests»

<u>Objectifs</u>: Ce chapitre vise à développer un modèle de prédiction des dommages reliés aux attaques de *Monochamus* spp. dans les peuplements brûlés de pins gris et d'épinettes noires, qui sera aisément utilisable par les aménagistes forestiers. Nous utiliserons des variables prédictives facilement disponibles, tels que l'essence, la surface terrière, le diamètre des tiges et la sévérité du feu (c'est-à-dire le degré auquel l'écosystème a changé à cause du feu (Lentile *et al.* 2006)). La caractérisation de la sévérité du feu est obtenue par imagerie satellitaire à partir de l'indice spectrale du « differenced Normalized Burn Ratio » (dNBR). Nos travaux permettront aussi d'estimer les taux de survie et de développement des *Monochamus* spp. entre les essences, de façon à contribuer à améliorer notre compréhension de la biologie de ces insectes.

Chapitre III

<u>*Titre:*</u> «High conservation value forests for burn-associated saproxylic beetles: an approach for developing sustainable post-fire salvage logging in boreal forest»

<u>Objectifs</u>: À travers ce chapitre, nous cherchons à recueillir des informations qui seraient aisément utilisables lors de la production de plans de récupération dans un contexte de conservation de la biodiversité. Dans une telle perspective, nous pensons que nos modèles devraient être fondés sur des variables prédictives qui sont couramment disponibles pour les aménagistes forestiers, comme l'essence, la surface terrière par essence, le diamètre des arbres, la sévérité du feu et la distance à la forêt non brûlée (Saint-Germain *et al.* 2004b;

Azeria *et al.* 2011b, 2012a; Boucher *et al.* 2012; Boulanger *et al.* 2013). Ces variables sont à la base de ce qui définira les forêts à haute valeur de conservation (FHVC) pour les espèces associées aux brûlis. L'identification des FHVC servira à améliorer la mise en œuvre de l'AFE dans les forêts boréales brûlées.

Nous avons émis comme hypothèse que (1) la richesse en espèces, une mesure largement utilisée dans la conservation de la biodiversité, ne saurait que fournir des recommandations générales dans l'identification de FHVC après feu. Cela est dû au fait que la réponse des espèces associées aux brûlis serait obscurcie par la présence d'espèces opportunistes et généralistes. Puisque les coléoptères saproxyliques peuvent montrer des patrons de réponses différents face aux caractéristiques de l'habitat brûlé (Azeria *et al.* 2012b), nous avons également émis l'hypothèse (2) que les espèces associées aux brûlis seraient plus écologiquement liées et se regrouperaient en groupes spécifiques. Finalement, nous nous attendons (3) à ce que la richesse de ces groupes et la présence d'espèces associées aux brûlis soient utiles dans l'identification de FHVC.
CHAPITRE I

Assessing the potential of the differenced normalized burn ratio (dNBR) for estimating burn severity in eastern Canadian boreal forests

Résumé

Il existe des variations considérables dans la sévérité du feu en forêt boréale. Afin de capter ces variations pour des forêts boréales de l'Ouest canadien, tant en termes de perspectives terrain et de télédétection, l'approche retenue fut l'utilisation combinée du « Composite Burn Index » (CBI) et du « differenced Normalized Burn Ratio » (dNBR). L'intérêt est de savoir comment cette approche peut performer pour des forêts boréales de l'Est du Canada. Cette étude a examiné la relation CBI-dNBR pour certains feux sélectionnés en forêt boréale de l'Est du Canada, tout en visant à contribuer à la généralisation d'un modèle pancanadien. Les résultats démontrent, pour la région étudiée, qu'il n'y a pas de différence dans la relation CBI-dNBR entre les peuplements dominés par l'épinette noire ou le pin gris, alors que cette relation a été la mieux décrite à travers un modèle additif généralisé (« Generalized Additive Model » (GAM)). Une cartographie de la sévérité du feu faite à partir du dNBR peut s'avérer utile afin de supporter la recherche et l'aménagement après feu, hors du territoire et du cadre temporel couvert par le système de cartographie déjà en place pour cette région. Le modèle de croissance saturée (« Saturated growth model ») proposé pour la région boréale de l'Ouest a bien performé pour nos forêts boréales de l'Est, ce qui supporte davantage le développement d'un modèle pancanadien.

Mots clés

Sévérité du feu, télédétection, Landsat, « differenced normalized burn ratio », « composite burn index », feu de forêt

Abstract

There is considerable variation in the degree of burn severity in boreal fires. One approach that has been used to capture this variation from field and remote sensing (RS) perspectives for western Canadian boreal forests is the Composite Burn Index (CBI) and differenced Normalized Burn Ratio (dNBR). Of interest was how well these methods may perform for fires in eastern Canada. This study investigated the CBI-dNBR relationship for selected fires in the eastern boreal forests of Canada, with a view towards contributing to the generalization of a Canada-wide model. Results for the sampled region showed no difference in the CBI-dNBR relationship between black spruce and jack pine dominated stands, whereas this relationship was best described by the Generalized Additive Model (GAM). The dNBR derived maps would also be useful to support research and post-fire management in burns outside the studied territory and time frame covered by the existing burn severity mapping system already used in this region. The Saturated growth model proposed for the western boreal region also performed well for our eastern boreal region, thus further supporting the development of a national model.

Key words

Burn severity, remote sensing, Landsat, differenced normalized burn ratio, composite burn index, wildfire

I. Introduction

The annual burned area has doubled in North American boreal regions in the last 40 years (Kasischke *et al.* 2008), which has consequences for a wide range of ecosystem processes, as well as new challenges to land managers (French *et al.* 2008; Sommers *et al.* 2014). Burn severity has been identified as a key variable that influences most ecological processes (Weber and Stocks 1998; Volney and Hirsch 2005) and as a result, quantifying and mapping this attribute is of prime interest for sustainable land management (Lentile *et al.* 2006). Burn severity is the widely-used term for describing the degree to which the ecosystem has changed owing to fire (Lentile *et al.* 2006). Burn severity quantification and mapping help us to better assess the spatial distribution of damage caused by fire to vegetation and timber (Lindenmayer *et al.* 2008), to support salvage logging and site rehabilitation (Lindenmayer *et al.* 2015) and the potential for soil erosion and induced water quality issues (Neary *et al.* 1999; Wood 2011). Moreover, strong arguments were stated for the need to incorporate burn severity into studies of wildlife response to fire (Smucker *et al.* 2005; Kotliar *et al.* 2007).

Burn severity has typically been evaluated *in situ* after fire by measuring soil characteristics, such as char depth, organic matter loss and color, along with above-ground vegetation consumption, scorch, mortality and recovery (Morgan and Tatar 1972; Ryan and Noste, 1985). It has often been partitioned into broad classes ranging from low to high severity for practical purposes (Lentile *et al.* 2006; Miller and Thode 2007). It is a rather subjective measurement and therefore varies according to the issue addressed, creating confusion in its definition and interpretation (Hutto 2006; Safford *et al.* 2008). Such confusion should be reduced by using a common burn severity mapping method for post-fire impact monitoring and planning (Lentile *et al.* 2006). It is also known that the biophysical symptoms of burn severity vary in a continuous manner, e.g. from stands of living trees with few snags, up to stands with 100% mortality (Kennedy and Fontaine 2009). This has led some authors such as Jain *et al.* (2004) to recommend estimating and mapping burn severity as a continuous variable rather than a categorical one.

Acquiring *in situ* burn severity data is often limited by the lack of accessibility and the high costs for surveying large areas. These constraints have brought up remote sensing (RS) products as an interesting alternative for providing spatially explicit information at lower cost (Wulder et al. 2009; Soverel et al. 2010). A consistent RS-based method is also useful for managers and researchers to provide a comparative baseline between burns and a temporal comparison and assessment of changes in fire regimes (Key and Benson 2006; Lentile et al. 2006). In such a context, many researchers have reported statistical relationships between field and remote sensed (RS) evaluations of burn severity to varying degrees throughout a variety of forest and woodland types (e.g., Cocke et al. 2005; Epting et al. 2005; Fox et al. 2008; Lhermitte et al. 2011; Randerson et al. 2012; Edwards et al. 2013). This has mainly been done using the remotely sensed index called the differenced Normalized Burn Ratio (dNBR) validated and calibrated with the *in situ* evaluation of burn severity defined as the Composite Burn Index (CBI) proposed by Key and Benson (2006). In the United States, CBI-dNBR relationships are now systematically used to map burn severity after wildfires (Cocke et al. 2005; Eidenshink et al. 2007). The dNBR is obtained from the difference between pre-fire and post-fire Normalized Burn Ratio (NBR). NBR is derived from two Landsat Thematic Mapper (TM) or Enhanced Thematic Mapper (ETM+) spectral bands (Eq. 1) and renders a continuous value index (García and Caselles 1991; Key and Benson 2006). NIR and SWIR Landsat TM or ETM+ bands (Eq. 1) respectively represent portions of the near infrared and of the shortwave infrared of the optical spectrum bandwidth. Following a fire event, the NIR reflectance diminishes due to leaf consumption and loss, while the SWIR reflectance rises due to reduction in canopy humidity and shade (van Wagtendonk et al. 2004). In Eq.1, the NIR-SWIR difference is normalized by the sum of the two bands enabling for spatial and multi-temporal comparison of NBR values (Key and Benson 2006). When computing the dNBR (Eq. 2), the subtraction of the post-fire from the pre-fire NBR isolates burned from unburned areas, providing a quantitative measure of change (Key and Benson 2006). Whereas dNBR theoretically ranges from -2.00 to +2.00, dNBR values within burned areas usually fall within +0.10 and +1.35 while those from unburned areas are generally within a range respectively of -0.10 to +0.10, and enhanced vegetative regrowth between -0.50and -0.10 (Key and Benson 2006).

$$NBR = (NIR - SWIR) / (NIR + SWIR)$$
(1)

In Canada, the CBI-dNBR relationship has been explored in western boreal forest (Hall *et al.* 2008; Soverel *et al.* 2010, Soverel *et al.* 2011). Hall *et al.* (2008) found that a Saturated growth model was able to quantify the relationship between *in situ* burn severity (CBI) and dNBR, which was also confirmed by the work of Soverel *et al.* (2010). Differences in the magnitude of dNBR values between vegetation types were also observed (Hall *et al.* 2008) due to their different fuel structures (Forestry Canada Fire Danger Group 1992). Surprisingly, statistical relationships have not yet been investigated for eastern Canada where wildfires are frequent, especially in the boreal region (Bergeron *et al.* 2004a; Bergeron *et al.* 2004b; Girardin *et al.* 2010), and where fire-adapted tree species like black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) are consequently well represented (Doucet and Côté 2009).

1. Objectives

The goal of this paper was to describe the relationship between *in situ* burn severity from CBI ratings and RS burn severity assessment using dNBR ratings in eastern boreal forests of Canada, as well as to contribute to the generalization of a model that could be applied throughout all the Canadian boreal forests. The study focused on stands dominated by black spruce (BS) and jack pine (JP) as they are common boreal tree species most affected by wildfires (Weber and Stocks 1998; Doucet and Côté 2009) and subsequently salvaged logged in eastern Canadian boreal forest (Annexe 1).

Two objectives were established to address this goal:

1. Modelling regional burn severity by:

i) Analyzing the differences in mean NBR, dNBR and CBI values between BS and JP stand types and differences in NBR values for time frame (pre-fire and post-fire).

ii) Developing regional statistical models over a representative region of eastern boreal forest for both BS and JP stand types and determining if these models varied statistically between them iii) Comparing the regional CBI-dNBR models for mapping burn severity with burn severity maps produced by the ministère des Forêts, de la Faune et des Parcs du Québec (MFFP). Since 2010, the MFFP has been using a different methodology and RS imagery type to derive maps from segmented and classified 5 m RapiEye satellite multispectral imagery (pers. com. Antoine Leboeuf, Head of imaging and remote sensing at MFFP). Obtaining maps derived from thresholded dNBR values that are comparable to the MFFP's maps would be useful to characterize burns beyond the targeted commercially used forest or for historical burns prior to 2010.

For this first objective, we used the "initial assessment" strategy proposed by Key and Benson (2006), that produces dNBR images using post-fire scenes taken the same year of the fires. This strategy is known for being especially useful for rapid assessment of burn severity (Key and Benson 2006) aiming at salvage logging for example.

2. Testing the transferability of previously developed Saturated growth models (Hall *et al.* 2008) from western to eastern boreal forests. The work done by Hall *et al.* (2008) used the extended assessment strategy, i.e., dNBR images are obtained using post-fire scenes taken from the following growing season (Key and Benson 2006). Therefore, we compared our Saturated growth models obtained using the extended assessment as well as the initial assessment strategies with Hall *et al.*'s (2008) models as both assessment strategies are useful. The initial strategy allows for rapid burn severity assessment aiming at short-term post-fire response. The extended strategy is especially useful for assessing the mid- to long-term effect of fire as well as for coping with the potential lack of Landsat scenes for the fire year.

II. Material & methods

1. Study area

The study area includes five burns that occurred in early summer of 2010 in the Haute-Mauricie region, Quebec, Canada (Figure 1, Table 1). These burns were all naturally ignited by lightning (Société de protection des forêts contre le feu (SOPFEU) data). The total burned area was approximately 137,000 ha and burns were selected due to their accessibility and their similar ignition date (Table 1). They overlap the western balsam fir-yellow birch and the western balsam

fir-white birch bioclimatic sub-domains, comprised between latitudes 47°N and 49°N (Doucet and Côté 2009). These bioclimatic sub-domains mainly support mixed stands dominated by balsam fir and birch species, in which fire-related species such as jack pine and black spruce are well represented (Doucet and Côté, 2009). Pre-fire composition of the forest was dominated by coniferous stands (54%), followed by mixed (37%) and deciduous (9%) stands. The forest of the pre-fire coniferous strata were mainly dominated by pure black spruce stands followed by pure jack pine stands accounting respectively for 65 % and 16% of the forest.

2. Field estimation of burn severity

In order to calibrate CBI-dNBR models, we established a total of 60 circular plots (11.28 m radius) in May 2011 across the five burns, with respectively 31 and 29 plots in BS and JP stands (Figure 1). Plot selection was guided by ecoforest and burn severity maps produced by the MFFP. First, ecoforest maps were used to stratify the study area into groups of forest stand polygons dominated by BS or JP species along with height and density classes. Second, resulting strata were intersected with MFFP burn severity maps providing four classes of burn severity (i.e., unburned, low, moderate and high; see Table 2). The resulting strata allowed sampling the widest possible range of pre-fire forest and burn severity conditions. Then, plot locations were selected through stratified random sampling which was spatially constrained to areas accessible at reasonable cost. Plots had to be established in forest stands that were locally homogeneous and large enough to include four 30×30 m Landsat pixels (Key and Benson 2006). Eight additional plots – four for each tree species – were randomly selected in nearby unburned stands (minimum distance of 2 km) to represent unburned forest conditions (Figure 1).

The 60 burned plots were revisited in August 2011 for forest inventory and burn severity estimation at the tree and plot levels. At the tree level, species was identified and we measured dbh (diameter at breast height, 1.30 m from the highest root). At the plot level, species-level basal area served to classify the plot as being dominated by either BS or JP using a 67% basal area threshold. Then, we followed the evaluation protocol from Key and Benson (2006) for field sampling of CBI rating. A team of two people visually estimated through consensus the burn severity rating in the plot within a 15 m radius by evaluating the level of fire consumption of up to 23 biophysical variables along five vertical stand strata: A) soil substrate, B) herbs, low shrubs

and small trees less than 1 m, C) tall shrubs and trees from 1 to 5 m, D) intermediate trees (subcanopy, pole-sized trees) and E) big trees (upper canopy, dominant and co-dominant trees). The percentage of living trees in the C stratum, as well as the char height and the percentage of mortality and of green/brown/black trees in the D and E strata, were determined using the inventory data. The completion of the CBI rating grid returned a global rating as a decimal value between 0 and 3 for each of the 60 burned plots whereas the 8 unburned plots were assigned 0. For more details on CBI rating please refer to Key and Benson (2006) CBI sheet.

3. Remote sensing estimation of burn severity

Pre-fire and post-fire satellite imagery were acquired from the United States Geological Survey (USGS) as Landsat TM-5 Climate Data Records (CDR) produced from the Landsat Ecosystem Disturbance Adaptive Processing System (LEDAPS) expert software (United States Geological Survey, 2013). Orthorectified Landsat surface reflectance images are readily useable and comparable through space and time, and include convenient cloud and cloud shadow masks. The pairs of pre-fire and post-fire Landsat scenes that were needed to cover the five burns of the study area (path 15, rows 26-27; Table 1) were acquired in the midst of the growing season to avoid phenological effects. Pre-fire scenes were acquired on August 27, 2007 (Julian day number 239), while post-fire scenes were acquired on July 2, 2010 (Julian day number 183) and August 6, 2011 (Julian day number 218) respectively for the initial and the extended assessment. The pairs of pre-fire and post-fire scenes were mosaicked and projected into NAD83 Quebec Lambert projection with 30 m pixel size. Pre-fire and post-fire NBR as well as dNBRinit (initial assessment) and dNBR_{ext} (extended assessment) were calculated using Eqs. 1 and 2. Resulting NBR and dBNR images were masked out for clouds and cloud shadows. This step led to the elimination of some burned plots that were masked by either clouds or cloud shadow, thus leaving 49 burned plots (25 in BS and 24 in JP stands), useable for assessing the initial assessment CBI-dNBR relationship, and 48 burned plots (24 in BS and 24 in JP stands) for the extended assessment. Finally, pre-fire/post-fire NBR, dNBRinit and dNBRextvalues for each burned and unburned plot were extracted by taking the mean value of all pixels within a radius of 15 m from the plot centroids whereas the pixel including the centroid was counted twice to provide extra weight in the mean calculation, as proposed by Key and Benson (2006).

4. Statistical analysis

4.1. NBR, dNBR and CBI variation between stand types

First we explored the difference between stand types (black spruce or jack pine dominated stands), by assessing how pre-fire and post-fire (calculated using the 2010 Landsat scenes) NBR values differed between them. The differences in mean NBR values between time frames (pre-fire and post-fire) and stand types was further assessed using linear mixed effects modelling (LME). The LME model made it possible to include the plots as a random effect, to account for temporal correlation between pre-fire and post-fire data, as well as to include a variance structure that considered both stand type and time frame variances. We also looked at the difference between stand types in terms of mean field (CBI) and mean remotely sensed (dNBR_{init}) estimates of burn severity using one-way ANOVA. These analyses were done using the 49 burned plots only, since we were interested in comparing the stand type spectral response to fire. LME model was done using the "nlme" package (Pinheiro *et al.* 2013), while the ANOVA was implemented in the "stats" package for R (R Core Team 2013).

4.2. Regional models

We modelled CBI ratings from dNBR_{init} values through different statistical regression models and used all of the 8 unburned and 49 burned plots. First, Generalized Additive Modeling (GAM) was explored as it uses adaptive spline-based smoothers and cross-validation to automatically determine the optimal smoothing thus fitting the best curve through the scatterplots (Zuur *et al.* 2009). The produced model is hypothesized to be the best at expressing the relationship between CBI and dNBR_{init} values. However, it serves only as a reference to find the best equivalent non-linear model as no definite model equation can be obtained from GAM, which is challenging for application purposes (Zuur *et al.* 2009; Wood 2011). Secondly, nonlinear regressions were explored using the DataFit 9 software, which includes a library of around 300 pre-defined regression models using the Levenberg-Marquardt non-linear least squares curve fitting algorithm (Oakdale Engineering 2002). All selected model forms produced by DataFit 9 were visually assessed to ensure a logical fit with the CBI- dNBR_{init} scatterplot (Hall *et al.* 2008) (not reported). Then, two models were kept for further investigation: a natural logarithm model (Eq. 3) and a third-order polynomial model (Eq. 4). Thirdly, we explored the Gompertz growth model (Eq. 5) modified by Baty and Delignette-Muller (2015), which allows a non-symmetrical curve fitting around the inflection points (Zwietering *et al.* 1992). This model could better fit the unburned portion of the dNBR_{init} range (CBI ratings = 0) than symmetrical sigmoidal models would do. Moreover, the parameter "b" of Eq. 5 is the maximum predicted CBI value which should reach the theoretical maximum CBI value of 3. As a fourth step, following the work done in western Canadian boreal forests by Hall *et al.* (2008) their Saturated growth model was fitted to our data (Eq. 6). It is to be noted that the first-order linear model, frequently investigated in the past (e.g., Allen and Sorbel 2008; Hall *et al.* 2008) was rejected based on the obvious non-linear shape of the CBI- dNBR_{init} scatterplot.

Natural logarithm:

$$CBI = \ln(a \cdot dNBR + b)$$
(3)

Third-order polynomial:

$$CBI = a \cdot dNBR^3 + b \cdot dNBR^2 + c \cdot dNBR + d$$
(4)

Gompertz model:

$$CBI = a + (b - a) \cdot exp[-exp[c \cdot exp(1) \cdot (d - dNBR)/((b - a) \cdot log(10)) + 1]]$$
(5)

Saturated growth model:

$$CBI = dNBR \cdot (a \cdot dNBR + b)^{-1}$$
(6)

Each of these models was fitted by including the two tree species as a fixed factor allowing testing for differences in the CBI- dNBR_{init} relationship between tree species. Then, models were re-fitted without tree species as a factor. All model fits at both steps were ranked using the Akaike information criterion (AIC; Akaike 1974) with the best model having the lowest AIC. For each model form, we compared the fit with or without tree species using ANOVA (Zuur *et al.* 2009) to determine if the CBI- dNBR_{init} relationships were significantly better with tree species as a factor. The model fittings and ANOVAs were done through the use of "mgcv" (Wood 2011) and "stats" R packages (R Core Team 2013).

4.3. Mapping of burn severity

The two best regional models were used to predict and map CBI in a manner comparable to what is presented on the map produced by the MFFP. CBI values from the initial 60 burned plots were classified according to the MFFP severity classes (unburned, low, moderate and high, see Table 2) through field visual estimation done while completing CBI ratings. Assuming a normal distribution of observed CBI values within each burn severity class, we calculated the mean CBI and its standard deviation for each severity class. CBI values found at the intersection of the overlapping normal distributions were used as upper bounds of the MFFP burn severity classes while the CBI values ranking between 0.00 - 0.29 was used for the unburned class (Hall et al. 2008). The two best CBI- dNBR_{init} models were then inverted to transform CBI upper bounds to threshold the dNBR_{init} distribution into upper bounds delimiting the MFFP burn severity classes (Hall et al. 2008). We then classified all dNBRinit pixels from the five burns into burn severity classes and mapped burn severity according to these classes. Finally, we compiled the areas classified in each severity class for each resulting map, and identified the overall total percentage and the relative percentage of rightfully classified areas based on the reference MFFP map. We also visually compared the three maps (MFFP and dNBR-derived map from our two best models). We present only maps of the Parent burn, which is representative of the other burns.

4.4. Generalization of the CBI-dNBR model

The transferability of two western models from Hall *et al.* (2008) to eastern boreal forest was assessed for generalization purposes at the national level. First, we modeled the extended assessment CBI-dNBR_{ext} relationship using the Saturated growth model (Eq. 6) to be comparable to Hall *et al.*'s (2008) methodology. Our predicted CBI values using both initial and extended Saturated growth models were then plotted against those obtained from the two western Saturated growth models (Eq. 6) from Hall *et al.* (2008); i.e., a general one including all their fires and a regional one developed for the Northwest Territories (NWT) (coefficients are presented in Table 6). This latter model is considered a better candidate as the NWT vegetation types most resemble ours. Prediction scatterplots were visually analyzed relative to a 1:1 slope, and Pearson's correlation (r), as well as root mean square deviation (RMSD), was calculated to assess the level of prediction agreement.

III. Results and Discussion

1. NBR, dNBR and CBI variation between stand types

We observed, in the case of pre-fire conditions, that NBR values for the unburned plots (n = 8) ranged from 0.537 to 0.648, which is similar to those of the burned plots (n = 49) for which NBR values ranged from 0.385 to 0.680. For post-fire conditions, we observed that unburned plot NBR values ranged from 0.523 to 0.622, and that burned plot NBR values were lower and covered a wider range from -0.399 to 0.440. As expected, post-fire mean NBR was lower compared with the pre-fire one. Finally, dNBR_{init} values ranged from -0.031 to 0.051 and from 0.144 to 1.011 respectively for the burned and unburned plots, and CBI ratings for burned plots ranged from 0.57 to 2.74 while unburned plots were assigned a CBI rating of zero.

The use of the LME model showed that there was a significant effect of stand type (BS: n = 25; JP: n = 24) and time frame factors on NBR (Table 3). Significantly higher pre-fire mean NBR values for BS stands were observed compared with JP stands whereas no significant difference was noted in the post-fire case as found by Wulder *et al.* (2009) for other conditions. Lastly, no significant difference was found between BS and JP when comparing both mean CBI ratings and mean dNBR values (Table 4).

BS and JP stands have different ecophysiological and fuel type structures (Forestry Canada Fire Danger Group 1992) and therefore generate different spectral signatures in pre-fire NBR. However, this difference did not persist for post-fire NBR or the dNBR_{init}. This shows that the dNBR_{init} index, in addition to the CBI rating, are both well designed and suited to evaluating the degree of change as it appears to be independent of the pre-fire vegetation cover (Miller and Thode 2007).

2. Regional models

All five fitted models, using tree species as a factor, performed well in describing the CBIdNBR_{init} relationship with adj-R² ranging from 0.89 for the Natural logarithm model to 0.92 for the GAM model, which was the best, as expected (Figure 2; Table 5). For each model, ANOVA analysis showed no significant differences when excluding tree species as a factor (Table 5). In fact, all models provided nearly identical adj-R² values, whether tree species was included or not in the models. This was also supported by the fact that no significant differences were observed for the means of CBI ratings and dNBR_{init} values between the two tree species (Table 4), which is reflected in the species blending in the CBI-dNBR_{init} scatterplots (Figure 2). Therefore, because of their good performance and greater simplicity, we used tree-species-independent models for the rest of the paper. For practical management purposes, generalizing the use of simple models across various land cover types is highly desirable (De Santis and Chuvieco 2007; Wulder *et al.* 2009; Soverel *et al.* 2011).

The five tree-species-independent model fits (coefficient estimates in Table 5) provided very similar adj-R² (0.88 to 0.92) and ranking, with GAM being the best (AIC = 1.93) followed by Gompertz (AIC = 11.41), Third-order polynomial (AIC = 12.61), Saturated growth (AIC = 16.94) and Natural logarithm (AIC= 23.92) (Table 5, Figure 2). The GAM and Gompertz models both have a small curvature at the lower end of the dNBR_{init} range that better fits the unburned plots (CBI=0). The Gompertz model reaches an asymptote at CBI values of 2.29 ± 0.05 due to its "b" coefficient (Table 6, Figure 2). On the other hand, none of the GAM, the Natural logarithm, the Saturated growth or the Third-order polynomial models reach an asymptote in the sampled range of burn severity (Figure 2). Noticeably, the Third-order polynomial model showed an increasing slope at the highest burn severity values (Figure 2).

The Gompertz model provided a good fit for low estimates of burn severity but reached asymptote far too early thus underestimating burn severity at high severity, with maximum CBI value of 2.29, which is relatively far from the observed maximum value of 2.74. The Third-order polynomial model also provided a good fit overall although the decreasing slope followed by an increasing one is hardly explainable on a biophysical basis. The Natural logarithm model has been successfully reported in other studies (Miller and Thode 2007; Cansler 2011; Parks *et al.* 2014), and it exhibited a more realistic fit than the Third-order polynomial and the Gompertz models, especially for the moderate-high severity values. However, it provided the worst statistical fit of our study. Moreover, an issue arises when using a logarithmic model, as a bias has to be applied when back-transforming values. Though physically very similar to the Natural logarithm model, the Saturated growth model has a better statistical fit. On the other hand, the GAM model had the best fit of all models across the scatterplot (Figure 2). It exhibited a small

curvature at the beginning, which was well suited for the unburned range of dNBR_{init} values, as well as a relatively slow and constant slope for the moderate-high values of burn severity. While it resulted in our best regional model, it does not result in actual coefficient estimates for this model thus making it harder to compare with other models. The Saturated growth model thus offered a good compromise over the GAM model with a simple equation (Eq. 6) requiring the estimation of only two coefficients. In addition, this model provided the best fit in western Canadian burns (Hall *et al.* 2008), although with different coefficient estimates (Eqs. 8 and 9).We thus retained both the GAM and the Saturated growth models as our two best regional models.

3. Mapping burn severity

Classification of the CBI plot values into the MFFP burn severity classes yielded nine plots in the low severity class, 30 plots in the moderate severity class and 21 plots in the high severity class (Table 7). The derived CBI bounding values ranged from 0.30 to 1.75, 1.76 to 2.23 and 2.24 to 3.00 respectively for the low, moderate and high burn severity classes (Table 7). The calculated upper dNBR_{init} bounds for each severity class according to our two best models (i.e., GAM and Saturated growth models) varied among them (Table 7) due to their different model forms (Figure 2). Visual analysis of the two derived maps relative to the MFFP map showed similar spatial patterns of burn severity class, according to our two best models, with the reference map of the MFFP (Table 8), we found a better agreement with the MFFP low burn severity for the Saturated growth model (44.6%) than for the GAM model (28.8%). However, the reverse was true for the MFFP moderate severity class (GAM: 49.3%; Saturated growth: 37.5%), while both models provided good agreement with the MFFP high burn severity class (GAM: 78.2%; Saturated growth: 81.6%). Overall, the GAM and Saturated growth models respectively correctly classified 57.1% and 55.6% of burned areas based on the MFFP reference map.

Part of this mismatch certainly arises from the substantial differences between our approach and that of the MFFP. These include the resolution (30 m vs 5 m), spectral band width (lack of SWIR band for RapidEye), classification method (pixel-based spectral index thresholding vs segmentation and classification technique considering both spectral and spatial pattern characteristics) and time frame (pre-/post-fire vs post-fire only). Nevertheless, the substantial

agreement between the two map sources suggests that our approach should provide meaningful burn severity maps for burns located outside the territory and the time frame covered by the MFFP. However, a limitation is the accessibility to cloud-free Landsat scenes for rapid post-fire management issues (Epting *et al.* 2005), a key factor that led the MFFP to rely on RapidEye imagery with high revisit capacity to derive burn severity maps in due time after fire (pers. com. Antoine Leboeuf, Head of imaging and remote sensing at the MFFP). However, the use of continuous dNBR-derived burn severity maps provides a flexibility that is especially useful to customize maps for various burn severity classes through variable thresholding, for addressing various issues, such as assessment of biodiversity (e.g., birds (Azeria *et al.* 2011); beetles (Boucher 2010; Boulanger *et al.* 2010)), damage due to xylophagous insects (e.g. woodboring insects (Boulanger *et al.* 2013; Chapter II of this thesis)) or seedling regeneration. Finally, the 30 m resolution and the SWIR band provided by the free Landsat imagery archives allows greater sensitivity to burn severity, and opens the door to simple and cost-effective burn severity mapping of large burned areas.

4. Generalization of the CBI-dNBR model

Modelling the extended assessment CBI-dNBR_{ext} relationship using the Saturated model performed well with adj-R² of 0.66 (Table 5b), though not as well as with the initial assessment strategy as presented earlier (adj-R² of 0.90). Such a discrepancy in model fit could be due to a blurring effect caused by post-fire vegetation regrowth (Allen and Sorbel 2008) captured by the extended assessment, which was not considered during our field estimates of burn severity (through CBI ratings).

The two western General and NWT Saturated growth models (Hall *et al.* 2008) were overlaid onto the initial and extended assessment CBI-dNBR scatterplots along with our Saturated growth models (Figure 4). Comparing to our initial assessment Saturated growth model (Figure 4a), the western models show a similar fit for the first third or so of the dNBR_{init} spectrum, though they slightly overestimate CBI values. The western models largely tend to overestimate burn severity above dNBR_{init} values of around 0.300 for the NWT model and around 0.100 for the General model. However, as expected, the NWT model exhibits a better fit with our data compared with the General model. When comparing our extended assessment Saturated growth model with the western models (Figure 4b), we observe that the General model tends to slightly overestimate CBI values for most of the dNBR_{ext} range (-0.102 - 0.828) while there is almost no distinction between our extended assessment Saturated growth model and the NWT model (Figure 4b).

CBI predictions from the two western models using our dNBR_{init} and dNBR_{ext} datasets plotted against those from our Saturated growth models (Figure 5) showed similar and high correlation coefficients from r = 0.98 to 1.00 while RMSE ranged from 0. 03 to 0.54. Based on deviation from the 1:1 line (Figure 5), best model agreement was logically found with the NWT and the extended assessment Saturated growth models (r = 1.00 and RMSE = 0.03). On the other hand, the worst agreement was between the General and the initial assessment Saturated growth models, with r = 1.00 and RMSE = 0.54.

Differences that were observed in the moderate to high severity range between the initial assessment model and western models could be partly explained by methodological differences. Indeed, by using the extended strategy, Hall *et al.* (2008) used post-fire scenes from the following growing season and evaluated CBI around the same date. Therefore, lower dNBR values were expected for high burn severity rating on site when using the extended strategy, compared with the initial assessment strategy, due to the spectral influence of short-term vegetation regrowth usually observed in high burn severity classes (Key and Benson 2006; Allen and Sorbel 2008). This could partly explain higher CBI predictions from the western models compared with ours for the moderate-high severity range. This could also explain why we found a quasi-perfect agreement between our extended assessment Saturated growth model and those of Hall *et al.* (2008), especially when looking at our coefficient estimates and those of the NWT model (Table 6). The slight overestimation of the western General model on our dNBR_{ext} dataset could be due to different vegetation compositions found in the other areas studied by Hall *et al.* (2008), which could yield different post-fire vegetation regrowth such as that from the fast sprouting poplars, for example (Doucet and Côté 2009).

As a final remark, some studies assessed the CBI-dNBR relationship by predicting dNBR as a function of CBI (e.g., Cansler 2011; Soverel *et al.* 2011; Parks *et al.* 2014), while others such as ours have predicted CBI as a function of dNBR (e.g., van Wagtendonk *et al.* 2004; Allen and Sorbel 2008; Hall *et al.* 2008; Hoy *et al.* 2008; Soverel *et al.* 2010), making model comparison

challenging. CBI field estimates were designed and are needed to calibrate and validate remote sensing results of dNBR (Key and Benson 2006). Since remote sensing is used to predict *in situ* burn conditions, the CBI and the dNBR should be considered respectively as the dependent and independent variables.

IV. Conclusion

We showed that the dNBR spectral index is effective for estimating burn severity in eastern boreal forests for two important fire-adapted tree species, black spruce and jack pine. The regional statistical modelling showed that the species-independent Saturated growth model performed nearly as well as the optimal GAM model for linking the CBI field estimates of burn severity to remotely sensed dNBR using Landsat imagery. We demonstrated that the regional burn severity maps based on the CBI-dNBR relationship offer the flexibility to provide contextadapted burn severity classes.

Moreover, our results further confirmed the value of the Saturated growth model based on the extended assessment strategy, previously developed for western boreal conditions, through its successful transfer into our sampled area of eastern boreal forest. Such results promote the potential applicability of this model across the boreal forests of Canada. Future generalization work should include other key boreal stand types across more ecosystems prone to fires.

Regarding burn severity assessment strategies, the initial assessment strategy is useful for providing quick responses for planning salvage logging with considerations for biodiversity conservation, especially in the context of rapid degradation of timber value due to woodboring insects. The extended assessment strategy is more useful for mid- to long-term planning or for monitoring stand rehabilitation. Furthermore, it circumvents the frequent lack of post-fire Landsat scenes needed during the same year of the fire for initial assessment due to unfavorable conditions (clouds/haze, smoke plume). The establishment and respective usefulness of two Saturated growth models, either for the initial or for the extended assessment strategies, should be further evaluated towards their broader application across the boreal forests of Canada. Nevertheless, our study supports the generalization in the near future of the CBI-dNBR relationship, which along with the capacity offered by the huge Landsat archives, certainly paves the way for repetitive large area mapping of burn severity across the boreal forests of Canada.

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Tables

Burn name	SOPFEU*	Date of	Latituda	Longitudo	Area	Landsat TM-5
	code	ignition	Latitude	Longitude	(ha)	path/row
Parent	270	26/05/2010	48.127	-74.534	4 181	15/27
Relais	267	25/05/2010	48.015	-73.473	3 663	15/27
Smokey	281	25/05/2010	48.353	-73.325	105 254	15/26
Vermillon	248	24/05/2010	47.414	-74.020	5 840	15/27
Wemotaci	274	25/05/2010	48.006	-73.793	18 209	15/27
Total					137 147	

 Table 1. Description of the five selected burns.

*SOPFEU stands for "Société de Protection des forêts contre le feu", which is Quebec's agency in charge of fighting wildfires.

Table 2. Definition of burn severity classes according to the ministère des Forêts, de la Faune et des Parcs (MFFP)

Classes	Definitions
Unburned	Fire has not spread to the ground or the crown.
Low	Surface fire that burned all or part of ground vegetation (moss, shrubs, seedlings, etc.) or the organic matter (slash, litter, etc.). In forested stands less than 50% of tree crowns are affected (brown or charred).
Moderate	Surface fire or intermittent crown fire. At least 50% of tree crowns were partly or entirely affected by fire (brown or charred) and crowns of more than 50 % of these affected trees were brown.
High	Continuous or intermittent crown fire. At least 50% of tree crowns were partly or entirely affected by fire (brown or charred) and for more than 50% of these affected trees; fire consumed the leaves and blackened the stems.

	Time frame						
Tree species	$\operatorname{Pre-fire}^{\dagger}$	Post-fire ^{†*}					
Black spruce	0.596 ± 0.008	0.051 ± 0.045					
Jack pine	0.541 ± 0.014	-0.005 ± 0.045					
	t-value	P-value					
Tree species	-3.475	0.001					
Time frame	12.249	0.000					

Table 3. Results from linear mixed effects model (LME) showing the significant difference in terms of NBR values between tree species and time frame.

 $^{\dagger}Mean \pm standard \ error$

*NBR values obtained using the 2010 Landsat scenes (initial assessment strategy)

Table 4. Comparison of CBI and dNBR_{init} statistics between tree species (black spruce and jack pine) using one-way ANOVA (*n*=49).

Burn severity variables	Range	Mean \pm SE		F-value	P-value
		Black spruce	Jack pine		
CBI	0.57 - 2.74	2.04 ± 0.11	2.13 ± 0.07	0.57	0.45
dNBR _{init}	0.144 - 1.011	0.610 ± 0.062	0.659 ± 0.046	0.41	0.53

Table 5. Comparison of CBI-dNBR models using A) initial assessment strategy: various models with or without tree species as an
independent factor along with F-statistic and P-value from ANOVA and B) extended assessment strategy for the Saturated growth
model only.

Tree species		Models [†]	df	R ²	adj-R ²	AIC	F-statistic	P-value
		Third-order polynomial	49	0.92	0.90	17.35		
		Natural logarithm	53	0.89	0.89	23.49		
ent	HLL	Gompertz	49	0.92	0.90	18.25		
ssme	×	GAM	48.5	0.93	0.92	7.93		
sses		Saturated growth	53	0.90	0.89	19.78		
A) Initial <i>e</i>	WITHOUT	Third-order polynomial	53	0.91	0.91	12.61	0.72	0.58
		Natural logarithm	55	0.88	0.88	23.92	2.14	0.13
		Gompertz	53	0.91	0.91	11.41	0.25	0.91
		GAM	51.8	0.93	0.92	1.93	0.17	0.93
		Saturated growth	55	0.90	0.90	16.94	0.55	0.58
B) Extended assessment		Saturated growth	54	0.66	0.66	84.50		

[†]For model equations, see Eqs. 3 to 6.

Model [†]		Madal [†]	Coefficient estimate \pm SE							
		Widdel	а	b	с	d				
		Third-order polynomial	6.22 ± 1.38	-12.63 ± 2.08	8.99 ± 0.85	-0.03 ± 0.09				
Initial	nitial ssment	Natural logarithm	1.11 ± 0.10	11.71 ± 0.59						
A) (A) asse	Gompertz	-0.11 ± 0.18	2.29 ± 0.05	18.27 ± 2.58	0.03 ± 0.04					
	Saturated growth	0.31 ± 0.02	0.09 ± 0.02							
nded	nent	Saturated growth	0.21 ± 0.03	0.11 ± 0.01						
B) Exter assessm	General Saturated growth *	0.22	0.09							
	NWT Saturated growth*	0.20	0.12							

Table 6. Coefficient estimates for A) the tree species-independent initial assessment models, and B) our extended assessment and Hall *et al.* (2008) General and NWT Saturated growth models.

[†]Refer to Eq. 3 to 6; ^{*}Models from Hall *et al.* (2008)

CBI values						Modelled	
Severity class	Number of field plots [†]	Mean	Standard deviation	Range	GAM	Saturated growth	
Unburned	8	0	-	0.00 - 0.29			
Low	9	1.36	0.41	0.30 - 1.75	0.078	0.032	
					0.293	0.362	
Moderate	30	2.06	0.21	1.76 - 2.23	0.729	0.684	
High	21	2.39	0.24	2.24 - 3.00			

Table 7. CBI bounds and modeled dNBR_{init} thresholds for mapping burn severity as classes

[†]All 68 plots were included as CBI values are not affected by cloud coverage in satellite images.

MEED Deference alogges	GAM model				Saturated growth model			
MIFFF Reference classes	Unburned [†]	Low	Moderate	High	Unburned [†]	Low	Moderate	High
Low	19.7	28.8	37.0	14.4	11.2	44.6	26.7	17.5
Moderate	1.8	10.7	49.3	38.2	0.7	17.2	37.5	44.6
High	0.6	3.3	17.8	78.2	0.3	5.3	12.9	81.6
Total percentage of correctly 57.1% classified areas 57.1%						55.0	5%	

Table 8. Compiled percentage of areas classified in each burn severity class (all five burns included) according to the two best regional models compared with the reference maps of the MFFP.

[†]Areas classified as unburned according to our two best models (i.e., GAM and Saturated growth models)

Figures



Figure 1. Study area is located in the Haute-Mauricie region of Quebec, Canada (black star in bottom right frame) along with the spatial distribution of the 68 sampling plots (60 burned plots: black dots; 8 unburned plots: black triangles) within the five studied burns (grey areas in the left frame).





Figure 3. Comparison of the burn severity maps for the 2010 Parent burn, based on A) the GAM model, (B) the Saturated growth model and (C) the MFFP severity map.



Figure 4. Visual comparison of potential Canada wide models for A) initial and B) extended assessment. The solid and dashed grey lines represent respectively the General and the NWT models (Eq. 6; Table 6) from Hall *et al.* (2008), the solid black lines represent our Saturated growth models. Black spruce and jack pine plots are represented respectively by grey dots and black triangles.



Figure 5. Correlation between the predicted values of our A) initial and B) extended assessment Saturated growth models (x-axes) and the General (All fires) and the NWT models from Hall *et al.* (2008) study (y-axes) and their deviation from the 1:1 line (dashed lines). In each frame, we indicated Pearson's correlation coefficient (r) and the root mean square error value (RMSE).

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CHAPITRE II

Predicting post-fire *Monochamus* spp. attacks in black spruce and jack pine forests

Résumé

La valeur marchande du bois récupéré après feu est souvent dépréciée en raison de la présence de galeries larvaires (trous de vers) de longicornes (Monochamus spp.), qui compromettent la rentabilité de la coupe de récupération. Nous manquons actuellement d'information pour mieux comprendre les liens entre la biologie de ces insectes et leur impact économique sur la ressource ligneuse. Cette étude vise à développer un modèle prédictif de la densité d'attaque (trous d'entrée \cdot m⁻² de surface de tige) de ces insectes en se basant sur des variables faciles à acquérir telles que la surface terrière par essence, le diamètre des tiges et la sévérité du feu, en utilisant le « differenced Normalized Burn Ratio » (dNBR). À la suite d'incendies en forêt boréale du Québec, Canada, des parcelles ont été installées dans des peuplements dominés par l'épinette noire (EN; Picea mariana) ou le pin gris (PG; Pinus banksiana). Nous avons écorcé une section de 50 cm sur sept arbres de ces parcelles dans lesquelles nous avons dénombré les trous d'entrée des larves et de sortie des adultes. Les analyses ont montré que les taux de développement et de survie étaient plus élevés sur le PG, bien que la densité des attaques était plus importante sur l'EN. Le modèle de prédiction de la densité des attaques a montré une augmentation de la densité en fonction du diamètre des tiges et un effet quadratique de la sévérité du feu : les densités d'attaques étaient plus grandes dans les feux de sévérité moyenne pour l'EN et dans les feux de sévérité élevée pour le PG.

Mot clés

Longicornes, Monochamus, prédiction des attaques, brûlis, trous de vers, sévérité du feu.

Abstract

Post-fire harvested wood's merchantable value is often reduced due to the presence of larval galleries (wormholes) of longhorn beetles (*Monochamus* spp.), which compromise the profitability of salvage logging. We are currently lacking information to better understand the links between the biology of these insects and their economic impact on timber resources. This study aims to develop a model for predicting the density of attack (entrance holes · m⁻² of bole surface) of the insects, based on easily acquirable variables such as basal area by tree species, stem diameter and burn severity, using the differenced Normalized Burn Ratio (dNBR). Following wildfires in the boreal forest of Quebec, Canada, plots were set in stands dominated by black spruce (BS; *Picea mariana*) or jack pine (JP; *Pinus banksiana*) trees. We barked off a 50 cm section on seven trees from these plots, in which we counted larval entrance holes and adult exit holes. Analyses showed higher developmental and survival rates on JP, although the density of attacks was greater on BS. The model predicting the density of attacks showed increased density with increased tree diameter, and a quadratic effect of burn severity: densities of attacks were greater in medium burn severity for BS and in high burn severity for JP.

Key words

Longhorn beetles, Monochamus, attack prediction, post-fire, wormhole, burn severity.

I. Introduction

Boreal landscapes are largely shaped by wildfires, making their forests the most fire-driven biome of the Northern Hemisphere (Burton *et al.* 2008). Large wildfires generate tremendous amounts of dead trees, that are increasingly salvaged to reduce economic losses resulting from this natural disturbance (Lindenmayer *et al.* 2008). However, most post-fire stands of the boreal forest are not easily accessible and wood quality is rapidly downgraded by woodboring insects, particularly longhorn beetles (Coleoptera: Cerambycidae) of the *Monochamus* genus (Saint-Germain and Greene 2009; Gardiner 1957). These insects promptly colonize recently dead trees, where they feed on subcortical tissues, and on the xylem (Haack and Slansky 1987). They are the main degradation agent of dead trees after natural disturbances, hindering the profitability of post-disturbance salvage logging operations (windthrow, insect epidemics, wildfire, etc.; Boucher and Hébert 2010; Post and Werner 1988; Raske 1972; Raske and Safranyik 1970; Ross 1960).

The whitespotted sawyer, Monochamus scutellatus scutellatus (Say), is known as the most damaging species in recently burned forests of Canada (Gardiner 1957). It thrives on all species of the Pinaceae family, but prefers spruces (Picea spp.) and pines (Pinus spp.) (Raske 1972), where densities exceeding 300 larvae per m² of bole surface have been reported (Saint-Germain et al. 2004a). As soon as they emerge as adults, Monochamus beetles converge rapidly toward recently burned forests, where they mate and lay eggs in the bark of burned trees (Bélanger 2013). Larvae go through four instars during their life cycle, which varies according to geographic location and environmental conditions. Overall, the life cycle of 75-90% individuals spans over 2 years, while that of the remainder extends over only 1 year (Appendix 1) (Bélanger et al. 2013; Cerezke 1977). Larvae of the two first instars thrive in the subcortical part of trees, but those of the third and fourth instars burrow galleries into the xylem (Raske 1972). Recent work on post-fire insects in eastern Canadian boreal forest reported another damaging Monochamus species, Monochamus mutator LeConte, commonly known as the spotted pine sawyer (Azeria et al. 2012; Boucher et al. 2012). As its common name suggests, M. mutator is only found on pine trees (Yanega 1996) and it appears to favour jack pine (Gardiner 1957). Both species are known to behave in the same manner (Belyea 1952; Craighead 1923), but the biology of *M. mutator* is fairly unknown since its larvae are yet indistinguishable from those of *M. s. scutellatus* (Gardiner 1957).

The larval galleries themselves cause less than 5% wood volume losses (Wilson 1962), but important economic impact may result from the downgrading of logs due to the presence of insects and holes in sawn lumber. Wood value losses related to woodborers such as Monochamus spp. have been evaluated to vary from 30-60% (NLGA 2014; Cerezke and Volney 1995; Raske 1972; Raske and Safranyik 1970). If we take the year of 2010 as an example, where 223,400 ha of forest burned in the province of Quebec, Canada (SOPFEU) 2015), of which 2 million m³ of wood was salvaged (pers. comm., Marie-Claire Dumont, Head of the Direction du soutien aux opérations Faune Forêts of the Ministère des Forêts, de la Faune et des Parcs du Québec), yielding revenues of about CAD\$ 216 M (Boulay 2013). This would represent economic losses attributable to woodborers of CAD\$ 65 M, for this sole year, based on a 30% depreciation value. That is equivalent to a loss of CAD\$ 30 m⁻³ of salvaged wood. Moreover, international phytosanitary trade agreements do not allow moving lumber that contains insects to European countries (Vallentgoed 1991), thus further depreciating the value of lumber intended for overseas markets. Being able to predict Monochamus spp. attacks is thus of prime interests in order to maximize benefits from post-fire salvage logging.

Several studies have reported that many environmental variables affect the level of *Monochamus* attacks, such as tree species, tree diameter and age, host tree vigour, wood moisture content, stand basal area, distance to unburned matrix and burn severity (Azeria *et al.* 2012; Bélanger *et al.* 2013; Boulanger *et al.* 2010, 2013; Breton *et al.* 2013; Gervais 2010; Saint-Germain *et al.* 2004a). Indeed, it has been suggested that burn severity may reduce the tree's natural defences, cortical and cambial water content and alter the chemical composition of the phloem (Boulanger *et al.* 2013; Gervais 2010), making fire-killed snags more acceptable or suitable to longhorns than live trees. Burn severity could also alter phloem chemical composition to such an extent that it could reduce longhorns attacks or developmental success (Boulanger and Sirois 2006; Boulanger *et al.* 2013; Gervais 2010). Some also showed a quadratic relationship between burn severity and longhorn beetle

attacks (Boulanger *et al.* 2013; Gervais 2010), while Saint-Germain *et al.* (2004a, b) outlined the existence of interactions between tree species, tree diameter and burn severity.

However, a model predicting post-fire longhorn beetle attacks does not exist. Our study aims to develop a model forecasting *Monochamus* spp. attacks in burned stands of black spruce and jack pine, that would be readily usable by land managers. We used variables that can be easily acquired, such as stand basal area, tree species, stem diameter, as well as burn severity (i.e., the degree to which the ecosystem has changed owing to fire (Lentile *et al.* 2006)) acquired through the differenced normalized burn ratio (dNBR) characterization presented in Chapter I of this thesis. Our work also allowed assessing differences in *Monochamus* spp. survival and development rates between tree species, which will contribute to improve our understanding of the biology of these insects.

II. Materials and methods

1. Study area and stand selection

The study was carried out in five burns naturally ignited by lightning in late May 2010, in the Haute-Mauricie region, Quebec, Canada (Figure 6). These burns were selected because of their relative proximity, accessibility and similar ignition date (Table 9), which limits possible bias (Bélanger 2013; Saint-Germain *et al.* 2004a). Overall, these burns covered around 137,000 ha of forest land. Selected burns were located between 47° and 49° N, where mean annual temperature varies between 0-2.5°C and annual precipitation totals 900-1,100 mm (Wilson 1971). Forests of this region consists of mixed stands dominated by balsam fir and birch, in which fire-prone species such as jack pine and black spruce are well represented (Doucet and Côté 2009).

Plot selection was guided by ecoforest and burn severity maps produced by the Ministère des Forêts, de la Faune et des Parcs du Québec (MFFP). Selected stands needed to cover at least 4 ha and to be homogeneous in terms of burn severity, species composition, tree density and height. Through stand selection, we also aimed at covering the widest range of burn severity available in our study area. Field validation was done in May 2011, and we retained 31 black spruce stands and 29 jack pine stands distributed across the five burns

(Figure 6, Table 9). Stand selection was greatly restricted by stand availability (post-fire salvage logging was carried out until late winter 2011) and accessibility (i.e., poor quality of the road network).

2. Plot inventory and Monochamus spp. attack assessment

In each of our 60 selected stands, we established a circular plot (11.28 m radius) for field surveys. Between August 8 and 23, 2011, we carried out forest inventory, in which each individual tree was identified and its DBH (diameter at breast height, 1.3 m from highest root) was measured within a 0.04 ha circular plot, thus allowing to estimate stand basal area for each tree species. Burn severity was remotely evaluated for each plot using the differenced Normalized Burn Ratio (dNBR; Key and Benson 2006). This spectral index produces continuous burn severity values (as opposed to nominal classes) which allows testing for quadratic effect. To assess the dNBR, we used Landsat 5TM scenes dating from August 27, 2007, for the pre-fire scene and from July 2, 2010, for the post-fire scene. They were acquired from the U.S. Geological Survey (USGS) Landsat 5TM Surface Reflectance Climate Data Record (CDR). The dNBR was computed for each pixel (30 m \times 30 m) through the difference between pre- and post-fire reflectance of two Landsat TM bands (bands 4 and 7) that respond to burning in divergent ways (Key and Benson 2006). Assessing burn severity of each plot involved calculating, using the dNBR image, the average of all pixel values within a radius of 15 m around the plot centre, and counting twice the pixel in which the plot centre was found, thus giving extra weight to the central pixel in the average as suggested by Key and Benson (2006) The calculation and extraction of dNBR values was done using the "raster" package (Hijmans 2013) of R (R Core Team. 2013). We also extracted the shortest distance from the centre of the plot to the continuous green forest outside the extent of the burn using ArcGIS (ESRI 2011), as it could serve as a source habitat for Monochamus (Boucher 2010; Boulanger et al. 2013; Gervais 2010; Saint-Germain et al. 2004a).

In this same visit of August 2011, as a proxy of damage caused by *Monochamus* spp., we evaluated the density of attacks by counting the number of entrance holes (ovoid shape) made by third instar larvae on seven trees randomly selected in each plot among the dominant tree species (i.e., either black spruce or jack pine). In the meantime, we also

counted the number of exit holes (round shape) made by emerging adults (Figure 7). Counts were done on a 50 cm section, centred on the DBH, that was previously debarked on each selected tree. In October 2012, 28 months after fire, we revisited each plot to record the final number of exit holes on the debarked section of each selected tree. To trace back the relationship between the time of our counts and the life cycle of *Monochamus*, please refer to Appendix 1.

4. Statistical analysis

Predictive variables are presented in Table 10, where we give for each a short description and sampled range by tree species. All variables were standardized by subtracting their average from each value and dividing it by the standard deviation, as suggested by Zuur *et al.* (2009). Then, we checked for correlation between the predictive variables and discarded the basal area of coniferous trees, which was correlated with the average diameter of sampled trees (r = 0.82). We kept tree diameter since it was the only variable that characterized the insect's habitat at the tree scale. Then, we assessed multicollinearity using the variance inflation factor (VIF) between the residuals of predictive variables, VIF values ranging between 1.07 and 1.12 (pers. comm. Dr. A.F. Zuur; O'Brien 2007).

4.1. Survival and developmental rates

To estimate *Monochamus* spp. survival rate from the third larval instar to adult emergence, we calculated the ratio of final count of exit holes over that of entrance holes. The relative developmental rate of *Monochamus* from the third larval instar to the adult stage was estimated by calculating the ratio of the first count of exit holes (number of individuals that completed their life cycle within 1 year, refer to Appendix 1) over the final count of exit holes (number of individuals that completed their life cycle in 1 or 2 years, refer to Appendix 1). All trees or sites for which no entrance hole was recorded were discarded from the calculation of the survival rate, leaving a total of 57 sites and 316 trees. For the calculation of the developmental rate, we also discarded trees or sites where no exit hole was recorded, thus leaving 51 sites and 240 trees for the analysis. To determine which factors affect the survival and developmental rates of *Monochamus* spp., we tested the effect of tree species (black spruce or jack pine), DBH and burn severity (dNBR) on both of

these ratios. This was done separately for each ratio through a generalized linear mixed model (GLMM), using a negative binomial distribution, which is useful for handling data sets showing high proportions of zeros (24% and 46% for survival and developmental rates, respectively) and overdispersion (Zuur *et al.* 2009). Plots were included as a random effect in the models since the debarked trees were statistically nested within plots.

4.2. Predicting longhorn beetle attack density

To predict longhorn beetle attack density, we first transformed raw counts of entrance holes into density of entrance holes (i.e., number of holes per m² of bole surface) as done by Saint-Germain et al. (2004a). We used a Hurdle model because the data set contained a large proportion of zeros (27% of the data set) and was overdispersed. This involves a twostep process based on two separate generalized linear mixed models (Zuur et al. 2009). First, we considered only presence/absence of *Monochamus*, and we thus used a binomial GLMM in which plots were included as a random effect to model the probability of finding an entrance hole (Min and Agresti 2005; Zuur et al. 2009). Second, the non-zero observations were modelled using a negative binomial GLMM (Min and Agresti 2005; Zuur et al. 2009). These two parts of the modelling process were named the "zero-part" and the "count-part" of the Hurdle model, respectively. GLMM analyses were done using the "Ime4" package (Bates et al. 2014) in R (R Core Team. 2013). For this analysis, all 60 plots were used. The predictive variables tested in both parts of the Hurdle model were tree species (black spruce or jack pine), tree diameter, distance to the green forest, basal area of deciduous trees, burn severity (dNBR) and its quadratic form (i.e., dNBR²). We also tested all possible interactions between tree species, burn severity and its quadratic form, and tree diameter, as suggested by Saint-Germain et al. (2004a). The final models for both the zeropart and the count-part were obtained through a manual stepwise selection process, where only significant variables were kept after testing all possible models (Zuur et al. 2009). Finally, we calculated a pseudo-R² value for each part of the Hurdle model through an adaptation of Nagelkerke's (1991) definition of the coefficient of determination, based on the work of Nakagawa and Schielzeth (2013). However, the calculated pseudo-R² values must be interpreted with caution, especially for the count part of the model, since Nakagawa and Schielzeth's (2013) methodology was not developed to be used with negative binomial distribution.

III. Results

In this study, we debarked a total of 434 trees to estimate longhorn beetle attack density and recorded 4,025 entrance holes (mean of 36 holes \cdot m⁻², maximum of 192 holes \cdot m⁻²) and 831 emergence holes (mean of 9 holes \cdot m⁻², maximum of 60 holes \cdot m⁻²). Overall, 38.4% of these emergence holes were recorded one year after fire and 61.6% were recorded two years after fire.

1. Variables affecting survival and development rates

GLMM analyses indicate that only the tree species had a significant effect on survival rate (Table 11), with a greater survival on jack pine (26,4%) than on black spruce (19,4%) (Figure 8). Analyses also showed a faster developmental rate on jack pine, as well as a faster developmental rate at high burn severity, the pattern being similar in both tree species (Table 11 and Figure 8). Tree diameter had no effect on either the survival or developmental rate.

2. Predicting longhorn beetle attack density

In the zero-part of the Hurdle model, the variables that were significant for predicting the presence/absence of *Monochamus* entrance holes were tree species, DBH, and burn severity, including its quadratic form (Table 12). The model also depicted three significant interactions, one between tree species and burn severity, a second one between tree species and the quadratic form of burn severity, and a third one between DBH and burn severity (Table 12). According to pseudo-R², the model explained 47% of the variability observed in the presence/absence data. Coefficients produced by the model were then used to predict the probability of finding entrance holes for each tree species as a function of tree diameter and burn severity (Figure 9). The model indicates that for both tree species, larger DBH trees had a higher probability of being attacked. However, different patterns were obtained for burn severity for each tree species. In fact, the odds for the presence of entrance holes increased rapidly with burn severity in black spruce, reached a long plateau, and then

steeply decreased at high burn severity, especially for small diameters (Figure 9). On the other hand, the rise in odds of finding entrance holes in jack pine is not as steep as in black spruce and has a sigmoid shape, reaching the highest odds at high burn severity (Figure 9).

For the second step (i.e., the count-part) of the Hurdle model, the variables that were significant for predicting the density of Monochamus entrance holes were tree species, burn severity and its quadratic form, as well as the basal area of deciduous trees (Table 12). According to the model, this last variable had a negative effect on the density of entrance holes in both tree species (Table 12). Tree diameter was significant only in interaction with burn severity. The model also indicates that there are other interactions between tree species and burn severity and between tree species and the quadratic form of burn severity. The model explained nearly 45% of count data variability, according to pseudo-R² (Table 12). The coefficients produced by this model predict entrance holes density for each tree species as a function of tree diameter and burn severity (Figure 10). To facilitate visualization and understanding of the interactions, the effect of deciduous trees basal area was not illustrated in Figure 10, but it is shown specifically in Figure 11. However, most interesting are the different ways in which the model predicts the density of entrance holes with regards to tree species and burn severity. Indeed, a clear quadratic effect of burn severity is depicted in black spruce, where the highest counts of holes are predicted around mid-severity values of dNBR (Figure 10), but in the case of jack pine, the highest density of entrance holes occurred at both the lowest and highest burn severity values. However, this "inverse quadratic" relationship is so weak, although significant, that we could almost consider it as flat. The results also predict a higher mean density of entrance holes in black spruce than in jack pine (Table 12 and Figure 10). No effect of the distance to the green forest was detected in the models.

IV. Discussion

Our results show that it is possible to predict the levels of attack by *Monochamus* spp. after wildfire, using few easily acquirable variables such as basal area of deciduous trees, tree species, stem diameter and burn severity. Our work also provides further insights into the

post-fire ecology of *Monochamus* spp.. This will help to improve salvage logging plans and thus reduce timber economic losses due to sawyer beetles.

In this study, 31% and 50% of Monochamus spp. individuals completed their life cycle in only 1 year on black spruce and jack pine, respectively. This is much higher than the 10% observed for the boreal region of Quebec (C. Hébert unpublished data) or the 25% reported for Alberta (Cerezke 1977). Such substantial differences between our study and these previous ones could be explained by climatic differences between the sampled areas and sampling years. Even if Monochamus attack density was higher on black spruce, its survival and developmental rates were greater on jack pine. Thus, if the presence of woodborer holes in jack pine is an issue for specific lumber products, managers might want to salvage jack pine more rapidly. In accordance with our results, Breton et al. (2013) have shown, under laboratory conditions, that Monochamus s. scutellatus preferred attacking black spruce than jack pine. However, contrary to our results, Breton et al. (2013) and Bélanger et al. (2013) suggested faster development on black spruce than on jack pine. These two studies were performed under controlled laboratory conditions, whereas our study uses data collected under natural conditions, where inter- and intraspecific competition could occur freely. Also, we evaluated the survival and development rates of Monochamus spp. while it was feeding on xylem (i.e., third instar to the adult stage), not on subcortical (or cambial) tissues as in Breton et al. (2013), where 80% of larval mortality occurs (Rose 1957). Moreover, as opposed to these studies (Bélanger et al. 2013; Breton et al. 2013), a second Monochamus species was present in jack pine trees. Indeed, 50% of Monochamus adults that emerged from jack pine were in fact M. mutator (unpublished data), a species living only in pines (Yanega 1996). Due to its co-evolution with pines, M. *mutator* may perform better than *M. s. scutellatus* in jack pine. This could partly explain the faster development and higher survival of *Monochamus* spp. on jack pine in our study.

Interestingly, we observed a faster developmental rate (i.e., a higher proportion of individuals completed their life cycle within 1 year) at high burn severity. To our knowledge this has never been reported in the literature and could simply be explained by the fact that, if all other things are equal, stands affected by a higher burn severity should have a warmer ambient temperature. This would be due to lesser shade caused by a

reduction in live tree crown and poor coverage by soil vegetation, which is mostly blackened at high burn severity. Also, a higher proportion of boles is strongly blackened from scorching, which obviously reduces the albedo effect and generates a warmer microclimate that hastens woodborer development. In turn, higher temperatures have been shown to increase the developmental rate of *Monochamus s. scutellatus* (Bélanger *et al.* 2013). The wide distribution of this insect across North America (Cerezke 1977; Raske 1972; Yanega 1996) attests for its ability to survive in different climatic conditions. This, as well as the insulating properties of xylem wood, could partly explain why the survival rate was not affected by the different conditions found across our wide range of burn severities.

Many environmental factors affect tree colonization by *Monochamus* spp. in burned stands (Bélanger 2013; Boulanger *et al.* 2013; Breton *et al.* 2013; Saint-Germain *et al.* 2004a), but to fully understand the ecology of these insects, one would have to consider several other factors. There is a hefty variability in *Monochamus* spp. attack levels, even between trees within a stand; indeed, while some trees can be full of longhorn galleries, other seemingly similar trees can have barely none (pers. observ.). This issue was considered in the statistical analysis conducted using the Hurdle GLMM. This model first allows to determine what are the odds of finding entrance holes, according to a set of predictive variables, while the second part of the model aims to determine where the attacks will be higher when present.

In black spruce, both the odds of finding entrance holes and the density of entrance holes followed a quadratic relationship with burn severity, as expressed by dNBR values. *Monochamus s. scutellatus* usually lay their eggs in trees where wood moisture varies between 10 and 50% (Dyer and Seabrook 1978). They have a lower survival rate on hosts with higher moisture content (Hanks 1999), such as live conifer trees, in which moisture content averages 77% for black spruce and 51% for jack pine (Nielson *et al.* 1985). Since burn severity is indicative of the strength of heat released during fire (Key and Benson 2006), wood moisture content is expected to decrease with increasing burn severity through heat desiccation (Cadorette-Breton 2014). We could thus hypothesize that the range of suitable moisture content for *M. s. scutellatus* depend on burn severity and rises up to a level at which burning is so intense that it decreases the moisture content to a level outside

this range of suitability (Gervais 2010). This could also alter the nutritional quality of phloem and cambium.

The pattern observed for jack pine was slightly different since the odds of finding entrance holes increased with burn severity. However, the density of entrance holes showed a slightly inverse quadratic relationship with burn severity that could almost be considered as flat. Jack pine has co-evolved with wildfire (Beaufait 1960; Chandler *et al.* 1983; Gauthier *et al.* 1996; Lamont *et al.* 1991) and mature trees have developed a thick scale bark that acts as an insulating layer against fire, thus reducing the desiccation of subcortical tissues (Farrar 1995; Smirnova *et al.* 2008). This adaptation might partly explain why the odds of finding entrance holes on jack pine trees are greater with a high burn severity. Yet, all combinations of tree diameter and burn severity in jack pine yielded similar amounts of attacks. However, it is important to remember that the patterns observed in jack pine are hardly comparable to those observed in black spruce, due to the presence of *M. mutator* in jack pine.

As expected, larger trees yielded greater odds and density of entrance holes in both tree species. Interestingly, neither the survival nor the developmental rate was affected by tree diameter. This suggests that DBH influences Monochamus spp. development when it feeds on cambium and phloem, when being at the first, second and early third larval instars. This may result from the correlation between tree diameter and subcortical tissue thickness (Guyette and Stambaugh 2004; Reid and Glubish 2001). Larger trees may thus offer better conditions for *Monochamus* spp. since phloem and cambium are the basis of early instar nutrition (Rose 1957), which could lead to the better survival of early instar larvae. The interaction found between tree diameter and burn severity is due to the fact that burn severity has a stronger effect on small trees, which have thinner bark and are less insulated to fire than large trees (Guyette and Stambaugh 2004; Smirnova et al. 2008). The decreased density of entrance holes linked with increasing basal area of deciduous trees may result from a reduction in stand attractiveness to colonizing adults of Monochamus. Indeed, one could hypothesize that the attractive effect of volatiles emitted by dead and dying coniferous trees on colonizing adults of Monochamus spp. might have been diluted by the presence of volatiles from dead and dying non-hosts deciduous trees.

1. Conclusion: how to use the predictive model

The models produced in this study are substantially flexible and useable by land managers as they use easily available continuous input variables. In this study we measured basal area and DBH on site and used it in our analysis for more precision. Although, estimation of basal area and DBH are available for land managers from ecoforest maps linked with a database inventory (stock data) of basal area; where for each stand they can find an estimation of the number of boles per tree species and diameter classes. Burn severity maps can be produced from Landsat images by referring to the materials & methods section of this chapter, to the Chapter I of this thesis, or even to Key and Benson (2006). The continuous form of our variables (basal area, stem diameter, and burn severity) are of the main reasons for our models' flexibility, as they allow to identify non linear relationships. This emphasizes the necessity of mapping burn severity with a continuous index such as dNBR (Jain et al. 2004), since the use of classified mapping of burn severity would be detrimental to the flexibility of such models. Our model are also flexible in the way they could be applied to any other burned stands of jack pine and black spruce of this boreal region. Moreover, we think the approach developed here could be applied in other geographical region, to other xylophagous species, as well as to other perturbations.

Our work could greatly help to reduce economic losses caused by *Monochamus* spp. through a better planning of salvage operations. The priority in this process is to determine the *Monochamus* spp. attack threshold that would be acceptable to land managers. This threshold should depend on the products manufactured with the salvaged boles, and be closely linked with the tolerance of the clients for these products. For example, land managers may accept a maximum of 95% of boles with entrance holes, regardless of tree species, but 1) might be relatively intolerant and would not accept more than 30 holes $\cdot m^{-2}$, or 2) might be relatively tolerant and willing to accept a maximum of 60 holes $\cdot m^{-2}$. According to these scenarios, we used the models presented in Figures 9 and 10 and drew plots (Figure 12) showing areas that fit these tolerances. This clearly indicates that if land managers want to salvage black spruce trees, they either have to harvest before *Monochamus* larvae have reached the third instar, or to be substantially tolerant to the

presence of holes in lumber. It would be easier to find jack pine trees with no or low levels of entrance holes. Such tools would be useful to land managers to identify which stands to avoid, as determined by the ranges of tree diameter and burn severity (dNBR). Finally, the next step for optimizing salvage logging would be to determine economic thresholds by linking the density of attacks (entrance holes \cdot m⁻²) on the outer surface of boles to actual damage recorded on sawn lumber.

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Tables

Sites	SOPFEU* code	Latitude	Longitude	Area (ha)	Cause	Date of ignition
Parent	270	48.127	-74.534	4 181	lightning	26/05/2010
Relais	267	48.015	-73.473	3 663	lightning	25/05/2010
Smokey	281	48.353	-73.325	105 254	lightning	25/05/2010
Vermillon	248	47.414	-74.020	5 840	lightning	24/05/2010
Wemotaci	274	48.006	-73.793	18 209	lightning	25/05/2010

Table 9. Information relative to the five selected burns.

*Société de protection des forêts contre le feu (SOPFEU).

 Table 10. Description, range and units of the predictive variables.

X7 ' 11	D	Range (unit)			
Variables	Description	Black spruce plots	Jack pine plots		
Distance to green forest	Shortest distance from the plot to the continuous green forest outside of the burn perimeter	55 - 3,840 (m)	35 - 2,624 (m)		
Basal area of coniferous trees	Total basal area of coniferous trees (mainly black spruce and jack pine) recorded in each plot	11.37 - 39.20 (m ² ·ha ⁻¹)	1.71 - 40.12 (m ² ·ha ⁻¹)		
Basal area of deciduous trees	Total basal area of deciduous trees (mainly birch and poplar) recorded in each plot	$0 - 4.74 (m^2 \cdot ha^{-1})$	$0 - 7.36 (m^2 \cdot ha^{-1})$		
Burn severity	Mean of every dNBR pixel value within a radius of 15 m around the plot centre, giving double weight to the pixel in which the plot centre is found	0.144 - 1.011 (dNBR)	0.214 - 0.961 (dNBR)		
Tree diameter	Diameter at breast height (DBH) of every sampled trees	10.5 - 23.9 (cm)	4.0 - 26.0 (cm)		

	Variable	Estimate	Std. Error	t-value	p-value
	Intercept	-1.7053	0.2576	-6.621	0.0000
Survival rate	Black spruce	0	-	-	0
	Jack pine	0.3126	0.1151	2.716	0.0066
	Diameter (DBH)	0.0103	0.0131	0.785	0.4323
	Burn severity (dNBR)	-0.1750	0.2379	-0.735	0.4621
velopmental rate	Intercept	-1.5963	0.3220	-4.957	0.0000
	Black spruce	0	-	-	0
	Jack pine	0.4777	0.1388	3.443	0.0006
	Diameter (DBH)	-0.0217	0.0165	-1.313	0.1891
De	Burn severity (dNBR)	1.0999	0.3154	3.488	0.0005

Table 11. Generalized linear mixed model results for both the survival (third instar to adult) and developmental (first-year emergences/total emergences) rates, including the plots as a random effect and using a negative binomial distribution.

	Variable [*]	Estimate	Std. Error	t-value	p-value
	Intercept	3.5607	0.6832	5.21	0.000
ence/Absence)	Black spruce (BS)	0	-	-	0
	Jack pine (JP)	-1.9516	0.8219	-2.37	0.018
	Diameter (DBH)	1.1008	0.3334	3.30	0.001
	Burn severity (dNBR)	9.9292	2.7882	3.56	0.000
	dNBR ²	-9.5227	2.7734	-3.43	0.001
res	$BS \times dNBR$	0	-	-	0
Zero-part (P	$JP \times dNBR$	-8.0918	4.1805	-1.94	0.053
	$BS \times dNBR^2$	0	-	-	0
	$JP \times dNBR^2$	9.3504	4.3404	2.15	0.031
	$DBH \times dNBR$	1.0076	0.3330	3.03	0.002
				[†] Pseudo-R ²	0.475
Count-part (holes·m ⁻²)	Intercept	3.9394	0.0937	42.06	0.000
	Black spruce (BS)	0	-	-	0
	Jack pine (JP)	-0.6405	0.1422	-4.50	0.000
	Diameter (DBH)	0.0147	0.0718	0.20	0.838
	Burn severity (dNBR)	1.5384	0.5066	3.04	0.002
	dNBR ²	-1.5897	0.4872	-3.26	0.001
	Deciduous basal area	-0.2467	0.0761	-3.24	0.001
	$BS \times dNBR$	0	-	-	0
	$JP \times dNBR$	-2.2907	0.9214	-2.49	0.013
	$BS \times dNBR^2$	0	-	-	0
	$JP \times dNBR^2$	2.3629	0.9019	2.62	0.009
	$DBH \times dNBR$	0.2037	0.0820	2.48	0.013
				[†] Pseudo-R ²	0.447

Table 12. Hurdle model results for the presence/absence (binomial distribution) and density of entrance holes (holes m⁻²; negative binomial distribution), including the plots as a random effect. Final models were obtained from a stepwise model selection, in which we excluded the variables that were not significant.

*All continuous variables have been standardized (i.e., we subtracted the mean and divided by the standard deviation) prior to the analysis.

[†]Pseudo-R² obtained through an adaptation of Nagelkerke (1991) and MuMIN (Nakagawa and Schielzeth 2013) R package.

Figures



Figure 6. Study area is located in the Haute-Mauricie region of Quebec, Canada (black star in bottom right frame) along with the spatial distribution of the sampling plots (black dots) within the five studied burns (grey areas in the left frame; burn's name in text boxes).



Figure 7. Ovoid-shaped entrance hole made by a third instar larva, and round-shaped exit hole made by an adult of *Monochamus* spp. on a burned bole.



Figure 8. Results of the GLMM models showing increased survival rate (fitted values) with increased burn severity, and greater survival rate (left), and greater developmental rate (right) in jack pine.



Figure 9. Graphical visualisation of the odds of having an entrance hole as a function of burn severity (dNBR) and tree diameter (DBH). These graphs are based on the zero-part of the Hurdle model. Graphics at the top represent the black spruce model and the ones at the bottom represent the jack pine model; the left and right graphics are alternate views of the models.



Black spruce



Figure 10. Graphical visualisation of the density of entrance holes $(nb \cdot m^{-2})$ as a function of burn severity (dNBR) and tree diameter (DBH). These graphs are based on the Count-part of the Hurdle model. Graphics at the top represent the black spruce model and the ones at the bottom represent the jack pine model; the left and right graphics are alternate views of the models.



Figure 11. Graphical visualisation of the predicted density of entrance holes as a function of basal area of deciduous trees, obtained from the Count-part of the Hurdle model. Dots represent black spruce stands and triangles represent jack pine stands.



Figure 12. Exemplification of the use of the predictive model indicating where, in terms of tree species, tree diameter and burn severity, the odds of finding entrance holes (top plots) and the density of holes of *Monochamus* (middle and bottom plots) do not respect the "fictive" tolerance of land managers (orange areas). Shaded gray areas indicate where managers could salvage according to their tolerance. Plots on the left of the figure correspond to black spruce, while those on the right are for jack pine.

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Appendix



Appendix 1. One year (black) and two years (gray) life cycles of *Monochamus* spp. (adapted from Vallentgoed 1991), and indications of when the first and second field counts were done.

CHAPITRE III

High conservation value forests for burn-associated saproxylic beetles: an approach for developing sustainable post-fire salvage logging in boreal forest
Résumé

Les arbres tués par le feu sont considérés comme une perte de revenus potentiels et sont donc de plus en plus récupérés, non sans inquiétude pour la conservation de la biodiversité. En effet, une grande diversité de coléoptères saproxyliques associés aux brûlis utilisent des arbres récemment brûlés pour leur reproduction. Par conséquent, ces coléoptères fournissent des services écologiques importants (ils sont la base de l'alimentation d'oiseaux insectivores, contribuent à la décomposition du bois mort et au recyclage des éléments nutritifs). Cette étude vise à réduire les impacts potentiels de la coupe de récupération sur la biodiversité, en identifiant les forêts à haute valeur de conservation (FHVC) pour les espèces associées aux brûlis, qui sont considérées plus à risque. Dans cinq feux allumés naturellement en 2010 dans la forêt boréale du Québec, au Canada, nous avons sélectionné des peuplements dominés par l'épinette noire (n = 31) et le pin gris (n = 29), dans lesquels nous avons récolté trois bûches de 50 cm, qui ont été placées dans des cages d'émergence pour mesurer la colonisation des arbres par les coléoptères saproxyliques. De ces bûches, 7 235 coléoptères provenant de 103 taxons ont émergé, dont 67 sont considérés rares (<5% d'occurrence dans les bûches) et 36 taxons comme communs (>5% d'occurrence dans les bûches) ont été utilisés pour l'analyse. Parmi les espèces communes, nous avons identifié six groupes d'espèces écologiquement liées à l'aide de la classification hiérarchique basée sur la cooccurrence (co-occurrence-based hierarchical clustering). Parmi ces groupes, trois sont principalement formés d'espèces opportunistes, qui sont actuellement de peu d'intérêt dans un contexte de récupération après-feu. Les trois autres groupes ont été formés par des espèces associées aux brûlis qui pourraient être affectées par la coupe de récupération. Les FHVC inclues les peuplements de pins gris et les grosses tiges, de l'une ou l'autre des essences, affectées par des sévérités du feu faibles à moyennes. Nous recommandons également de maintenir la périphérie des peuplements brûlés, puisque ces écotones sont des habitats riches utilisés par plusieurs espèces associées aux brûlis. Ces espèces se retrouvent en faibles abondance en forêt verte, mais bénéficient d'habitats brûlés pour augmenter significativement leur population.

Mots-clés

Biodiversité, coléoptères saproxyliques, après-feu, conservation, sévérité du feu, coupe de récupération

Abstract

Fire-killed timber is considered as a loss of potential revenues and is thus increasingly salvaged, though not without concerns for biodiversity conservation. Indeed, a large diversity of burnassociated saproxylic beetles use recently burned trees. This study intends to reduce potential impacts of salvage logging on biodiversity by identifying High Conservation Value Forests (HCVFs) for burn-associated beetles, which are considered the most at risk. In five burns ignited naturally in 2010 in the eastern Canadian boreal forest, we selected 31 and 29 stands of black spruce and jack pine respectively. Three 50 cm bole segments were retrieved from each stand and placed in emergence cages to measure tree utilization by saproxylic beetles. This yielded 7,235 beetles from 103 taxa, of which 67 were considered rare (<5% occurrence in logs) and 36 as common taxa (>5% occurrence in logs). Among the common taxa, we identified six groups of ecologically related species using co-occurrence-based hierarchical clustering, among which three were mainly formed by opportunistic species that are currently of little concern in a postfire logging context. The three other groups were formed by burn-associated species that could be affected by salvage logging. HCVFs include jack pine stands and large trees of either tree species of low- to mid-range burn severity. We also recommend retaining the periphery of burned stands, as ecotones are rich habitats used by several burn-associated species that are found in low numbers in green forests but they benefit from burned habitats by increasing their populations significantly.

Key words

Biodiversity, saproxylic beetle, post-fire, conservation, burn severity, salvage logging, boreal forest, High Conservation Value Forest

I. Introduction

Stand-replacing wildfires in boreal forest generate large inputs of freshly killed trees at the landscape scale (Siitonen 2001; Drapeau *et al.* 2002; Kennedy & Fontaine 2009). Considered as a loss of potential revenues, this fire-killed timber is increasingly salvaged for lumber production (Dellasala *et al.* 2006; Lindenmayer *et al.* 2008) and is now also considered for bioenergy production (Gautam *et al.* 2010). Salvage logging is raising concerns for conservation (Dellasala *et al.* 2006; Lindenmayer *et al.* 2008) because deadwood provides habitat and food resources for a large diversity of saproxylic organisms (Vallauri *et al.* 2005; Stokland *et al.* 2012), i.e. those that depend on deadwood to complete at least part of their life cycle (Speight 1989). Beetles form a substantial portion of saproxylic organisms (Niemelä 1997; Siitonen 2001) and provide important ecological services. They constitute the basic diet of many vertebrate species (Morissette *et al.* 2002; Kennedy & Fontaine 2009; Nappi & Drapeau 2009; Nappi *et al.* 2010) and they are involved in deadwood decomposition (Speight 1989; Kim 1993; Boulanger & Sirois 2007), which contributes to forest nutrient cycling (Cobb *et al.* 2010).

Promptly after fire, many saproxylic beetles colonize burns, where they use recently killed trees as breeding substrates (Muona & Rutanen 1994; Hjältén et al. 2007; Boulanger & Sirois 2007; Boulanger et al. 2010; Cobb et al. 2011; Azeria et al. 2012b). This is due to the distinctive conditions found in burns, e.g. large amounts of deadwood are produced in a short period of time (Drapeau et al. 2002), deadwood is fully exposed to the sun (Jonsell et al. 1998), and subcortical tissues remain suitable for several weeks or months (Boulanger & Sirois 2006). These conditions have been shown to yield distinctive saproxylic beetle communities in burned habitats (Saint-Germain et al. 2004a; Boulanger & Sirois 2007; Boulanger et al. 2010; Boucher et al. 2012). Nevertheless, saproxylic beetle communities are not homogeneous within burns. They were shown to vary according to attributes such as burn severity, tree species and tree diameter (St-Germain et al. 2004; Boulanger et al. 2010; Azeria et al. 2012). Moreover, many saproxylic beetles found in burns are known as opportunistic species, i.e. they are also found in dead trees produced by other types of disturbances and thus colonize burned trees simply because of their great availability (Nappi et al. 2004; Saint-Germain et al. 2008; Boucher et al. 2012). On the other hand, other species are called "fire-favoured" (Johansson et al. 2007), "fire-associated" (Kouki et al. 2011) or "burn-associated" species because of their close association with the

burned substrate, and are considered more at risk in a salvage logging context (Boucher *et al.* 2012).

In Fennoscandian boreal forests, intensive forest management and extensive fire suppression have led several saproxylic species conspicuously favoured by fire to be considered as threatened (Wikars 1992, 1997; Siitonen 2001; Hyvärinen et al. 2006; Toivanen & Kotiaho 2007). Even the use of prescribed burning to restore natural ecological properties of these forests does not allow recovery of several red-listed species when landscapes have lost their ecosystem integrity for a long time (Kouki et al. 2011). In North America, logging history is much younger in the boreal forest and as a consequence, ecosystem integrity is much higher. Thus, large wildfires that were naturally ignited still offer an opportunity for promoting post-fire biodiversity conservation in natural landscapes. Orientations for implementing ecosystem-based management in burned forest have been provided recently in Quebec, Canada (Nappi et al. 2011). Roughly, it was recommended that 30% of burned forests be maintained at the landscape scale, with a minimum threshold of 15% in each burn. The identification of the key forest attributes needed to maintain burn-associated species, which are the most threatened by salvage logging, would improve these first recommendations. Such an approach, which would ensure conservation of specialized biodiversity associated with a specific type of disturbance such as wildfire, responds to the definition of the concept of High Conservation Value Forests (HCVFs), developed for certifying forestry practices (FSC 1996).

Our study is thus intended to gather comprehensive information and make it readily available for integrating biodiversity conservation when preparing salvage logging plans. In such a perspective, models should use variables already identified as good predictors of saproxylic beetle diversity, and that are easily available to land managers, such as burn severity, tree species and tree diameter (Saint-Germain *et al.* 2004b; Azeria *et al.* 2011b 2012a; Boucher *et al.* 2012; Boulanger *et al.* 2013). That will constitute the basis for identifying HCVFs for burn-associated species and serve to improve ecosystem-based management in burned boreal forests.

In this study, we hypothesized that (1) species richness, a widely used metric in biodiversity conservation, would only provide general guidelines for identifying post-fire HCVFs because it is blurred by the responses of burn-associated, opportunist and generalist species. As saproxylic

beetles can show contrasting patterns and responses to burned habitat characteristics (Azeria *et al.* 2012b), we also hypothesized that (2) burn-associated species might be more ecologically related and could co-occur in specific groups. Finally, we expected that (3) species richness in these groups and the presence of burn-associated species could be useful to identify HCVFs.

II. Materials and methods

1. Study area and plot selection

Five burns, ignited by lightning between May 24 and 26, 2010 were selected in the Haute-Mauricie region of Quebec, Canada (Figure 13). The burns were located between 47-49°N and totaled around 137,000 ha. In this boreal region, the forest landscape consists of mixed stands dominated by balsam fir (*Abies balsamea* (L.) Mill.) and white birch (*Betula papyrifera* Marsh.), but species prone to fire, such as jack pine and black spruce, are well represented (Doucet & Côté 2009). In selected burns, pre-fire forest composition was dominated by coniferous stands (54%), followed by mixed (37%) and deciduous (9%) stands. Burned coniferous stands were dominated by black spruce (*Picea mariana* (Mill.) BSP) followed by jack pine (*Pinus banksiana* Lamb.), which accounted respectively for 65% and 16% of the stands.

Stands were selected using the ministère des Forêts, de la Faune et des Parcs (MFFP) burn severity maps and ecoforest maps. These maps served to locate black spruce and jack pine dominated stands and to sample the widest range of burn severity. A field validation was done in May 2011 to retain pre-selected stands and establish a plot within each stand. Stands retained were homogeneous in terms of burn severity, species composition, tree density and height. We established 60 plots in residual forest stands among the five burns: 31 plots in black spruce stands and 29 plots in jack pine stands (Figure 13).

2. Beetle sampling

To measure burned tree colonization by saproxylic beetles, we selected three trees of the dominant species (black spruce or jack pine) in each plot with a diameter at breast height (DBH, measured 1.3 m from highest root) and burn severity that represented the average at the plot level. Trees were cut and 50 cm bole sections centred on the tree DBH were retrieved between

June 10 and 20, 2011, approximately 1 year after fire, once initial saproxylic beetle colonization was completed (Boulanger & Sirois 2007; Azeria *et al.* 2012b). In certain jack pine plots (six plots) where mean DBH was smaller than 9 cm (i.e. non-commercial size), we selected six trees and retrieved six bole sections to collect a sufficient number of insects for statistical analysis.

To identify close relationships between the progeny of beetle colonizers and their habitat needs (i.e. deadwood characteristics), we placed each bole section in a ventilated emergence cage. This method has proven its efficacy to translate the habitat suitability of the sampled piece of wood, as the emergence cages capture insects that successfully emerge (Wikars et al. 2005; Toivanen & Kotiaho 2010; Azeria et al. 2012b; Boucher et al. 2012; Boulanger et al. 2013). Overall, we collected a total of 198 bole sections that were placed in emergence cages from late June 2011 to early November 2012, thus ensuring the collection of insects with a 2-year life cycle, such as Monochamus species for instance (Peddle et al. 2002; Boucher et al. 2012; Bélanger et al. 2013). Prior to being placed in cages, both ends of logs were waxed to prevent excessive drying during the rearing period (Saint-Germain et al. 2004b; Wikars et al. 2005). Emergence cages consisted of 20 L plastic buckets, in which bole sections were suspended vertically to maintain their natural orientation. At the lower end of the bucket, a funnel led to a collecting vial filled with a preservative solution composed of 40% ethanol and 5% household vinegar (acetic acid). Emergence cages were installed in the field insectarium of the Laurentian Forestry Centre (LFC) of the Canadian Forest Service of Natural Resources Canada (CFS-NRCan) situated in Quebec City, QC, Canada. Vials were serviced bi-monthly throughout the study. Every beetle that emerged was identified to the lowest taxonomic level possible. Beetle identifications were verified at the René-Martineau Insectarium of the LFC.

3. Predictive variables

We recorded the DBH of each tree from which a bole section was retrieved to test the effect of host size on the saproxylic beetle community. We also carried out a forest inventory in each plot, within an 11.28 m radius (0.04 ha), in which each individual tree was identified and its DBH measured. This allowed us to calculate the basal area of coniferous and deciduous trees. Such an inventory is commonly used by foresters to estimate forest stand characteristics (Doucet & Côté 2009).

Burn severity is defined as the degree to which the ecosystem has changed owing to fire (Lentile et al. 2006). This is symptomatic of the strength of smouldering combustion that is expected to reduce cortical and cambial water content, alter the chemical composition of phloem, and thus affect the overall nutritional quality of fire-killed snags for saproxylic species (Boulanger & Sirois 2006; Boucher 2010; Azeria et al. 2012a). Burn severity was evaluated for each plot using the differenced Normalized Burn Ratio (dNBR; Key & Benson 2006). First, we produced the dNBR image from Landsat 5 Thematic Mapper Climate Data Records scenes (pre-fire: August 27 2007; post-fire: July 2 2010). The dNBR was computed for each pixel ($30 \text{ m} \times 30 \text{ m}$) through the difference between pre- and post-fire reflectance of two Landsat 5TM bands (band 4 and band 7) that respond the most, but in divergent ways, to burning (Key & Benson 2006). Then, each plot burn severity value was obtained by taking, from the dNBR image, the mean of every pixel value within a 15 m radius around the plot centre, giving a double weight to the pixel in which the plot centre was located (for more information on the methodology, please refer to Key & Benson (2006) and to Chapter I of this thesis. Since some saproxylic beetles are known for their non-linear response to burn severity, we also included a second-order polynomial (quadratic) term of burn severity in the analyses (Boulanger et al. 2010). We also extracted the shortest distance from the centre of the plot to the continuous green forest (distance to green forest) outside the extent of the burn as it could serve as a source habitat for colonizing saproxylic beetles (Saint-Germain et al. 2004c; Boucher 2010; Gervais 2010; Boulanger et al. 2013). This was done using ArcGIS (ESRI. 2011).

4. Statistical analysis

4.1. Identification of habitat attributes favouring richness of saproxylic beetles

We examined how species richness of saproxylic beetles per bole relates to a post-fire environment with generalized linear mixed models (GLMM). Trees were considered as the experimental unit in the analysis. Plots were included in the model as a random effect, since the selected trees from which we retrieved the bole sections were statistically nested within the plots. GLMM was performed with species richness of all captured species, with richness of common (i.e. species present in more than 5% and less than 95% of plots) and rare (i.e. species present in less than 5% of the plots) species as dependent variables.

Before running the GLMM analysis, we standardized all continuous predictive variables (listed in Table 13) by subtracting the mean from each value and dividing it by the standard deviation (Zuur *et al.* 2009). We then assessed correlation between predictive variables, and found that the basal area of coniferous trees was correlated with the average diameter of sampled trees (r = 0.82). We thus discarded the basal area of coniferous trees and kept the tree diameter because it was our only tree-scale variable, and Boulanger *et al.* (2010) reported that tree diameter had a stronger influence on diversity than basal area. Finally, we assessed multicollinearity using the variance inflation factor (VIF) between the residual predictive variables. This did not reveal any problems, as VIF values ranged between 1.07 and 1.12 (Zuur *et al.* 2009).

4.2. Species groups from co-occurrence patterns of pairwise associations

We aimed at identifying groups of ecologically related species by classifying saproxylic beetles into species groups using their spatial co-occurrence in bole sections. To do so, we combined a null model of species co-occurrence with a cluster analysis allowing the identification of groups of species that should co-occur beyond random expectations (Azeria et al. 2009). We discarded rare (i.e. present in less than 5% of plots) and ubiquitous species (i.e. present in more than 95% of plots; only Acmaeops p. proteus) due to the limited information they provide on cooccurrences, leaving 36 common species for the analysis (Appendix 2). We followed the threestep approach proposed by Azeria et al. (2009). As a first step, we computed a dissimilarity matrix between all species pairs in the original presence-absence matrix (Disobs) using the Sorensen-based coefficient of dissimilarity. The second step was the calculation of the species pairwise dissimilarity matrix that would be expected by chance alone, given the species' frequencies. This was obtained by producing 1000 null matrices by randomizing the original distribution matrix using a fixed row-fixed column null model (Gotelli 2000; Azeria et al. 2009). We then extracted the mean DissimMean and standard deviation DissimsD from the 1000 simulated null matrices for each species pair. Subsequently, we computed the standardized effective species pairwise dissimilarity that occurs beyond "random" expectations as:

Disses = (Disobs - DissimMean) / DissimSD

The values of Disses were rescaled to distances between 0 and 1, where values near 0 indicate that species strongly co-occur (aggregate), and values near 1 indicate the inverse (segregate). The third step of the Azeria *et al.* (2009) approach is to derive species groups that best fit the rescaled Disses data using hierarchical clustering with Ward's agglomeration method. Finally, we determined the optimal number of clusters (species groups) in the hierarchical tree using the "kgs" function implemented in the maptree package for R (White 2010; R Core Team. 2013). Cluster analysis is a non-parametric approach that produces a classification that can be interpreted as hypotheses of ecological similarities between species. This classification is the result of species responses to habitat features as well as of interspecific interactions (Azeria *et al.* 2011a).

Thus, to validate this classification, still following the methodology proposed by Azeria *et al.* (2009), we tested if, as expected, species within groups co-occur more often, due to their ecological similarity, than between groups (Peres-Neto 2004; Azeria *et al.* 2009). As a mean of testing these expectations, we determined the frequency of significant aggregated (positive) and segregated (negative) pairwise associations within and between groups using the results of the species pairwise tests described above (Azeria *et al.* 2011a). The between-groups aggregated and segregated pairwise associations show how the groups relate to one another. We also outlined both strongest aggregated and segregated association between each group.

4.3. Identification of High Conservation Value Forests (HCVFs)

To identify HCVFs, we need to better understand what factors affect the distribution of saproxylic beetle diversity, and particularly "burn-associated" species. We thus ran the same type of GLMM analysis as previously explained to model the richness of each species group obtained by the hierarchical clustering, as a function of our six predictive variables. Again, we tested all predictive variables and all interactions between tree species, burn severity and its quadratic form, and tree diameter (Saint-Germain *et al.* 2004c; Chapter II of this thesis). The final models were also obtained through a stepwise selection process, where we only kept significant variables (Zuur *et al.* 2009).

We also modelled the presence/absence of each burn-associated species and the abundance (n/m^2) bole) of the ubiquitous *Acmaeops proteus proteus* (Kirby) (present in more than 95% of

plots). The use of GLMM allowed us to handle the non-Gaussian distribution of our data, characterized by many null or low species occurrences, by using the Poisson distribution, negative binomial distribution, and binomial distribution. The best distribution for each model was determined by looking at overdispersion, as well as through model comparison using the Akaike Information Criterion (AIC) (Akaike 1974; Bolker 2009; Zuur *et al.* 2009). We tested all predictive variables and all interactions between burn severity, the quadratic form of burn severity, tree species, and tree diameter (Saint-Germain *et al.* 2004c; Chapter II of this thesis). Final models were obtained through a stepwise selection process, keeping only significant variables (Zuur *et al.* 2009). GLMM analysis was run using the "lme4" package (Bates *et al.* 2014) for R (R Core Team 2013).

III. Results

A total of 7,235 beetles from 28 families and 103 taxa emerged from the bole sections, among which 33% of taxa were found only in black spruce and 25% only in jack pine. The 36 common species used in the cluster analysis represented 77% of overall abundance of saproxylic beetles, and 66 species were considered as rare species, since they were present in less than 5% of plots.

1. Identification of habitat attributes favouring richness of saproxylic beetles

Models aiming to predict the overall species richness and the richness of common species both indicated that there were more saproxylic species in larger diameter trees affected by low burn severity but there was no effect of tree species (Table 14). The number of common species was higher close to the green forest. The richness of rare species was greater in lower burn severity stands.

2. Species groups from co-occurrence patterns of pairwise associations

The co-occurrence-based hierarchical clustering yielded six groups of species (Figure 14, Table 15). From left to right in Figure 14, species groups #1 to #6 were formed respectively by 5, 7, 4, 5, 6, and 9 taxa. Group #2 contained the highest number of beetles, while group #6 had the lowest (Table 15). Group #5 contained the highest number of burn-associated species (3), while groups #1, #3, #4 and #6 each had one such species. Group #2 was the only one with no burn-associated species, though it contained four opportunistic species (Figure 14). Groups #4 and #5 also contained one opportunistic species. These groups were respectively dominated by *B*.

unicolor and *S. virescens*. Interestingly, out of the eight staphylinid taxa, four species were found to co-occur with *Monochamus s. scutellatus* in group #1. Three staphylinid taxa co-occured with *Acmaeops pratensis* (Laicharting), the most abundant species of group #6. In the case of group #3, the most abundant taxon was immature Corylophidae sp.1, followed by the burn-associated *C. fusca*. Along with these results and to simplify the reading of the paper, we renamed the species groups according to the dominant burn-associated species: group #1 became "scutellatus group", group #3 "fusca group", group #4 "mutator group", group #5 "virescens group", and group #6 "pratensis group". Group #2 was renamed the "bark beetles group" since there were no burn-associated species in this group and bark beetles dominated it.

The cohesion of species groups was further validated by stronger aggregated (positive) than segregated (negative) pairwise species associations within groups (Table 16). Species of the bark beetles group had the strongest aggregated pairwise species associations within the group, followed by the fusca group, whereas the virescens group had the lowest aggregated pairwise associations within its group, followed by the pratensis group (Table 16). The virescens group also had strong segregated associations with the scutellatus and mutator groups. The virescens and pratensis groups were the only ones to always show more segregated than aggregated associations with the other groups. The strongest aggregated association between groups was observed for the scutellatus and mutator groups.

3. Identification of High Conservation Value Forests (HCVFs)

Models on the presence/absence of burn-associated species yielded significant results only for *Monochamus scutellatus scutellatus* (Say), *Clypastraea fusca* (Harold) and *Sphaeriestes virescens* (LeConte) (Table 17). The occurrence of *Monochamus s. scutellatus* was maximized in large black spruce trees affected by mid-range burn severity. The probability of encountering *Clypastraea fusca* was also maximized in mid-range burn severity stands. The model for *Sphaeriestes virescens*, though marginally significant, indicated that the odds of finding this species were higher in smaller trees. Finally, the abundance (n/m² bole) of the ubiquitous species *Acmaeops p. proteus* was higher in stands of large black spruces with low burn severity and low basal area of deciduous trees.

Modelling species richness of each group provided different responses to habitat variables (Table 18). The species richness of the scutellatus group was higher in black spruce, larger diameter trees and in the mid-range of burn severity. A significant interaction was also depicted between tree diameter and burn severity. Modelling showed that species richness of the bark beetles group was maximized in black spruce and in low burn severity. Species richness of the fusca group was higher in mid-range burn severity while that of the mutator group was maximized in large-diameter jack pine trees close to the continuous green forest, also in mid-range burn severity. A significant interaction between tree diameter and burn severity was also depicted in the latter model. Species richness of the virescens group, to which belonged three burn-associated species, was higher in small diameter trees that were somewhat close to continuous green forest, while species richness of the pratensis group was maximized in large diameter trees of stands with low burn severity.

IV. Discussion

1. Identification of habitat attributes favouring richness of saproxylic beetles

As expected in our first hypothesis, species richness provides only general information for defining ecosystem-based management guidelines for post-fire salvage logging, with no reference to tree species. Our results showed that overall species richness was highest in large, slightly burned trees. This is similar to unburned conditions, as it is already known that larger diameters are correlated with thicker bark and phloem (Reid & Glubish 2001), which offers better conditions for the development of saproxylic beetles (Rose 1957; Boulanger et al. 2010; Breton et al. 2013). Snags in low burn severity plots were mainly killed by root and stump girdling due to fire heat (field observations), in which the nutritional quality of the cambium is assumed to be less deteriorated than those of scorched trees (Wikars 2002; Johansson et al. 2006). However, it should be noted that tree diameter does not always influence species richness as only minor differences were found in species number between diameter classes of four tree species in Sweden (Jonsell et al. 2007). In stands of low burn severity, we also observed higher heterogeneity in fire-killed tree characteristics (e.g. percentage of residual live crown) as compared with higher burn severity stands (field observations). Conditions found in low burn severity stands could also yield many saproxylic species that usually thrive in unburned forests containing fresh snags resulting from other disturbances (Boucher et al. 2012). However, cooccurrence analysis allowed us to capture more complex responses among species assemblages (Marquet *et al.* 2004) compared with what had been highlighted through species richness analysis. Analyses of biodiversity based on species richness are rather rough and could even be misleading (Fleishman *et al.* 2006; Koivula & Spence 2006; Azeria *et al.* 2009), especially when it comes to issues such as wildfire, where it is likely that a few specialized species may depend on such an extreme type of habitat. Their responses are blurred by the mass of opportunist and common generalist species.

2. Identifying groups of ecologically related species

Saproxylic beetle diversity in post-fire habitat is spread across the environment due to the specific needs of species (Boucher & Hébert 2010; Boulanger et al. 2010). Yet, some species have a similar affinity to their environment, as expressed by their co-occurrence in burned boles (Azeria et al. 2012b). Our work permitted us to identify six groups of ecologically related species in burned boles of black spruce and jack pine. However, burn-associated species were not grouped in one or two of these groups as hypothesized but rather spread among five out of the six groups. This indicates that they respond differently to various environmental attributes of burned forests. We also observed that the strength of cohesion within groups varied, and could be due to interspecific interactions and habitat requirements (Azeria et al. 2012b). For instance, lower aggregated pairwise species associations found within the virescens and pratensis groups could be explained by a lower abundance and occurrence of taxa, and the opposite could explain the strong aggregated pairwise species associations observed for the bark beetles group, which had the highest abundance. Though the bark beetles and pratensis groups were both favoured by low burn severity stands, they showed more segregated than aggregated pairwise associations between them. This could be explained by interspecific competition due to high abundance of scolytids in the bark beetles group, or even to some other unmeasured variables. Azeria et al. (2012b) indicated that A. pratensis, the most abundant member of the pratensis group, tends to show segregated patterns with other competing phloem-feeder species, such as Acanthocinus pusillus Kirby and scolytids forming the bark beetles group. This could also partly explain the lower cohesion (or aggregated pairwise associations) between species in the pratensis group. It suggests that this latter group could be defined mainly by interspecific interactions rather than by habitat attributes. This could be a major challenge for implementing conservation guidelines as

most policies are based on habitat attributes. Lower group cohesion could also result from more generalist species in their habitat choice.

3. Identification of High Conservation Value Forests (HCVFs)

The first three groups appear to be of low conservation concern in the context of post-fire salvage logging. Even if they have been found to be statistically associated with burns (Boucher *et al.* 2012), *M. s. scutellatus* and *C. fusca* are known for thriving in unburned forest (Légaré 2010; Boucher *et al.* 2012). Indeed, *M. s. scutellatus* is recognized as a major economic pest by the forest industry (Ross 1960; Chapter II of this thesis). All other species of these groups, as well as those of the bark beetles group, are known for thriving in unburned coniferous forests (Saint-Germain *et al.* 2008; Légaré 2010; Boucher *et al.* 2012; Brunke *et al.* 2012) and should not be directly of concern in post-fire management decisions. Nevertheless, they represent important food sources for bark-insectivore bird species that are associated with burns, such as the black-backed woodpecker (*Picoides arcticus*) and the three-toed woodpecker (*Picoides tridactylus*) (Murphy & Lehnhausen 1998; Imbeau *et al.* 1999; Nappi *et al.* 2003; Azeria *et al.* 2011c). We should thus attenuate the statement that there are no conservation issues concerning species of the scutellatus, bark beetles, and fusca groups, as a potential decrease in their occurrence (or abundance) due to salvage logging activities could hinder the ecological services they render by negatively affecting species of higher trophic levels (Azeria *et al.* 2011c).

Species that belong to the last three groups could be potentially threatened by post-fire salvage logging. For instance, the mutator group was the only one to be clearly linked to jack pine, and it contained *Monochamus mutator* LeConte, which is specific to pine trees (Azeria *et al.* 2012b; Boucher *et al.* 2012), as well as *Boros unicolor* Say, which is known to be associated with jack pine (though also occasionally found on black spruce) and to co-occur with *M. mutator* due to facilitative interaction (Azeria *et al.* 2012b). Indeed, *B. unicolor* feeds on frass of phloem feeders such as *M. mutator* (Savely 1939). In our study area, jack pine stands also have a high conservation value because they represent only 16% of coniferous stands. It means that less than 5% of the territory might be left as burned jack pine stands, if 70% of burned stands were to be salvaged as allowed by current guidelines in Quebec. Moreover, jack pine burn-associated beetles might have adapted more markedly to fire as they have closely co-evolved with a tree species well adapted to recurrent wildfires (Farrar 1995; Pausas *et al.* 2004). If this hypothesis is

deemed true, then salvage logging in jack pine stands might increase stand fragmentation to such an extent that it could exceed the resilience of burn-associated beetles (McPeek & Holt 1992; Le Goff *et al.* 2008). More generally, post-fire salvage logging might threaten host-specific insects of any stand type poorly represented at the regional scale. This could become even worse if stands left over by salvage logging were to be considered for late harvesting by the bioenergy industry (Barrette *et al.* 2013).

The virescens group counts the highest number of burn-associated species. Moreover, Cortinicara gibbosa (Herbst) is considered as opportunistic in the eastern Canadian boreal forest, but this Holarctic species has been identified as fire-favoured in Sweden (Lundberg 1984; Wikars 2006; Milberg et al. 2014). This group could thus be considered to be more at risk when it comes to the salvage logging effect due to its close association with fire-killed trees. However, the fact that S. virescens is more prevalent and that the overall group is richer in small trees could provide some protection to this group, since post-fire salvage logging is aimed at harvesting commercial trees (DBH > 9 cm in Quebec). However, this group might be rapidly threatened if the bioenergy industry were to harvest non-commercial burned trees. Also, the richness of this group, as well as that of the mutator group, was higher when close to the green forest, suggesting that interactions between these habitats (green forests and burned forests) are important at the regional scale. The green matrix around burns provides important resources for several species such as *M. s. scutellatus*, whose adults feed on green twigs of coniferous trees (Gardiner 1957). Saint-Germain et al. (2008) and Boulanger et al. (2010) even hypothesized that these green (unburned) forests may act as source habitats for beetles that colonize burns. Green forests might be sub-optimal habitats for several saproxylic beetles but, by maintaining populations of these insects, even at low levels, these forests could serve as source populations for colonizing nearby burned forests. The resilience of burn-associated beetles may depend on the source-sink dynamics that involve burned and green forests.

The richness of the pratensis group is higher in large-diameter trees affected by low burn severity. We ought to mention that *A. pratensis*, the sole burn-associated species of this group, was previously found to be more associated with higher burn severity by Azeria *et al.* (2012b). The association between *A. pratensis* and burned habitat has been shown to increase through time (Boucher *et al.* 2012) and to persist in burns for up to 10 years after fire (C. Hébert, unpubl.

data). This species is also known to be associated with burns in Europe where it is on some red lists (Moretti *et al.* 2010). This raises the conservation importance of this species in post-fire habitat, which could be considered as a bio-indicator of mid- to long-term sustainability of post-fire management practices (C. Hébert, unpubl. data). Interestingly, the two other most abundant species in the pratensis group, the predaceous (Bousquet 1991) Melyrid larvae (Melyridae sp.1) and mould-feeding *Sericoderus lateralis* (Gyllenhal) (Yavorskaya *et al.* 2014), form a three-level trophic network with the xylophagous *A. pratensis*. We have no information yet on the actual presence of direct interspecific interaction between these species. Nevertheless, such assemblages of species are also the target of biodiversity conservation policies, and could thus be considered important attributes to preserve in an ecosystem-based management approach (Gauthier *et al.* 2008; Nappi *et al.* 2011).

4. Conclusion

The approach presented in this study could be easily implemented by land managers as we used easily available environmental variables as well as information on the burn itself, such as burn severity (dNBR) acquired through the use of satellite imagery. In our regional context, salvage logging of severely burned black spruce might be more appropriate to ensure biodiversity conservation because species richness is lower in these trees and economic losses to woodborers is incidentally lower (Chapter II of this thesis). More generally, we could also recommend:

- At the regional scale: increase retention of poorly represented burned stand types, as they
 make a substantial contribution to regional diversity and are more at risk because these
 species were already facing high fragmentation before the disturbance.
- 2) At the regional scale: keep an eye on non-commercial stands. These are left over from conventional salvage logging, which collects only commercial sized trees (DBH > 9 cm in Quebec). However, if these stands were to be harvested for other purposes, such as for the bioenergy industry, some species may rapidly become threatened. Moreover, we observed that most non-commercial black spruce stands were scarified and planted within a few years after fire for site reforestation.
- 3) At the burn scale: maintain short distances between burned and green forests as numerous species obviously use both habitats. The simplest way to do that would be to maintain the

periphery of burned stands as much as possible as it represents an ecotone. Ecotones are known as rich habitats for biodiversity. Ecotones could also be maintained around unburned forest patches within burns, since Nappi *et al.* (2011) recommended retaining these unburned patches. The connectivity between residual stands should also be maximized when designing salvage logging plans. Future studies should try to better define ecotones after wildfire, particularly their width, for management purposes.

These guidelines aim to improve ecosystem-based management in burned forests to make postfire salvage logging sustainable. The efficacy of these guidelines could be assessed by measuring habitat use by a species such as *A. pratensis*, a burn-associated species found in both Europe and North America and for which habitat is poorly defined. As this species is red-listed in several European countries where fires are scarce, it could be a powerful indicator of sustainable postfire salvage logging in North America. This would require developing a standardized sampling protocol for validating habitat use by *A. pratensis*.

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Tables

Variables	Description	Range (unit)
Distance to green forest	Shortest distance from the plot to the continuous green forest outside of the burn perimeter	35 - 3,840 (m)
Basal area of coniferous trees	Total basal area of coniferous trees recorded in each plot	1.71 - 40.12 (m ² ·ha ⁻¹)
Basal area of deciduous trees	Total basal area of deciduous trees recorded in each plot	0 - 7.36 (m ² ·ha ⁻¹)
Burn severity	Mean dNBR, based on all pixel values within a radius of 15 m around the plot centre, giving double weight to the pixel in which the plot centre is located	0.144 - 1.011 (dNBR)
Tree diameter	Diameter at breast height (DBH) of sampled trees	5 - 26 (cm)

 Table 13. Description, range and units of predictive variables used in GLMM models.

Variables	Estimate	Std. Error	z-value	p-value
Richness of all species ¹				
Intercept	5.547	0.224	24.749	0.000
Diameter (DBH)	1.001	0.234	4.270	0.000
Burn severity (dNBR)	-0.848	0.220	-3.860	0.000
Richness of common species ¹				
Intercept	4.134	0.185	22.365	0.000
Diameter (DBH)	0.779	0.193	4.027	0.000
Burn severity (dNBR)	-0.496	0.186	-2.668	0.010
Distance to green forest	-0.390	0.184	-2.118	0.039
Richness of rare species ²				
Intercept	-0.616	0.101	-6.079	0.000
Burn severity (dNBR)	-0.462	0.094	-4.911	0.000

Table 14.Regression models predicting richness of all species, of common species, and of rare species. Final models were determined using a stepwise model selection approach.

¹Modelled using Gaussian distribution, so t-values are presented instead of z-values. ²Modelled using Poisson distribution.

Species group	Species	Species (code)*	Number of occurrence in plots	Number of occurrence in boles	Number of specimens emerged
Group 1	Monochamus s. scutellatus	Cera Mono scut	42	91	256
or only of	Nudobius cephalus	Stap Nudo ceph	30	44	61
	Placusa tacomae	Stap plac taco	7	7	7
	Phloeostiba lapponica	Stap Phlo lapp	49	89	289
	Placusa vaga	Stap Plac vaga	13	14	16
	0			Total	629
Group 2	Dryocoetes affaber	Curc_Dryo_affa	28	32	252
	Orthotomicus caelatus	Curc_Orth_cael	5	6	12
	Coleoptera sp.2	Coleo_sp.2	10	11	43
	Cryptophagidae sp.1	Cryp_sp.1	4	4	42
	Acanthocinus pusillus	Cera_Acan_pusi	7	7	10
	Crypturgus borealis	Curc_cryp_bore	12	21	1,783
	Polygraphus rufipennis	Curc_poly_rufi	18	29	748
				Total	2,890
Group 3	Clypastraea fusca	Cory_clyp_fusc	31	51	135
	Corylophidae sp.1	Cory_sp.1	47	90	445
	Chrysobothris verdigripennis	Bupr_Chry_verd	4	4	4
	Lepturinae sp.1	Cera_Lept_sp.1	7	8	11
				Total	595
Group 4	Rhagium inquisitor	Cera_Rhag_inqu	4	4	4
	Cerambycidae sp.1	Cera_sp.1	5	5	6
	Boros unicolor	Bori_Boro_unic	15	25	47
	Monochamus mutator	Cera_Mono_muta	10	10	19
	Staphylinidae sp.1	Stap_sp.1	45	78	1,046
				Total	1,120
Group 5	Cleridae sp.1	Cler_sp.1	5	5	5
	Cortinicara gibbosa	Lath_Cort_gibb	5	5	5
	Sphaeriestes virescens	Salp_Spha_vire	14	30	81
	Trixagus carinicollis	Thro_trix_cari	7	7	7
	Dryocoetes autographus	Curc_Dryo_auto	24	31	73
	Epuraea planulata	Niti_Epur_plan	7	8	8
				Total	179
Group 6	Acmaeops pratensis	Cera_Acma_prat	18	22	46
	Melyridae sp.1	Mely_sp.1	15	23	37
	Placusa tachyporoides	Stap_Plac_tach	9	9	9
	Melanophthalma sp.1	Lath_Mela_sp.1	5	5	5
	Placusa incompleta	Stap_Plac_inco	5	5	5
	Sericoderus lateralis	Cory_Seri_late	22	26	31
	Dinaraea pacei	Stap_Dina_pace	4	4	6
	Gnathotrichus materiatus	Curc Gnat mate	4	4	4

Table 15. Beetle species forming each group, number of specimens emerged from tree boles, and occurrence in plots and boles.

Epuraea terminalis	Niti Epur term	5	5	5
-			Total	148

*Species codes presented on the dendrogram of Figure 14.

Table 16.Percentage of significant pairwise associations ((+) positive; (-) negative) of saproxylic beetle species within and between groups given by the proportion of potential species pairwise tests done using fixed-fixed null model. The number of species for each group is given in parentheses in the left-most column. The highest percentage of positive (green) and negative (red) pairwise associations between groups is in bold.

Species groups	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6
Group 1 (5)	34.3 (+) , 0.3 (-)					
Group 2 (7)	11.5 (+), 6.1 (-)	45.9 (+) , 1.5 (-)				
Group 3 (4)	4.8 (+), 13.6 (-)	1.2 (+), 11.6 (-)	40.9 (+) , 0.7 (-)			
Group 4 (5)	13.6 (+), 9.1 (-)	4.2 (+), 10.8 (-)	12.9 (+), 11.2 (-)	38.7 (+) , 1.0 (-)		
Group 5 (6)	5.8 (+), 19.5 (-)	7.3 (+), 11.0 (-)	2.6 (+), 9.7 (-)	3.1 (+), 14.5 (-)	16.1 (+) , 3.3(-)	
Group 6 (9)	7.5 (+), 10.8 (-)	8.8 (+), 10.5 (-)	5.5 (+), 12.0 (-)	2.3 (+), 8.2 (-)	6.5 (+), 12.7 (-)	18.2 (+) , 4.6 (-)

Variables	Estimate	Std. Error	z-value	p-value
Acmaeops pratensis				
Intercept	-2.652	0.546	-4.853	0.000
Black spruce	0	-	-	0
Jack pine	0.500	0.523	0.956	0.339
Diameter (DBH)	0.548	0.289	1.898	0.058
Burn severity (dNBR)	-0.264	0.250	-1.054	0.292
Acmaeops p. proteus ¹				
Intercept	3.349	0.178	18.825	0.000
Black spruce	0	-	-	0
Jack pine	-0.602	0.232	-2.597	0.009
Diameter (DBH)	0.444	0.125	3.558	0.000
Burn severity (dNBR)	-0.291	0.119	-2.448	0.014
Deciduous basal area	-0.570	0.132	-4.317	0.000
Cleridae sp.1				
Intercept	-4.978	1.092	-4.560	0.000
Black spruce	0	-	-	0
Jack pine	1.349	1.146	1.178	0.239
Diameter (DBH)	0.779	0.556	1.400	0.161
Burn severity (dNBR)	0.611	0.572	1.067	0.286
Clypastraea fusca				
Intercept	-1.321	0.258	-5.122	0.000
Burn severity (dNBR)	2.809	1.301	2.159	0.031
dNBR ²	-2.993	1.308	-2.287	0.022
Dryocoetes autographus				
Intercept	-1.391	0.331	-4.208	0.000
Black spruce	0	-	-	0
Jack pine	-0.908	0.484	-1.874	0.061
Diameter (DBH)	-0.295	0.251	-1.176	0.240
Burn severity (dNBR)	0.013	0.219	0.060	0.953
Monochamus mutator				
Intercept	-22.657	617.495	-0.037	0.971
Black spruce	0	-	-	0
Jack pine	20.400	617.495	0.033	0.974
Diameter (DBH)	0.334	0.291	1.149	0.251

Table 17.Regression models predicting the presence of burn-associated species, as well as the abundance (number \cdot m⁻²) of the ubiquitous species *Acmaeops p. proteus*. Models were done using binomial distribution. Final models were determined using a stepwise model selection approach.

Burn severity (dNBR)	0.108	0.385	0.281	0.779
Monochamus s. scutellatus				
Intercept	1.501	0.610	2.460	0.014
Black spruce	0	-	-	0
Jack pine	-3.362	0.941	-3.572	0.000
Diameter (DBH)	1.144	0.444	2.580	0.010
Burn severity (dNBR)	5.801	2.335	2.485	0.013
dNBR ²	-5.559	2.319	-2.397	0.017
Sphaeriestes virescens				
Intercept	-3.939	1.365	-2.886	0.004
Diameter (DBH)	-1.008	0.514	-1.961	0.050

¹Modelled using negative binomial distribution.

Variables	Estimate	Std. Error	z-value	p-value
Group 1				
Intercept	0.238	0.108	2.210	0.027
Black spruce	0	-	-	0
Jack pine	-0.377	0.108	2.210	0.012
Diameter (DBH)	0.491	0.094	5.255	0.000
Burn severity (dNBR)	1.042	0.427	2.443	0.015
dNBR ²	-1.227	0.427	-2.877	0.004
$DBH \times dNBR$	0.272	0.105	2.578	0.010
Group 2				
Intercept	-0.656	0.195	-3.371	0.001
Black spruce	0	-	-	0
Jack pine	-0.575	0.268	-2.147	0.032
Burn severity (dNBR)	-0.546	0.129	-4.223	0.000
Group 3				
Intercept	-0.297	0.084	-3.528	0.000
Burn severity (dNBR)	1.355	0.490	2.767	0.007
dNBR ²	-1.498	0.498	-3.010	0.003
Group 4				
Intercept	-1.036	0.169	-6.149	0.000
Black spruce	0	-	-	0
Jack pine	0.616	0.201	3.065	0.002
Diameter (DBH)	0.498	0.107	4.672	0.000
Burn severity (dNBR)	0.984	0.586	1.678	0.093
dNBR ²	-1.223	0.600	-2.038	0.042
Distance to green forest	-0.222	0.105	-2.112	0.035
$DBH \times dNBR$	0.347	0.126	2.757	0.006
Group 5				
Intercept	-1.094	0.169	-6.495	0.000
Diameter (DBH)	-0.359	0.134	-2.679	0.007
Distance to green forest	-0.355	0.167	-2.122	0.034
Group 6				
Intercept	-0.813	0.132	-6.161	0.000
Diameter (DBH)	0.369	0.123	3.003	0.003
Burn severity (dNBR)	-0.305	0.103	-2.967	0.003

Table 18.Regression models predicting richness within each species group. These models were done using Poisson distribution. Final models were determined using a stepwise model selection approach.

Figures



Figure 13. Study area in the Haute-Mauricie region of Quebec, Canada (black star in bottom right frame) and spatial distribution of the sampling plots (black dots) within the five studied burns (grey areas in the left frame; burn's name in text boxes).

Cluster Dendrogram



Figure 14. Dendrogram showing saproxylic beetle species groups as categorized by co-occurrence-based hierarchical clustering and Ward's agglomeration algorithm. Species names are expressed as the first four letters of the family, followed by the first four letters of the genus and the four first letters of the species. Asterisks (*) designate species recognized as burn-associated species and daggers (†) indicate opportunistic species according to Boucher *et al.* (2012).

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Appendix

Family	Species	Burn- associated*	Black spruce	e Jack pine	Total
Anobiidae	Stephanopachys hispidulus (Csy.)	Unknown	1	0	1
Boridae	Boros unicolor Say	Unknown	1	46	47
Buprestidae	Chrysobothris verdigripennis Frost	Unknown	4	0	4
	Phaenops fluvoguttata (Harr.)	Unknown	1	0	1
Cerambycidae	Acanthocinus pusillus Kirby	Unknown	9	1	10
	Acmaeops pratensis (Laicharting)	Yes	27	19	46
	Acmaeops proteus proteus (Kirby)	Yes	925	497	1,422
	Asemum striatum (Linné)	No	2	0	2
	<i>Lepturinae</i> sp.1 [†]	Unknown	4	7	11
	Lepturinae sp.2	Unknown	1	1	2
	Monochamus mutator LeConte	Yes	0	20	20
	Monochamus scutellatus scutellatus (Say)	Yes	218	38	256
	Monochamus sp.1	Yes	14	8	22
	Phymatodes dimidiatus (Kirby)	Unknown	4	1	5
	Pogonocherus penicillatus LeConte	No	26	0	26
	Rhagium inquisitor (Linné)	No	1	3	4
	sp.1	Unknown	2	4	6
	Tetropium cinnamopterum Kirby	No	2	2	4
	Tetropium parvulum Kirby	Unknown	0	9	9
Cleridae	sp.1 (prob. Thanasimus undatulus)	Yes	1	4	5
Colydiidae	Lasconotus borealis Horn	Unknown	1	0	1
Corylophidae	<i>Clypastraea fusca</i> (Harold)	Yes	77	58	135
	Orthoperus micros Csy.	Unknown	1	0	1
	<i>Sericoderus lateralis</i> (Gyllenhal)	Unknown	10	21	31
	sp.1	Unknown	219	226	445
Cryptophagidae	Atomaria (anchicera) lewisi Reit.	Unknown	3	0	3
	Cryptophagus coticinus C.G.Thomson	Unknown	4	0	4
	sp.1	Unknown	41	1	42
Curculionidae	Barypeithes pellucidus (Boh.)	Unknown	0	1	1
	Crypturgus borealis Swaine	No	1,779	4	1,783
	Crypturgus pusillus (Gyllenhal)	Unknown	2	0	2
	Dryocoetes affaber (Mannerheim)	No	235	17	252
	Dryocoetes autographus (Ratzeburg)	Yes	52	21	73

Appendix 2. Number of beetles emerged from burned boles of black spruce and jack pine.

	Dryophthorus americanus Bedel	Unknown	1	0	1
	Gnathotrichus materiatus (Fitch)	Unknown	3	1	4
	Ips latidens (LeConte)	No	1	49	50
	Ips pini (Say)	No	4	0	4
	Orthotomicus caelatus (Eichhoff)	No	3	9	12
	Pissodes nemorensis Germar	Unknown	0	2	2
	Pissodes rotundatus LeConte	No	2	0	2
	Pityogenes plagiatus (LeConte)	No	0	11	11
	Pityophthorus sp.1	Yes	1	0	1
	Polygraphus rufipennis (Kirby)	No	736	12	748
	sp.1	Unknown	4	0	4
	Trypodendron lineatum (Olivier)	No	1	0	1
	Tychius picirostris (F.)	Unknown	1	0	1
	Xyleborus sayi (Hopkins)	Yes	0	1	1
Dermestidae	Anthrenus fuscus Olivier	Unknown	4	0	4
	sp.1	Unknown	0	1	1
Laemophloeidae	Laemophloeus fasciatus Melsh.	Unknown	1	0	1
	Placonotus modestus (Say)	Unknown	2	0	2
Lathridiidae	Cartodere constricta (Gyllenhal)	Unknown	2	1	3
	Corticaria dentigera LeConte	Yes	1	5	6
	Corticaria elongata (Gyllenhal)	Unknown	0	2	2
	Corticaria saginata Mannerheim	Unknown	0	1	1
	Cortinicara gibbosa (Herbst)	No	2	3	5
	Enicmus tenuicornis LeConte	No	0	1	1
	<i>Melanophthalma</i> sp.1 Motschulsky	Unknown	3	2	5
Melandryidae	Serropalpus substriatus Hald.	Unknown	3	0	3
Melyridae	sp.1	Unknown	17	20	37
Monotomidae	Monotoma longicollis (Gyllenhal)	Unknown	0	1	1
Mordelidae	Mordellaria borealis (LeConte)	Unknown	1	0	1
Mycetophagidae	<i>Typhasa</i> sp.1	Unknown	0	1	1
Nitidulidae	Epuraea boreades Parsons	Unknown	1	1	2
	Epuraea obtusicollis Reit.	Unknown	1	0	1
	<i>Epuraea planulata</i> Erichson	Unknown	4	4	8
	<i>Epuraea terminalis</i> Mannerheim	Unknown	2	3	5
	Epuraea truncatella Mannerheim	Unknown	0	2	2
	sp.1	Unknown	4	1	5
Oedemeridae	sp.1	Unknown	1	0	1

Ptiliidae	Pteryy sp.1	Unknown	0	1	1
	sp.1	Unknown	1	0	1
Pyrochroidae	sp.1	Unknown	0	2	2
Pythidae	sp.1	Unknown	19	0	19
Ripiphoridae	Pelecotoma flavipes Melsh.	Unknown	1	0	1
Salpingidae	Sphaeriestes virescens (LeConte)	Yes	13	68	81
Silvanidae	Dendrophagus cygnaei Mannerheim	Unknown	0	1	1
	Silvanus bidentatus (F.)	Unknown	0	1	1
Staphylinidae	Acidota subcarinata Erichson	Unknown	0	1	1
	Amischa analis (Grav.)	Unknown	1	0	1
	Atheta sp.1	Unknown	0	2	2
	<i>Dinaraea pacei</i> Klim.	Unknown	1	5	6
	Myrmecocephalus cingulatus (LeConte)	Unknown	0	1	1
	Nitidotachinus tachyporoides Horn	Unknown	0	1	1
	Nudobius cephalus (Say)	Unknown	30	31	61
	Oligota parva Krtz.	Unknown	0	1	1
	Oligota sp.1	Unknown	0	1	1
	Parascydmus corpusculus (Csy.)	Unknown	1	0	1
	Philhygra clemens (Csy.)	Unknown	0	1	1
	Philhygra sp.1	Unknown	2	0	2
	Phloeonomus laesicollis (Makl.)	Unknown	0	1	1
	Phloeostiba lapponica (Zett.)	Unknown	116	173	289
	Placusa incompleta Sjöb	Unknown	3	2	5
	Placusa pseudosuecica Klim.	Unknown	1	2	3
	Placusa tachyporoides Waltl	Unknown	5	4	9
	Placusa tacomae Csy.	Unknown	2	5	7
	Placusa vaga Csy.	Unknown	10	6	16
	Silusa densa Feny.	Unknown	1	1	2
	sp.1	Unknown	285	761	1,046
Throscidae	Trixagus carinicollis (Schaeffer)	Unknown	4	3	7
	Trixagus chevrolati (Bonvouloir)	Unknown	0	1	1
(unknown)	sp.1	Unknown	0	1	1
	sp.2	Unknown	16	30	46
	Total		4,986	2,249	7,235

Species in bold were found in >5% and <95% of the plots and were included in the hierarchical clustering analysis

*Burn-associated species according to Boucher *et al.* (2012) *Most of the unidentified species (sp.) were at the larval stage

CONCLUSION GENERALE

I. Retour sur les résultats

Le premier chapitre de cette thèse propose une approche de caractérisation de la sévérité par télédétection, sous la forme d'un index continu, qui permettra de bonifier les outils d'aménagement disponibles. Les objectifs et résultats des deux autres chapitres s'articulent autour de cet élément principal qu'est la caractérisation de la sévérité du feu, de manière à optimiser la récupération après feu, tout en respectant le cadre de l'aménagement forestier écosystémique, des points de vue économique et écologique. Dans nos analyses, afin d'avoir plus de précision, nous avons utilisé la surface terrière et le diamètre des tiges que nous avons mesuré sur le terrain. Toutefois, une estimation de ces variables est disponible pour les aménagistes à travers les cartes écoforestières liées aux tables de stock, sous la forme du nombre de tiges par essences et classes de diamètre par peuplements.

1. La sévérité du feu comme outil d'aménagement des forêts brûlées

Malgré une certaine pensée populaire, les feux ne font pas que générer des habitats homogènes. Au contraire, ils génèrent toute une diversité de nouveaux habitats, de l'échelle du micro-habitat à celle du paysage (Kennedy et Fontaine, 2009; Nappi et al., 2011). De façon générale, le régime de feu en zone boréale au Canada peut être qualifié de sévérité mixte (« mixed severity fire regime »), où les brûlis résultent souvent en un mélange complexe d'aires affectées par des sévérités différentes (Bergeron et al., 2002; Agee, 2005). Par exemple, on y retrouve des zones non brûlées, de faible sévérité, où le feu peut avoir été de peu intense, de sévérité modérée, où peut-être un tiers à deux tiers de la végétation est tuée, et finalement de sévérité élevée, où presque toute la végétation est tuée (Agee, 2005). Cette variabilité de l'impact du feu à l'échelle du brûlis a des impacts visuellement évidents à court terme sur la mortalité de la végétation et la consumation de la matière organique (Lentile et al. 2006), qui se traduisent par des impacts à moyen terme, sur les communautés d'insectes (Boucher et al. 2012) ou sur la régénération (Crotteau et al. 2013) par exemple. À plus long terme, les divers types de végétations qui sont affectés par des sévérités de feu différentes suivront des trajectoires de rétablissement écologiques diverses (Weber et Stocks 1998). Ces trajectoires se manifestent à travers des modifications dans la composition et dans la structure d'âge des espèces végétales, par des changements dans le recyclage des éléments nutritifs, dans la productivité de l'habitat et dans la biodiversité (Volney et Hirsch 2005). Tout comme le feu lui-même, sa sévérité peut donc avoir un impact majeur à l'échelle du paysage forestier.

Une cartographie juste de la sévérité du feu est donc un complément indispensable dans les outils d'aménagement écosystémique des forêts brûlées, puisqu'elle permet de synthétiser de façon spatiale l'impact qu'a eu le feu sur le milieu. La caractérisation de la sévérité du feu peut être utile dans plusieurs facettes de l'aménagement et de la gestion des forêts brûlées. En effet, ses utilités peuvent être aux niveaux de la gestion des risques pour la santé (ex.: qualité de l'eau (Fowler, 2003)) et l'environnement (ex. : émissions de carbone (Meigs *et al.*, 2009; Arnett *et al.*, 2015)), de problématiques économiques (ex. : dommages reliés aux longicornes (Boulanger *et al.*, 2013; Cadorette-Breton, 2014), de la remise en production en essences forestières (Greene *et al.*, 2004; Crotteau *et al.*, 2013)), ainsi qu'au niveau de problématiques écologiques (ex. : diversité aviaire (Smucker *et al.*, 2005; Nappi *et al.*, 2010; Azeria *et al.*, 2011) et diversité entomologique (Boucher, 2010; Boulanger *et al.*, 2012a)).

Les travaux faits dans le cadre du Chapitre I ont permis de valider que le dNBR offre une représentation fidèle (R² = 92.4%) des conditions observées sur le site du brûlis (CBI), pour des forêts boréales de l'Est du Canada. Le dNBR offre d'ailleurs un rendement comparable que ce soit en peuplement d'épinettes noires ou de pins gris. De tels résultats indiquent que le dNBR pourrait être utilisé en complémentarité avec les outils déjà disponibles dans le cadre de l'aménagement des forêts brûlées au Québec. Nous avons d'ailleurs pu établir les plages de valeurs de dNBR correspondant aux classes de sévérité utilisées lors de la cartographie faite par le MFFP (Figure 15). Il est d'ailleurs intéressant d'observer sur la Figure 15 qu'il existe une grande variabilité en termes de sévérité du feu (CBI) à l'intérieur des classes de sévérité du MFFP. Dans le contexte québécois, l'obtention de cartes de sévérité du feu comparables à celles du MFFP et obtenues à partir de valeurs de dNBR seuillées (voir Figure 3 au Chapitre I), pourrait être utile afin de cartographier les brûlis hors de la zone de la forêt commerciale, soit au-delà de la limite nordique d'exploitabilité

de la forêt par exemple, ou encore dans le cadre d'études historiques concernant des feux datant d'avant 2010.

De plus, la relation entre le dNBR et le CBI observée pour notre région d'étude est comparable à ce qui a été observé dans l'Ouest canadien par Hall *et al.* (2008). Ces derniers résultats nous permettent d'envisager l'établissement d'un modèle unique pour l'ensemble de la forêt boréale commerciale du pays. En effet, malgré que des validations restent à faire, particulièrement pour la taïga et les zones feuillues, certains travaux sont déjà en cours afin que le dNBR soit utilisé pour cartographier la sévérité du feu à l'échelle du Canada (communication personnelle avec Luc Guindon, spécialiste en SIG, base de données et télédétection au SCF-RNCan). Une telle cartographie utilisant le dNBR pourrait s'avérer fort utile dans le cadre de comparaisons internationales, de suivis historiques des feux et de leur sévérité, pour mieux définir la propension des forêts à brûler, ainsi que pour la production de bilans de carbone (Sommers *et al.*, 2014; Arnett *et al.*, 2015). Dans les chapitres subséquents, nous avons d'ailleurs démontré que cet indice spectral (dNBR) est un intrant important, permettant de prédire les attaques de *Monochamus* spp. causant des pertes économiques et d'identifier les forêts à haute valeur de conservation pour la biodiversité des coléoptères saproxyliques associés aux brûlis.

2. Améliorer la rentabilité des opérations de récupération après feu par une meilleure prédiction des attaques de Monochamus spp.

Grâce aux travaux présentés au Chapitre II, les pertes économiques reliées *Monochamus* pourront définitivement être diminuées en ciblant mieux les peuplements ayant subis des niveaux d'attaques dépassant les seuils économiquement rentables fixés par les aménagistes. L'exemple présenté en conclusion du Chapitre II illustre bien la simplicité avec laquelle nos modèles peuvent être utilisés.

Nos résultats démontrent qu'il est possible de prédire les niveaux d'attaque des *Monochamus* spp. après feu en utilisant l'essence, la surface terrière en feuillus, le DHP et la sévérité du feu, obtenue à travers la méthodologie présenté au Chapitre I. Il a été fort intéressant de constater dans nos travaux, que malgré une densité d'attaques plus élevée de *Monochamus* spp. chez l'épinette noire, le taux de survie et le taux de développement de

ces insectes sont quant à eux plus élevés chez le pin gris. De plus, nous avons dénoté une augmentation du taux de développement en fonction de la sévérité du feu, chose qui n'avait jamais été démontrée par le passé. D'un point de vue de la planification de la récupération, cela indique que si la présence de galeries larvaires dans le pin gris est un problème pour certains produits de bois d'œuvre, les gestionnaires pourraient vouloir récupérer le pin gris plus rapidement, et ce plus particulièrement dans les peuplements de pins gris où la sévérité du feu est élevée. C'est d'ailleurs au niveau de sévérité plus élevées, que nous retrouvons les plus hauts risques d'attaques chez le pin gris. Cette relation avec la sévérité est bien différente chez l'épinette, car les plus hautes densités d'attaques se retrouvent à des sévérités moyennes.

3. Réduction des impacts potentiels de la récupération après feu sur la diversité des coléoptères associés aux brûlis

Les travaux présentés au Chapitre III de cette thèse s'inscrivent dans un cadre d'aménagement écosystémique après feu. En effet, en cernant mieux les forêts à haute valeur de conservation, cela nous permettra de réduire les impacts potentiels de la coupe de récupération après feu sur les coléoptères saproxyliques associés aux brûlis.

Notre approche a permis d'identifier six groupes d'espèces écologiquement liées, colonisant les arbres tués par le feu. Parmi ces groupes d'espèces, la moitié sont identifiés comme ayant peu d'intérêt en termes de conservation après feu, puisqu'on les retrouve dans plusieurs milieux où il y a du bois mort d'autre provenance que le feu. Cependant, le rôle écologique que ces espèces jouent auprès de certains oiseaux, par exemple, pourrait justifier un plus grand intérêt de conservation. Les trois autres groupes sont considérés comme étant potentiellement à risque dans un contexte de récupération du bois brûlé, puisqu'ils contiennent des espèces saproxyliques associées aux brûlis. D'après nos travaux, il serait plus approprié de récolter l'épinette noire sévèrement brûlée afin de conserver la biodiversité, puisque la richesse en espèce y est plus faible. De façon plus générale, nous recommandons: (1) À l'échelle régionale: d'augmenter la rétention des types de peuplements brûlés sous-représentés, car ils contribuent substantiellement à la diversité régionale et sont plus à risque, puisqu'ils étaient déjà confrontés à une fragmentation élevée avant les perturbations (feu et récupération); (2) À l'échelle régionale: garder un œil sur les

peuplements non-commerciaux. Ceux-ci sont laissés de côté par la coupe de récupération conventionnelle, qui recueille des tiges aux dimensions commerciales (DHP > 9 cm au Québec). Toutefois, si ces peuplements étaient récoltés à d'autres fins, comme pour l'industrie de la bioénergie, certaines espèces pourraient rapidement devenir menacées. En outre, nous avons observé que la plupart des peuplements d'épinettes noires avaient été scarifiés et plantés que quelques années après le feu; (3) À l'échelle du feu: maintenir de courtes distances entre la forêt brûlée et la forêt verte (non brûlée), puisque plusieurs espèces semblent utiliser ces deux habitats. La façon la plus simple de le faire serait de maintenir autant que possible la périphérie brûlée des brûlis, car elle représente un écotone. Les écotones sont connus comme de riches habitats pour la biodiversité. Ce type d'écotone pourrait aussi être maintenus autour des îlots de forêts non brûlés à l'intérieur des brûlis, surtout que Nappi *et al.* (2011) ont recommandé de conserver ces îlots non brûlés. La connectivité entre les peuplements résiduels devrait également être maximisée lors de la conception des plans de récupération. À des fins de gestion, les études futures devraient tenter de mieux définir les écotones après feu, plus particulièrement leur largeur.

II. Intégration des chapitres

1. Avantages d'utiliser un gradient de sévérité sous forme continue dans l'étude des patrons biologiques

Avant nos travaux, les études s'étant interrogées sur l'impact de la sévérité du feu sur la répartition des *Monochamus* avaient utilisé une caractérisation de la sévérité sous forme de classes (ex.: Richmond et Lejeune, 1945; Ross, 1960; Saint-Germain *et al.*, 2004; Gervais *et al.*, 2012; Breton *et al.*, 2013), rendant ainsi les résultats difficilement transférables dans le temps ainsi qu'à d'autres régions. À notre connaissance, seuls Boulanger *et al.* (2013) ont utilisé un indice de sévérité du feu sous une forme continue, soit le NBR_{après-feu}. Bien que sous une forme continue, le NBR_{apès-feu} rend les résultats tout de même difficilement comparables à d'autres études puisque cet indice spectrale n'est pas normalisé par les conditions avant le feu, comme c'est le cas pour le dNBR (Key et Benson, 2006).

Afin de montrer comment l'utilisation d'une mesure de sévérité du feu sous forme de classes pourrait être contraignante dans un cadre de gestion des dommages reliés aux

Monochamus, nous avons placé sur la Figure 12 présentée au Chapitre II des lignes correspondant aux classes de sévérité du MFFP (Figure 16). Il devient évident que toute la subtilité de la relation entre la densité d'attaques des longicornes et la sévérité du feu exprimée par nos modèles serait perdue en utilisant une description de la sévérité à classes fixes (Figure 16). Toutefois, la classification de la carte de sévérité provenant du dNBR en fonction des tolérances des aménagistes face au dommages reliés aux *Monochamus* serait surement une voie envisageable à la lumière de nos résultats.

L'importance d'utiliser un indice de sévérité sous forme continue est aussi vraie lorsque l'on traite de la diversité des coléoptères saproxyliques. C'est d'ailleurs l'auteur de la présente thèse qui a présenté les premiers résultats montrant une relation entre le dNBR et la diversité des coléoptères saproxyliques après feu à travers ses travaux de maîtrise (Boucher, 2010). Afin d'illustrer l'avantage d'une telle caractérisation de la sévérité, nous présentons ici sous forme graphique les résultats présentés au Tableau 18 du Chapitre III, concernant la relation entre les groupes d'espèces et la sévérité du feu, où nous avons ajouté des lignes correspondant aux classes de sévérité du MFFP (Figure 17). Il devient encore une fois évident, qu'une grande partie de la relation observée serait ignorée en utilisant des classes de sévérité (Figure 17).

En effet, ce n'est que grâce à l'utilisation d'un indice continu comme le dNBR que nous avons pu dénoter l'existence de relations de type quadratique avec la sévérité du feu. Ce type de relation a été observé tant au niveau des attaques de *Monochamus*, qu'au niveau de la richesse de certains groupes d'espèces saproxyliques (Figure 9, 10, et 17). L'utilisation du dNBR a aussi permis de mettre à jour des différences importantes dans l'effet de la sévérité du feu en fonction des essences. D'autres travaux en cours sur la régénération du pin gris et de l'épinette noire semblent aussi démontrer l'existence de tels patrons en lien avec la sévérité du feu (Boucher *et al.*, résultats non-publiés).

2. Réduire les pertes économiques reliées aux Monochamus spp. tout en préservant la diversité entomologique associée aux brûlis

D'un point de vue de l'AFE, est-ce utopique de penser qu'en laissant de côté les peuplements les plus attaqués par les *Monochamus* nous préserverons du même coup la

diversité entomologique associée aux brûlis? Voilà une question fréquemment posée lors de discussions entourant l'entomologie et la récupération après feu. En général la réponse est : ça dépend! En fait, ça dépend de bien des facteurs dont deux importants et non examinés dans cette thèse. C'est-à-dire la tolérance de l'industrie forestière aux dommages reliés aux *Monochamus* et à quel point, en tant que société, nous désirons conserver la diversité saproxylique associée aux brûlis. Évidemment, si l'industrie est totalement intolérante aux galeries de *Monochamus*, aucune récupération ne se fera et ainsi toute la biodiversité sera préservée. Au contraire, si les longicornes ne sont plus un enjeu, dans ce cas les peuplements commerciaux sont tous à risque d'être récupérés et ainsi toute la diversité saproxylique associée à ces peuplements serait menacée.

En se basant sur les résultats présentés aux Chapitres II et III de cette thèse nous pouvons tout de même répondre en bonne partie à cette question. Premièrement, ça dépend de l'essence considérée, car tel qu'établi plus tôt, les insectes démontrent des partons de réponses biens différents entre le pin gris et l'épinette noire. Dans le cas de l'épinette noire, les plus hautes densités d'attaques de Monochamus se retrouvent dans les grosses tiges atteintes par des sévérités moyennes à élevées, là même où nous retrouvons le plus grand nombre d'espèces des groupes scutellatus et fusca (voir Chapitres II et III). En évitant de récupérer dans les peuplements d'EPN de sévérités moyennes à élevées, nous préservons par le fait même les espèces de ces groupes, qui rappelons-le ne sont pas d'un très grand intérêt en termes de conservation dans les brûlis. Tout comme les espèces opportunistes du groupe scolytes (« bark beetles » au Chapitre II) qui se retrouvent quant à elles plus présentes dans des grosses tiges d'épinettes noires atteintes par de faibles sévérités de feu. Cependant, ce sont aussi dans ces tiges intéressantes pour l'industrie, du fait que les densités d'attaques de Monochamus sont moindres, que l'on retrouve le plus grand nombre d'espèces associées au groupe pratensis, et pour lequel nous avons émis certaines inquiétudes quant à sa conservation dans un contexte de récupération après feu. Chez le pin gris, la situation est quelque peu différente. La densité d'attaque de Monochamus y est largement plus basse que chez l'épinette noire, ce qui peut contribuer à rendre cette essence intéressante lors de la récupération. Par contre, les Monochamus s'y développent plus rapidement et ce dans les sévérités les plus élevées, où l'on retrouve aussi les plus hautes chances de retrouver des galeries. La particularité la plus importante du pin gris, est la présence *Monochamus mutator*, dont l'impact économique est important chez cette essence, soit environ 50% des dommages. La présence de cette espèce est d'ailleurs indicatrice de la présence des espèces du groupe mutator, dont *Boros unicolor*. Cela confère au pin gris une contribution importante à la biodiversité saproxylique régionale après feu. La rétention de tiges de pin gris attaquées par les longicornes, dont *M. mutator*, contribuerait ainsi à préserver la biodiversité associée à ce milieu. Finalement, en termes de conservation de la biodiversité, récupérer du bois d'épinette noire serait probablement plus approprié dans notre contexte régional. Plus particulièrement, dans les peuplements atteints par des sévérités plus élevées, où la richesse en espèces est plus faible et où les densités d'attaques de longicornes sont incidemment plus basses relativement aux sévérités moyennes.

III. Implication des travaux dans l'aménagement et perspective d'avenir

Ce projet de doctorat découle de la vision de l'étudiant pour un aménagement intégré des forêts brûlées. Plusieurs travaux de recherches ont été faits concernant divers aspects de l'écologie et de l'aménagement après feu. Cependant, l'intégration de ce savoir est difficile dû au fait que les variables utilisées dans ces travaux ne sont pas tout à fait compatibles aux outils d'aménagement disponibles, comme la cartographie écoforestière par exemple. Cette cartographie écoforestière, couplée aux tables de stock, est l'outil à la base de l'aménagement des forêts. Après feu, cet outil demeure indispensable, mais il est d'une aussi haute importance d'y associer une caractérisation de la sévérité du feu, et plus particulièrement à partir d'un indice spectral continu.

Dans une optique d'optimisation de l'AFE en forêts brûlées, l'intégration de nos travaux de recherche et leur mise en œuvre pourraient être faites à travers des plateformes informatiques utilisées lors de l'aménagement des forêts, telles que celles développées par FPInnovations, comme FPInterfaceTM par exemple. Toutefois, certaines validations resteraient à faire afin de démontrer que l'utilisation d'information provenant des tables de stock (surface terrière et DHP) serait aussi performante que celle mesurée directement sur le terrain et utilisée dans nos analyses.

L'auteur est d'avis que des travaux du même type que ceux présentés dans cette thèse devraient être réalisés dans le cadre d'autres perturbations, car il semble que la description

de la sévérité des perturbations soit aussi un enjeu de taille dans le cadre de l'aménagement post-épidémie d'insectes ou post-chablis. L'apparition de bois mort suite à de telles perturbations occasionne aussi des problématiques reliées aux *Monochamus* et à la conservation de la biodiversité des organismes saproxyliques (Belyea, 1952; Bouget et Duelli, 2004; Boucher et Hébert, 2010), de même qu'au niveau du comportement d'un incendie ayant subséquemment cours dans une telle forêt perturbée. La méthodologie utilisée dans les travaux de cette thèse pourrait certainement servir de cadre général dans la réalisation de travaux de recherches sur l'écologie et l'aménagement forestier écosystémique post-perturbation en forêt boréale.

Figures



Figure 15. Diagramme de dispersion des sites d'épinettes noires (points gris) et de pins gris (triangles noirs), montrant la relation CBI-dNBR tel qu'exprimée par le meilleur modèle régional (modèle GAM). Les lignes de couleurs réfèrent aux classes de sévérité du feu du MFFP tel que représenté par les valeurs de CBI et de dNBR (pour plus de détails, se référer au Chapitre I de cette thèse). La ligne verte réfère aux limites inférieures de la classe Affecté (ou supérieures de la classe Vert ou non-brûlée), alors que les lignes orange et rouge réfèrent respectivement aux limites inférieures des classes Roussi et Carbonisé.



Figure 16. Exemple de l'utilisation du modèle prédictif présenté au Chapitre II indiquant où, en termes d'essences, de diamètre et de sévérité du feu, les chances de trouver des trous d'entrée (graphiques du haut) et la densité de trous de longicornes (graphiques au centre et au bas) ne respectant pas la tolérance "fictive" des gestionnaires (zones orange). Les zones grises ombragées indiquent où les gestionnaires pourraient récupérer en fonction de leur tolérance. Les graphiques de gauche correspondent à l'épinette noire, tandis que ceux de droite sont pour le pin gris. Les traits verts, orange et rouges présents sur les graphiques représentent respectivement les limites inférieures des classes de sévérité Affecté, Roussi et Carbonisé du MFFP.



Figure 17. Graphique illustrant la richesse prédite des groupes d'espèces en fonction de la sévérité du feu tel que présenté au Tableau 18 présenté au Chapitre III. Les traits verts, orange et rouges présents sur les graphiques représentent respectivement les limites inférieures des classes de sévérité Affecté, Roussi et Carbonisé du MFFP.

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Annexes

Annexe 1. Résultats de travaux faits dans le cadre de mon projet de fin d'études de baccalauréat et portant sur l'effet de la coupe de récupération sur la proportion des peuplements conifériens résiduels. J'ai fait la description des superficies, avant et après les travaux de récupération, pour les peuplements soumis à quatre feux ayant sévis au cours de l'été 2005 dans la région de Chibougamau (Québec, Canada). Les résultats ont démontré que les niveaux de récupération dans les peuplements commerciaux d'épinettes noires, de pins gris et de sapins baumiers étaient respectivement de 35.6%, 63.5% et 42.3%.

Date	Code	Superficie	Superficie	Niveau de
d'ignition	SOPFEU*	forestière	récupérée	récupération
		(ha)	(ha)	(%)
14/07/2005	792	3 162.13	1 780.62	56.3
31/05/2005	301	27 856.25	2 103.67	7.6
31/05//2005	298	9 489.05	3 409.99	35.9
03/06/2005	373	1 198.96	528.22	44.1
	Total:	41 706.39	7 822.50	18.8

Superficies brûlées et récupérées, ainsi que le niveau de récupération pour les brûlis de 2005 étudiés

*SOPFEU: Société de protection des forêts contre le feu

Superficies totales brûlées et récupérées, ainsi que le pourcentage de récupération par groupement d'essences résineuses aux dimensions commerciales, soit de classes d'âges 50 ans et plus (incluant JIN et VIN).

Groupement	Superficie brûlée	Superficie récupérée	Récupération
d'essences	(ha)	(ha)	(%)
Pessière noire	15 267.5	5 431.7	35.6
Pinède grise	2 071.8	1 315.3	63.5
Sapinière	327.9	138.6	42.3
Total :	17 667.2	6 885.6	39.0