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IMPACTS DE LA COUPE DE RÉCUPÉRATION APRÈS FEU SUR LES COLÉOPTÈRES ASSOCIÉS AUX BRÛLIS EN FORÊT BORÉALE : UNE DYNAMIQUE TEMPORELLE

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Résumé

Il y a désormais plusieurs évidences quant au fait que la coupe de récupération nuirait au rétablissement des processus écologiques naturels, telle la régénération d'espèces végétales. En effet, si certaines espèces saproxyliques boréales sont adaptées aux habitats brûlés avec lesquels elles ont évolué, la coupe de récupération pourrait excéder leur résilience. Ainsi, cette étude à comme but d'identifier les espèces associées aux brûlis et de déterminer l'effet réel de la réduction en surface terrière commerciale, dans le temps suivant la coupe de récupération après feu, sur les assemblages de coléoptères associés aux brûlis de la forêt boréale de la province de Québec au Canada. La coupe de récupération a été effectuée d'août 2005 à mai 2006 suite aux feux de forêt de 2005 ayant eu lieu dans la région de Chibougamau. Nous avons échantillonné les coléoptères au cours des trois premières années suivant la coupe de récupération (2006 - 2008) à l'aide de pièges à impact multidirectionnels. Dix pièges furent installés dans dix sites également répartis entre des peuplements non-brûlés dominés soit par l'épinette noire (*Picea mariana* Mill. B.S.P.) ou le pin gris (*Pinus banksiana* Lamb.), où 11 arbres avaient été annelés afin de générer des chicots récents. Trente-six autres pièges ont été installés dans 36 sites brûlés répartis entre des peuplements résiduels à la coupe de récupération d'épinette noire ou de pin gris, de façon a couvrir le plus large éventail de niveau de récupération. Pour chacun des sites brûlés, nous avons mesuré des attributs de l'habitat, affectés par la récupération et pouvant affecter la structure des assemblages associés aux brûlis, dont : la surface terrière des tiges résiduelles par essence et par classe de diamètre à diverses échelles (0.04 ha et 7 ha). Nous avons aussi mesuré la distance entre les sites et la forêt non-brûlée continue et la sévérité du feu en utilisant le « delta Normalized Burn Ratio (dNBR)». En étudiant les assemblages de coléoptères des familles retenues (Buprestidae, Cerambycidae, Cleridae, Corylophidae, Curculionidae, Elateridae, Lathridiidae et Salpingidae) des sites brûlés et des sites non-brûlés contenant des arbres annelés, nous avons identifié 18 espèces associées aux brûlis. Ces coléoptères associés aux brûlis n'ont répondu à la coupe de récupération qu'à l'année no.2 (2007) après l'intervention. Les assemblages de coléoptères associés aux brûlis ont été principalement façonnés par trois groupes de facteurs environnementaux : 1) les conditions de la forêt avant feu, tel la composition en essences; 2) les conditions générées par le feu, soit la distance à la forêt non-brûlée, directement influencée par la forme du brûlis, et la sévérité du feu; 3) la quantité d'aire récupérée et la réduction associée en chicots de conifères matures (dhp > 9 cm).

Abstract

There are a few evidences that salvage logging could hamper natural ecological recovery processes, such as the regeneration of plant species. Indeed, if some boreal saproxylic species are adapted to postfire habitat with which they have evolved, salvage logging might exceed their resilience. This study aimed to identify burn-associated species of the northern boreal forest of the province of Quebec in Canada, and to determine the effect of reducing the merchantable tree basal area through time following salvage logging after fire, on the assemblages of these burn-associated species. Salvage logging was conducted from August 2005 to May 2006 after wildfires that prevailed in 2005, in the Chibougamau region. We sampled beetles over three years after salvage logging (2006 - 2008) using multidirectional flight-interception traps. Ten traps were installed in ten plots equally distributed between unburned black spruce (*Picea mariana* Mill. B.S.P.) and jack pine (*Pinus banksiana* Lamb.) dominated stands, where 11 mature trees (dbh > 9 cm) were girdled in order to generate recent snags. Thirty-six other traps were set in 36 plots distributed between burned black spruce and jack pine dominated stands residual from salvage logging in order to cover the largest gradient of salvage logging levels. For each burned plot, we measured habitat attributes affected by salvage logging which could influence burn-associated assemblages' structure, such as the basal area of residual trees by species and diameter classes at different scales (0.04 ha and 7 ha). We also measured the distance from the sites to the unburned continuous forest and fire severity, using the delta Normalized Burn Ratio (dNBR). By studying beetle assemblages from selected families (Buprestidae, Cerambycidae, Cleridae, Corylophidae, Curculionidae, Elateridae, Lathridiidae and Salpingidae) found in burned and unburned plots with girdled trees, we identified 18 burn-associated species. These burn-associated beetles only responded to salvage logging starting from year no.2 (2007) after salvage logging. Burn-associated beetle assemblages were mainly shaped by three groups of environmental factors: 1) prefire forest conditions such as tree species composition; 2) conditions generated by fire event such as the distance to the unburned forest, which is directly affected by the shape of the burned area, as well as burn severity; 3) the amount of salvage logged area and the associated reduction of the amount of mature size coniferous snags (dbh > 9 cm).

Avant-Propos

Le chapitre au cœur de ce mémoire « Impacts of postfire logging on burn-associated beetles in boreal forest : temporal dynamics » a été rédigé en anglais dans le but de le soumettre pour publication dans un journal scientifique arbitrée. Ce chapitre est précédé d'une introduction et d'une conclusion toutes deux rédigées en français. Le candidat à la maîtrise a récolté les échantillons de la troisième année du projet ainsi que les données relative aux attributs de l'habitat sur le terrain, fait l'identification de la plupart des insectes, en plus de tout le travail d'extraction des données environnementales à l'aide d'un système d'information géographique (SIG), la description de la sévérité du feu, ainsi que l'analyse des données. Ce mémoire fut rédigé en entier par le candidat à la maîtrise soutenu par les commentaires et critiques de son directeur Jacques Ibarzabal, de son co-directeur Christian Hébert et d'Ermias T. Azeria chercheur post-doctoral. Ces travaux de recherches furent réalisés et financés grâce au Fonds québécois de la recherche sur la nature et les technologies (FQRNT), La Fondation de l'Université du Québec à Chicoutimi et Le Service canadien des forêts de Ressources Naturelles Canada (SCF-RNCan).

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1. Introduction générale

Avant l'apparition des organismes photosynthétiques et des plantes terrestres, l'atmosphère ne contenait pas suffisamment d'oxygène, ni de combustible pour que le feu puisse exister sur Terre (Pausas et Keeley, 2009). L'apparition du feu sur notre planète est donc intimement liée à celle des plantes, celles-ci étant responsables de la production de deux des trois éléments essentiels au feu, soit l'oxygène et le combustible (Pausas et Keeley, 2009). Le troisième élément est une source de chaleur, qui était probablement déjà disponible depuis le début de l'histoire de la Terre (principalement par les éclairs, les volcans, les météorites, etc.) (Pausas et Keeley, 2009). Les premières traces du feu remontent à la période du Silurien (440 millions d'années) et elles ont été trouvées sur des résidus de végétation calcinés provenant de plantes parmi les premières à porter des stomates (Glasspool et al., 2004). Il existe d'ailleurs certaines évidences, datant du Paléozoïque et du Mésozoïque, de la présence de régimes de feux similaires à ceux que l'on retrouve encore aujourd'hui, tels les régimes de feux de surfaces et de couronnes (Falcon-Lang, 2000; Pausas et Keeley, 2009).

1.1 Influence évolutive du feu

Le feu ne semble avoir eu un impact majeur sur la biogéographie du paysage et sur les fonctions des écosystèmes que depuis la fin du Tertiaire et ce malgré sa présence depuis le Silurien (Pausas et Keeley, 2009). En effet, il semble que la propagation des herbes en C_4 et des prairies ouvertes et savanes de la fin du tertiaire soit liée à l'impact du feu (Pausas et Keeley, 2009). Depuis la fin du Tertiaire, ce processus naturel influence donc les patrons et processus globaux des écosystèmes, incluant la répartition et la structure de la végétation, la production de biomasse, les cycles géochimiques, le climat et la biodiversité (Weber et Flannigan, 1997; McCullough et al., 1998; Bourgeau-Chavez et al., 2002; Bowman et al., 2009). Par exemple, dans les communautés de plantes sujettes au feu (c'est-à-dire où le feu est une force évolutive importante), le fait de posséder des traits d'histoire naturelle permettant une régénération rapide et efficiente après feu est fondamentale dans le succès et la persistance des populations ; le feu change donc la structure des communautés de plantes en accroissant la représentativité des espèces ayant une forte capacité à germer après feu (Pausas et al., 2004). Ainsi, les espèces végétales vivant dans des communautés où la fréquence des feux est élevée sont plus apparentées phylogénétiquement, puisque la pression évolutive est plus grande (Pausas et Verdú, 2008). Le feu ne fait donc pas qu'éliminer des espèces et simplifier la structure végétative d'un milieu; il entraîne aussi la formation de nouveaux habitats, allant de l'échelle du micro-habitat à celle du paysage, ce qui est définit comme la structure pyrogénique (Kennedy et Fontaine, 2009). À l'échelle du paysage en forêt boréale, le passage de feux de forêts représente la principale source générant du bois mort (chicots et arbres en voie de mourir) (Siitonen, 2001; Drapeau et al., 2002; Nappi et al., 2004; Kennedy et Fontaine, 2009).

1.2 Importance des brûlis pour les coléoptères saproxyliques

Les arbres tués simultanément par le feu sont des habitats pour une large diversité d'espèces saproxyliques invertébrées (Wikars, 1992; Saint-Germain et al., 2004a; Boulanger et Sirois, 2007), lesquels jouent un rôle important dans la décomposition du bois et le recyclage des éléments (Speight, 1989; 1993; Boulanger et Sirois, 2007). Ces invertébrés représentent aussi une part non-négligeable de la diète de plusieurs espèces vertébrées (Morissette et al., 2002; Purdon et al., 2002; Nappi et al., 2004; Kennedy et Fontaine, 2009). Les invertébrés saproxyliques sont définis comme des espèces dépendantes, durant une partie de leur cycle vital, de un ou plusieurs des items suivants : 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). Parmi les trois ordres d'insectes les mieux représentés en terme de nombre d'espèces saproxyliques (Coleoptera, Diptera, Hymenoptera), les coléoptères sont les plus diversifiés, les mieux représentés en forêt boréale et les plus connus en termes de taxonomie et d'écologie (Niemela, 1997; Siitonen, 2001). De plus, les coléoptères saproxyliques sont parmi les plus à risque d'extinction dans les forêts boréales de Fennoscandie, à cause de la réduction dans la quantité de bois mort disponible (Hyvärinen et al., 2006), principalement causé par l'aménagement forestier intensif (Siitonen, 2001) et la suppression extensive des feux de forêts (Wikars, 1992).

Les organismes saproxyliques étant ostensiblement favorisés par le feu sont définis comme pyrophiles (Wikars, 1997b). La plupart des espèces pyrophiles se développent à l'état de larves dans les arbres tués par le feu ou dans les sols brûlés où elles se nourrissent soit de proies, de champignons, de l'aubier et/ou du phloème des arbres (Wikars, 1997a). Les conditions retrouvées en forêts brûlées sont particulièrement importantes pour les espèces d'insectes qui ont de la difficulté à surmonter les mécanismes de défense des arbres sains (flux de sève chez les feuillus, néoformation de résine secondaire chez les résineux). Ainsi, ces insectes se limitent à la colonisation d'arbres morts ou préalablement affaiblis (Bouget et al., 2005). L'occurrence imprévisible des feux et les caractéristiques spéciales des habitats générés par ceux-ci imposent des exigences particulières aux organismes qui dépendent des feux pour leur survie à long terme. Les espèces capables d'arriver rapidement sur le site brûlé devraient avoir un avantage comparativement aux espèces arrivant plus tardivement dans le milieu (Wikars, 1997a). Certaines espèces ont donc développé des caractéristiques adaptées au contexte des feux comme une grande capacité de dispersion, une reproduction et une croissance rapide (Wikars, 1997a). La fumée et les allélomones (signal chimique entre individus d'espèces différentes; ici on parle du type kairomone, dont le signal d'une espèce bénéficie à une autre qui le reçoit) transportées par le vent, ainsi que la chaleur dégagée par le feu pourraient être un facteur important pour guider les insectes pyrophiles vers les sites brûlés (Wikars, 1997a). Il semblerait que ce soit effectivement le cas pour certains buprestes (Coleoptera : Buprestidae) du genre *Melanophila*, possédant des récepteurs permettant la détection des radiations infrarouge émises par les feux de forêts sur de longues distances (Evans, 1966; Evans et Kuster, 1980).

Cependant, il existe une controverse autour du terme « pyrophile ». En effet, comparativement à Wikars (1997b), Nappi et al. (2004) soutiennent que pour qu'une espèce soit pyrophile, elle doit avoir évoluée sous un régime de feux récurrents et être maintenant dépendante du feu. Jusqu'à maintenant, aucun lien direct entre les adaptations sensoriel de certaines espèces n'a été établi avec le feu ou les brûlis récents. En effet, des adaptations, telle la détection d'infrarouge, pourrait être utilisées pour détecter un meilleur gîte de ponte sur un chicot trouvé en forêt non-brûlée. Étant donné cette controverse, nous préférons utiliser les termes *espèces associées aux brûlis*, pour définir les espèces préférant (retrouvées en plus grandes abondances/fréquence) les habitats brûlés aux habitats non-brûlés contenant du bois mort récents. Suite aux hypothèses de certains auteurs (Wikars, 2002; Nappi et al., 2004) nous pensons que les espèces associées aux brûlis utiliseraient les chicots produits par le feu pour accroître leur population, ce qui pourrait permettre leur persistance dans des habitats non-brûlés sub-optimaux jusqu'au prochain passage du feu. De telles espèces seraient ainsi plus sujettes à être négativement affectées par une réduction de la disponibilité en habitats brûlés comparativement à des espèces saproxyliques opportunistes qui sont retrouvées en grande abondance dans les brûlis, due à l'abondance de bois mort récent, mais qui préfèrent d'autres sources de bois mort.

1.3 Problématique

1.3.1 Impacts de la récupération après feu

Bien qu'encore commun dans le paysage de la forêt boréale canadienne, l'importance régionale des brûlis récents pourrait diminuer dans les années à venir, dû en partie à la diminution de la fréquence du feu reliée aux changements climatiques, principalement prévue pour l'ouest du Québec (Bergeron et al., 2001; Flannigan et al., 2001). Cependant, on présume que la coupe de récupération après feu aura un plus grand impact sur la réduction de la disponibilité des habitats brûlés, puisqu'elle est facilitée par le développement du réseau routier forestier qui améliore l'accessibilité aux brûlis (Nappi et al., 2004; Schmiegelow et al., 2006). De plus, les progrès technologiques dans les usines de transformation permettent d'utiliser le bois brûlé de plus en plus efficacement (Saint-Germain et Greene, 2009). En fait, une intensification généralisée de la récupération après feu en forêt boréale a été observée, ce qui a soulevé certaines inquiétudes au niveau des problématiques de conservation (Dellasala et al., 2006; Lindenmayer et al., 2008). En effet, dans l'éventualité où les espèces saproxyliques boréales seraient bien adaptées à la récurrence des feux avec laquelle elles ont évoluées (McPeek et Holt, 1992), la récupération après feu pourrait excéder leur résilience (Le Goff et al., 2008). Il y a déjà plusieurs indications que la récupération après feu interfère avec le rétablissement de certains processus écologique naturel (Lindenmayer et Ough, 2006) et qu'elle a plusieurs impacts négatifs sur la flore et la faune (Nappi et al., 2004). Parmi ces impacts, il y a l'élimination d'habitats de nidification et d'alimentation. En effet, l'extraction de chicots qui entretiennent une grande quantité de larves d'insectes diminue la disponibilité de proies pour les oiseaux insectivores (Morissette et al., 2002; Purdon et al., 2002). Il a aussi été démontré que 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, l'extraction de chicots de dimensions commerciales réduit les sources *in situ* de semences pour la régénération des arbres. 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-étages dû à une augmentation de la température du sol et de la dessiccation (Purdon et al., 2002). Cela tend à homogénéiser et à réduire le couvert végétal ainsi que la diversité en espèces des plantes (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).

1.3.2 Lois protégeant la biodiversité

Afin de réduire les effets négatifs des perturbations anthropiques sur les milieux naturels, le gouvernement fédéral, par le biais du Conseil canadien des ministres des forêts (CCMF), a adopté en 1992 le concept d'aménagement durable des forêts (CCMF, 2003), définit en 1987 par la commission Brundtland (Brundtland, 1987). Ce concept vise à maintenir et à améliorer à long terme la santé des écosystèmes forestiers au bénéfice de tous les êtres vivants, tout en assurant aux générations actuelles et futures de bonnes perspectives environnementales, économiques, sociales et culturelles (Brundtland, 1987; CCMF, 2003). Le gouvernement québécois identifie en tant que premier critère d'aménagement durable des forêts, la conservation de la diversité biologique ; et indique que pour y arriver, il faut assurer la diversité des écosystèmes, la diversité des espèces et la diversité génétique au sein des espèces, ainsi que les interactions entre les espèces et celles entre les espèces et leur milieu (MRNF, 2003). Selon Kim (1993), la biodiversité est la ressource biotique de base pour soutenir la vie humaine. Le CCMF, comme le gouvernement québécois, a identifié l'aménagement écosystémique comme une approche pertinente pour parvenir à mettre en application le concept d'aménagement forestier durable (CCMF, 2003; Coulombe et al., 2004). 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).

Puisque les effets de la coupe de récupération après feu semblent affecter la diversité biologique, certaines provinces canadiennes ont inclus, dans leur loi sur les forêts, des directives d'aménagement quant à la récupération après feu. Ces directives ont comme but principal de préserver des portions de la variabilité de l'habitat après feu. De façon concrète, cela est fait en limitant les superficies soumises à la récupération dans un même brûlis, en laissant des tiges résiduelles sur le parterre de coupe, ou même en ne récupérant pas du tout dans certains brûlis (Saint-Germain et Greene, 2009). Toutefois, certaines provinces obligent toujours la récupération après feu dans leur loi sur les forêts et ce, sans aucune directive spécifique à la récupération, ni même quant aux opérations sur le terrain ; c'est d'ailleurs le cas de la province de Québec (Schmiegelow et al., 2006; Saint-Germain et Greene, 2009). La nature obligatoire des plans de récupération au Québec a entraîné, dans les années 90, une hausse des volumes récupérés (Purdon et al., 2002). Récemment, des 278 030 ha de forêts brûlées au Québec en 2007, 20 % ont été soumis à la coupe de récupération (Parent, 2009). En effet, au Québec, la récupération résultent principalement en coupe totale des peuplements brûlés, sans rétention d'arbres ou de groupes d'arbres résiduels dans l'aire récupérée. Seul ceux n'ayant pas brûlés, qui ne sont pas marchand (avec un diamètre à hauteur de poitrine (dhp) $\leq$9 cm) ou ceux étant inaccessibles sont laissés sur l'aire récupérée (Nappi et al., 2004). Concrètement, de tels plans ont provoqué la récupération de 39 % des 17 667 ha de peuplements conifériens marchands brûlés issus de quatre brûlis de la région de Chibougamau en 2005 et couvrant un total de 41 706 ha (J. Boucher, résultats non-publiés).

1.4 Contexte de l'étude

Afin d'évaluer l'impact de la coupe de récupération après feu sur les espèces associées aux brûlis, nous avons spécifiquement travaillé sur huit familles de coléoptères (Buprestidae, Cerambycidae, Cleridae, Corylophidae, Curculionidae, Elateridae, Lathridiidae et Salpingidae) reconnues pour contenir plusieurs espèces saproxyliques et/ou pour posséder plusieurs espèces étant le plus souvent retrouvées dans les brûlis (Wikars, 1992; Wikars, 1997a; Siitonen, 2001; Saint-Germain et al., 2004a; Boulanger et Sirois, 2007). En effet les familles des Buprestidae et des Cerambycidae se développent à l'état larvaire dans le phloème ou même directement dans le xylème des arbres récemment morts ou moribonds, les premiers spécimens retrouvés de ces familles indiquent que leur existence date de la fin du Jurassique pour les Burprestidae et du Crétacé pour les Cerambycidae (Grimaldi et Engel, 2005). Les Curculionidae, contenant la sous-famille des Scolytinae, datent du début du Jurassique; certains fossiles démontrent qu'ils se nourrissaient et creusaient déjà sous l'écorce depuis au moins la moitié du Crétacé (Grimaldi et Engel, 2005). Les Elateridae, dont les larves sont reconnues pour creuser des galeries dans le bois en décomposition imprégné de pourriture fongique où elles se nourrissent d'autre larves xylophages ou de racines de plantes, existent aussi depuis au moins la fin du Jurassique (Grimaldi et Engel, 2005). Les familles récentes de Cucujoidea (Cleridae, Corylophidae, Lathridiidae et Salpingidae) se sont formées durant le Crétacé. Certaines de ces familles, comme les Cleridae et les Salpingidae ont un rôle de prédateurs saproxyliques, alors que les Corylophidae et les Lathridiidae sont des mycétophages saproxyliques (Grimaldi et Engel, 2005). Puisque ces familles de coléoptères existaient déjà il y plus de 100 millions d'années et qu'elles avaient déjà un rôle d'organismes saproxyliques dans les écosystèmes préhistoriques, on peut imaginer, que comme les plantes et autres organismes des écosystèmes, les coléoptères de ces familles ont eux aussi évolué en développant certaines adaptations au feu et sont donc des groupes à risque de contenir plusieurs espèces associées aux brûlis.

Peu de chercheurs ont directement évalué la réponse des communautés de la forêt boréale à la coupe de récupération. Certains comme Morissette et al. (2002), Cahall et Hayes (2009) et Azeria et al. (en révision) ont étudié les communautés d'oiseaux et Bradbury (2006) a étudié les communautés de bryophytes. La réponse des Carabidae épigés à la coupe de récupération a été étudiée, indiquant des communautés différentes entre la forêt brûlée et la forêt récupérée (Phillips et al., 2006). Il a d'ailleurs été noté que la réponse des Carabidae à la coupe de récupération est différente de leur réponse à la coupe forestière en forêt non-brûlée, ce qui suggère que l'aménagement des brûlis requiert des considérations différentes de l'aménagement en forêt non-brûlée (Phillips et al., 2006). Cependant, à notre connaissance, il n'existe aucune étude sur les communautés de coléoptères saproxyliques directement associés aux arbres retirés lors de la récupération.

L'objectif de cette étude était de déterminer l'effet d'une réduction de la surface terrière marchande suite à la récupération après feu sur les assemblages de coléoptères associés aux brûlis. Plus spécifiquement, les objectifs étaient de : 1) vérifier si l'abondance de coléoptères, leur richesse en espèces et les assemblages observés dans les brûlis différaient de ceux observés dans d'autres perturbations contenant des chicots récents ; 2) identifier, parmi les huit familles étudiées, les espèces associées aux brûlis de celles qui sont opportunistes ; et 3) explorer les effets de la coupe de récupération après feu, de la sévérité du feu et de la distance à la forêt non-brûlée, sur l'abondance, la richesse en espèces, les renouvellements d'espèces dans le temps et sur les assemblages d'espèces associées au brûlis.

CHAPITRE PRINCIPAL

Impacts of postfire logging on burn-associated beetles in boreal forest: temporal dynamics

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Abstract

There are a few evidences that salvage logging could hamper natural ecological recovery processes, such as the regeneration of plant species. Indeed, if some boreal saproxylic species are adapted to postfire habitat with which they have evolved, salvage logging might exceed their resilience. This study aimed to identify burn-associated species of the northern boreal forest of the province of Quebec in Canada, and to determine the effect of reducing the merchantable tree basal area through time following salvage logging after fire, on the assemblages of these burn-associated species. Salvage logging was conducted from August 2005 to May 2006 after wildfires that prevailed in 2005, in the Chibougamau region. We sampled beetles over three years after salvage logging (2006 - 2008) using multidirectional flight-interception traps. Ten traps were installed in ten plots equally distributed between unburned black spruce (*Picea mariana* Mill. B.S.P.) and jack pine (*Pinus banksiana* Lamb.) dominated stands, where 11 mature trees (dbh > 9 cm) were girdled in order to generate recent snags. Thirty-six other traps were set in 36 plots distributed between burned black spruce and jack pine dominated stands residual from salvage logging in order to cover the largest gradient of salvage logging levels. For each burned plot, we measured habitat attributes affected by salvage logging which could influence burn-associated assemblages' structure, such as the basal area of residual trees by species and diameter classes at different scales (0.04 ha and 7 ha). We also measured the distance from the sites to the unburned continuous forest and fire severity, using the delta Normalized Burn Ratio (dNBR). By studying beetle assemblages from selected families (Buprestidae, Cerambycidae, Cleridae, Corylophidae, Curculionidae, Elateridae, Lathridiidae and Salpingidae) found in burned and unburned plots with girdled trees, we identified 18 burn-associated species. These burn-associated beetles only responded to salvage logging starting from year no.2 (2007) after salvage logging. Burn-associated beetle assemblages were mainly shaped by three groups of environmental factors: 1) prefire forest conditions such as tree species composition; 2) conditions generated by fire event such as the distance to the unburned forest, which is directly affected by the shape of the burned area, as well as burn severity; 3) the amount of salvage logged area and the associated reduction of the amount of mature size coniferous snags (dbh > 9 cm).

Keywords: Boreal forest; Fire ecology; Burn-associated species; Coleoptera; Salvage logging; Burn severity; Snags.

1. Introduction

Geological records of fossil charcoal, a proxy of fire, indicate that wildfires rapidly followed the appearance of terrestrial plants; this suggest that fire have had strong evolutionary impacts on biota along the history of terrestrial life (Glasspool et al., 2004; Scott and Glasspool, 2006; Bowman et al., 2009). This natural disturbance influences global ecosystem patterns and processes; these include vegetation distribution and structure, biomass production, geochemical cycles, climate and biodiversity (Weber and Flannigan, 1997; McCullough et al., 1998; Bourgeau-Chavez et al., 2002; Bowman et al., 2009). Wildfires do not only remove species and simplify vegetative structure; it also generates new habitat features, from micro-habitat to the landscape scale, which are referred as pyrogenic structures (Kennedy and Fontaine, 2009). These habitats are mainly characterized by open stands with warm and exposed mineral soils, by high abundances of fungi and as time goes, by an increasing shrub cover (Wikars, 1992; Nappi et al., 2004). At the landscape scale, wildfires represent the main cause for generating dead wood in boreal forests (Siitonen, 2001; Drapeau et al., 2002; Nappi et al., 2004; Kennedy and Fontaine, 2009).

Fire-killed trees are habitats for a large diversity of invertebrate saproxylic species (Wikars, 1992; Saint-Germain et al., 2004a; Boulanger and Sirois, 2007), which are important in wood decomposition (Speight, 1989; Kim, 1993; Boulanger and Sirois, 2007), and a non-negligible part of many vertebrate species diet (Morissette et al., 2002; Purdon et al., 2002; Nappi et al., 2004; Kennedy and Fontaine, 2009). Invertebrate saproxylic species are defined as species that depend, during a part of their life cycle, upon wood of moribund or dead trees (standing or fallen), or upon wood-inhabiting fungi, or upon the presence of other saproxylics (Speight, 1989). Amongst boreal forest's saproxylics organisms, beetles (Coleoptera) are the best known and the most diversified taxonomic group, both in terms of taxonomy and ecology (Niemela, 1997; Siitonen, 2001). Moreover, saproxylic beetles are the most vulnerable group of Coleoptera to extinction in boreal forests of Fennoscandia because of the reduction in the availability of dead wood (Hyvärinen et al., 2006) which is mostly due to intensive forest management (Siitonen, 2001) and extensive fire suppression (Wikars, 1992). Saproxylic organisms that are conspicuously favoured by fires are defined as pyrophilous (Wikars, 1997b). However, the term pyrophilous raises some controversy (see Nappi et al., 2004) and we prefer to use *burn-associated species*, to define species that are strongly associated (i.e. found in high abundance/incidence) with postfire habitats. Burn-associated species are expected to use snags produced by wildfire to increase their population level, which is hypothesized to allow their persistence in sub-optimal unburned habitats until the next regional wildfire (Wikars, 2002; Nappi et al., 2004). Such species would thus be more likely to be negatively affected by a reduction in the availability of postfire habitats than opportunistic saproxylic species, which are fund in burns with high abundance because of the massive snag recruitment, but are more associated to other sources of recently killed trees.

Even if it is still common in the Canadian boreal forest landscape, the regional importance of recent burns habitats is expected to decrease in the near future due to climate-related decrease in fire frequency, especially in western Quebec (Bergeron et al., 2001; Flannigan et al., 2001). Moreover, increasing pressure by salvage logging may have a stronger impact on the reduction of postfire habitat availability, as the development of extensive road networks is rapidly increasing, making burns more accessible (Nappi et al., 2004; Schmiegelow et al., 2006). In addition, the technology for treating fire-killed wood in lumber mills continues to improve (Saint-Germain and Greene, 2009). In fact, widespread trend in the intensification of postfire logging in boreal forest has been observed, which raised some concerns about conservation issues (Dellasala et al., 2006; Lindenmayer et al., 2008). Indeed, if boreal saproxylic species are presumably well adapted to fire recurrence with which they have evolved (McPeek and Holt, 1992), it is important to make sure that salvage logging following fire does not exceed their resilience (Le Goff et al., 2008). There is yet abundant theoretical and empirical evidence that salvage logging interferes with natural ecological recovery (Lindenmayer and Ough, 2006) and has several negative impacts at the extent of salvage activities, on both vegetation and wildlife (Nappi et al., 2004) at the extent of salvage activities. Amongst these impacts, one of the most important is the removal of foraging and nesting habitats for wildlife (e.g. snags), that harbour large numbers of insect larvae, thus reducing the availability of prey for insectivorous birds (Morissette et al., 2002; Purdon et al., 2002). It has also been reported that salvage logging reduces the average persistence of leftover snags, which are more vulnerable to windthrow when forest openings become abundant across the landscape, and it obviously reduces average diameters of lingering snags and stand densities (Russell et al., 2006). Moreover, the removal of merchantable snags reduces *in situ* seed sources that are important for establishing tree regeneration; full sun exposition also results in higher variations in soil temperatures (Greene et al., 2006) leading to desiccation and to a reduction in suitable seedbed and growth conditions for understory plants and trees (Purdon et al., 2002). This tends to homogenize and to reduce the cover and diversity of plant communities

(Purdon et al., 2002). Furthermore, patterns of within-stand structural complexity are altered as snags and residual living trees are removed (Lindenmayer et al., 2008); within these simplified stands, the assemblages of plants and animals are modified as functional groups decline or are lost (Lindenmayer and Ough, 2006).

To evaluate the impact of postfire salvage logging on burn-associated species, we specifically looked at eight beetle families (Buprestidae, Cerambycidae, Cleridae, Corylophidae, Curculionidae, Elateridae, Lathridiidae and Salpingidae) known to contain many saproxylic species and/or having many species that mostly occur in burns (Wikars, 1992; Wikars, 1997a; Siitonen, 2001; Saint-Germain et al., 2004a; Boulanger and Sirois, 2007; Moretti et al., 2010). Few studies have directly evaluated the response of boreal forest communities to salvage logging, most have considered bird communities (Morissette et al., 2002; Cahall and Hayes, 2009; Azeria et al., in revision) and one considered bryophyte communities (Bradbury, 2006). The response of epigeic carabid beetles to postfire salvage logging has been studied, and indicated that communities differ between burned forest and salvage logged forest (Phillips et al., 2006). The same study also outlined that carabid's response towards salvage logging was different from the one to harvesting in unburned forest, suggesting that postfire forest management requires particular considerations (Phillips et al., 2006). Although to our knowledge, our study is the first to address this issue by studying the response of saproxylic beetles' assemblages over time to postfire salvage logging.

The aim of this paper was to determine the effect of the reduction of merchantable basal area following postfire logging on the assemblages of burn-associated beetles.

Specific objectives were: 1) to verify if beetle abundance, species richness and assemblages found in burns differed from those found in unburned stands containing a patch of recent snags produced by girdling trees; 2) to identify burn-associated species versus opportunistic species in the eight studied families, and 3) to explore the effects of postfire logging, burn severity and distance from unburned forest on burn-associated species abundance, species richness, and species assemblages changes through time after salvage logging.

2. Methods

2.1. Study area and sampling plots

The study was conducted in four 2005 burns covering 41 706 ha of forested lands within the western spruce–moss bioclimatic subdomain of North-Western Quebec, Canada (Figure 1). This subdomain is typically dominated by black spruce (*Picea mariana* Mill. B.S.P.) with jack pine (*Pinus banksiana* Lamb.) and balsam fir (*Abies balsamea* (L.) Mill.) as companion species. Trembling aspen (*Populus tremuloides* Michx.) and paper birch (*Betula papyrifera* Marsch.) are also present in some stands. Due to the relatively short fire cycle (120 - 180 years), landscapes of this subdomain are dominated by even-aged forest stands (Bergeron et al., 2004). Studied stands varied in terms of pre-fire composition and structure (age - tree species), as well as in levels of postfire logging activities, which were carried out between August 2005 and May 2006. To cover these gradients in our sampling, thirty-six plots were established in leftover stands from postfire logging (hereinafter *burned plots*), which were dominated by either black spruce or jack pine, in order to measure the potential of these residual stands as habitat for saproxylic beetles. Burned plots were selected based on their accessibility, which was assessed using ecoforest maps, and in a way to cover the whole range of salvage logging levels, which was visually evaluated in a radius of roughly one hundred meters. The thirty-six burned plots thus covered a range of 0 - 80 % of salvaged area within this radius. Because of the poor accessibility to some sectors of the burns, none of the four burns permitted to establish plots covering this range of salvage logging. Thus, burned plots are distributed in burns based on the availability of accessible stands fitting our needs (i.e. that burns are not considered as statistical blocks). Ten other plots were equally distributed between unburned black spruce and jack pine dominated stands. In each of these plots 11 mature trees (dbh > 9 cm) were girdled at breast height in order to kill them (hereinafter *girdled plots*). The girdling treatment consisted in the removal of a 5 cm wide strip of bark around the bole, reaching the sapwood, before tree buds open (early June 2006). Girdled trees languished rapidly, and by the end of summer 2006 most of them showed significant signs of weakening (loss of needled and/or red needles). These plots were set kilometres (> 3 km) away from the closest 2005 burn. The girdling generated a micro-perturbation, of about 0.03 - 0.04 ha, that emulated the gap dynamics which characterise the disturbance regime of northern boreal forest stands escaping fire. These micro-perturbations aimed at attracting saproxylic beetles that could use unburned recently killed snags (Jacobs et al., 2007). This was intended to distinguish opportunistic saproxylic from burn-associated species. All plots were georeferenced and included in a Geographic Information System (GIS).

2.2. Beetle sampling

Beetles were sampled, in both burned plots and girdled plots, over three years after salvage logging (2006-2008; hereinafter *year no.1* for 2006, *year no.2* for 2007, and *year no.3* for 2008), during the active season of beetles (i.e. early June to late August). We used one multidirectional flight-interception trap (Saint-Germain et al., 2004a; Janssen et al., 2009) at the center of each plot. These traps were made of four 15 × 40 cm panels (two made of mosquito net and two made of Plexiglas®) mounted into a cross pattern, along a 10 cm diameter black ABS cylinder. Two funnels, leading to collecting vials, were placed above and below the cylinder; vials were filled with a 40 % ethanol solution in which a 5 % household vinegar (acetic acid) solution was added for preservation. Flight-interception traps are known for being efficient in trapping flying saproxylic beetles (Okland, 1996; Saint-Germain et al., 2004a). The samples were collected every two weeks and kept into a 70 % ethanol solution for preservation until identification.

Adult beetles were identified to species (13 432 specimens) whenever possible, at the genus level (409 specimens), or at the family level (2 specimens). These identifications were cross-checked at either the René-Martineau insectarium of the Canadian Forest Service (Quebec, Canada) (17.2 % of the specimens), or at the Canadian National Collection (CNC) of Insects, Arachnids and Nematodes (Ottawa, Canada) (1.8 % of the specimens). A reference collection of labelled and identified specimens is conserved in the Forest Insect Ecology and Diversity laboratory of the Canadian Forest Service of Natural Resources Canada (Quebec, Canada).

2.3. Habitat attributes

2.3.1. At the 0.04 ha scale

Habitat attributes of burned plots were characterized using a circular plot of 0.04 ha (11.28 m radius) centered on the flight-interception trap where we recorded tree species and diameter at breast height (dbh: 1.3 m) for all trees and snags of merchantable dimension (> 9 cm dbh). These values were also recorded for all trees and snags of non-merchentable dimension (≥9 cm dbh) within a 0.004 ha (3.57 m radius) circular subplot, also centered on the flight-interception trap. The amount of down dead wood (DDW) by tree species was measured on four transects of 11.28 m (for a total length of 45.12 m), each starting from the trap and going toward the four cardinals points, in order to neutralise the effect of non-random log orientation (Van Wagner, 1982). The diameter of every DDW larger than 5 cm of diameter and crossing the line transect was measured perpendicularly to the main axis of the logs (Warren and Olsen, 1964; Van Wagner, 1968; Ringvall and Stahl, 1999; Bohl and Brandli, 2007). The DDW were mostly constituted of black spruce and jack pine, so we did not considered the few pieces of other species.

2.3.2. At the 7 ha scale

Because we used flight-interception traps that catch beetles that are flying in or through our plots, we wanted to verify if insects that we trapped were affected by habitat attributes at a larger extent than the 0.04 ha scale. Therefore, to assess the importance of habitat attributes and the effect of salvage logging at a larger scale for beetles, we set a 7 ha circular plot (150 m radius) centered on each flight-interception trap. These 7 ha plots included almost only burned forest, very few live trees being observed. This radius length (150 m) was the largest we could use to avoid overlapping between plots and thus ensure the spatial independence of estimates from each 7 ha plot (Holland et al., 2004). We used ArcMap 9.2 (ESRI, 2009) to extract habitat attributes from ecoforest classification maps at the 7 ha scale. These maps constitute the baseline information on age structure and stand composition, as well as the area affected by postfire logging activities. These maps were combined with a database on stock inventory to evaluate the residual basal area by tree species at the 7 ha scale. This database on stock inventory includes basal area by diameter class (dbh) for each tree species. Thus, allowing estimates of residual basal area in stands still present after salvage logging at the 7 ha scale, according to their size (dbh $\leq$9 cm vs dbh > 9 cm). Because basal area by tree species is not available in the Stock database for young stands ($\leq$20 years old), we recorded their area in each 7 ha plot. We also estimated the proportion of salvaged area within the 7 ha scale (Sal.Area). Since the unburned continuous forest can be considered as a source habitat for species that colonize burns (Saint-Germain et al., 2008; Boulanger et al., 2010), we measured the shortest distance from the plot center to the interface between the burn edge and the unburned continuous (i.e. areas of more than hundreds of hectares) forest (Dis.GF), which is dependent of the burn shape. Thus, in irregular shaped burns, the shortest would be the distance from a random point in the burn to the unburned continuous forest.

Finally, we quantified burn severity using the Delta Normalized Burn Ratio (dNBR) index, which is derived from differences between pre- and postfire reflectance of two Landsat bands (TM Band 4 and Band 7) that most respond but in divergent ways, to burning (Key and Benson, 2006). The dNBR was computed using satellite images taken before salvage logging was carried out. Six field-corrected Landsat 5 TM 30-meter scenes (3 prefire and 3 postfire) obtained from the U.S. Geological Survey Earth Resources Observation and Science Center (USGS - EROS) were used. Prefire scenes were taken on September 10th and 19th 2004, and smoke-free postfire scenes were taken on July 11th 2005 and on September 6th 2005. We computed dNBR values for each pixel (30 m × 30 m) within the 7 ha scale, and considered the mean and standard deviation as a measure of burn severity (Brn.Sev) and heterogeneity (Brn.Het), respectively. The dNBR index has been an increasingly popular method in recent years because it is closely linked to burn severity as confirmed by field assessments (Key and Benson, 2006). To identify unburned areas within the 7 ha plots, dNBR values ranging between −74 and 93 were determined as unburned areas, using a 95 % confidence interval from the distribution of 316 484 pixels values (Standard deviation: 42.64) that were sampled in the unburned areas around the burns (methodology approved by J. Clark Remote Sensing Analyst USDA-USFS-RSAC).

2.4. Statistical analysis

All statistical tests were produced using the program R v.2.9.0 (R-Development-Team, 2009).

2.4.1. Abundance and species richness in burned versus girdled plots

We used ANOVA to compare abundance and species richness of beetles in burned and girdled plots. These analyses were made using the GLM procedure in the STATS package of R (Davies et al., 2010).

2.4.2. Species assemblages in burned versus girdled plots

We used Anderson's (2006) analysis of homogeneity of multivariate group dispersions (variances) to identify differences in beetle assemblages. It uses Euclidean distances based on Bray-Curtis index of dissimilarity. We composed a priori groups using burned (n = 36) and girdled (n = 10) plots as factors. All identified beetles from studied families and for each of the 46 plots were used in the analysis. The procedure used (Betadisper procedure in R, (Simpson, 2010)) calculates the average distance of group members (burned versus girdled plots) to the group centroids on the basis of the principal coordinate axes. To test whether dispersions (variances) of burned and girdled plots groups were different, the distances of group members to the group centroid are subject to ANOVA where a *P*-value is obtained by permuting observations 999 times (Anderson, 2004; Anderson, 2006; Anderson et al., 2006).

2.4.3. Burn-associated species

To identify species positively associated with burned forests, we used the point-biserial group-equalized phi coefficient (Pearson correlation) as described by De Cáceres and Legendre (2009), for each post-salvage year. We used the MULTIPATT procedure in the Indicspecies package for R (De Cáceres, 2010). Correlation coefficients produced by this analysis take into account the absences outside the target group (in our case burned versus girdled plots), and these absences contribute in increasing the power of the associations as well as presences in plots of that group. This makes the analysis more context dependent than indicator value indices (IndVal index, Dufrêne and Legendre, 1997) for the determination of species-habitat associations (De

Cáceres and Legendre, 2009). All species identified from the studied families in the 46 plots were used in this analysis.

2.4.4. Burn-associated species models relating abundance, species richness and species turnover to habitat attributes

We pursued the analysis using exclusively the burn-associated species, because we considered these saproxylic species to be more at risk of being affected by postfire logging, since their main breeding substrate, fire-killed trees, is harvested. To determine species – habitat relationship, we first verified the normal distribution of habitat attributes and applied the required transformations when needed (Table 1). We built a correlation matrix between habitat attributes to identify collinearity problems ($r \geq 0.7$). With this method we figured out that merchantable basal area of jack pine in 7 ha was correlated with merchantable basal area of jack pine in 0.04 ha and with merchantable basal area of black spruce in 7 ha. Therefore, the merchantable basal area of jack pine in 0.04 ha was dropped from the analyses, and merchantable basal area of jack pine and black spruce in 7 ha were pooled (BSP-JPI.M). Since unburned areas within the 7 ha plots were negatively correlated with burn severity, this habitat attribute was not used in the analysis. Basal areas of non-merchantable and merchantable balsam fir were strongly correlated in 7 ha, so we only considered the merchantable basal area in our analysis (BFI.M), given that salvage logging as a direct impact on merchantable trees. The same type of correlation was observed for deciduous tree species, so we only kept merchantable basal area (DEC.M). Using variance inflation factor (VIF), we tested for multicollinearity amongst selected habitat attributes (Table 1). Those which had a VIF value ranging from 1.84 to 6.65 were considered appropriate in our context (O'brien, 2007), and other variables were drawn back from the analysis.

To assess the impact of salvage logging through time (three years after salvage) on the abundance and species richness of burn-associated beetles, we used Bayesian Model Averaging (BMA) with habitat attributes (Table 1) for each of the three years after salvage. We used the BIC.GLM procedure in the BMA package for R (Raftery et al., 2005), which selects the most probable models based on the Bayesian information criterion (BIC) using the "leaps and bounds" algorithm. We then fitted linear regression using the most supported habitat attributes which had a posterior model probability (PP) higher than 40 from BMA (Azeria et al., 2009a).

To understand what drives the changes in insect assemblages through time (three years after salvage logging), and assess the impact of salvage logging on these assemblages, we measured species turnover between years via Bray-Curtis dissimilarity indices using the VEGDIST procedure from Vegan package in R (Oksanen et al., 2010). We calculated the dissimilarity between species assemblages of each burned plot on different years as a metric of changes in the structure of assemblages through time (species turnover). To ensure a comparable base from year to year, we considered all listed (Table 2) burn-associated species. Bray-Curtis dissimilarity index has a value of 0 when perfect overlap occurs in assemblages structure between two years for a same burned plot (i.e. same species and same abundance by species), and it equals 1 when dissimilarity in assemblages is complete (i.e. no species in common). We modeled the

Bray-Curtis dissimilarity index between years with habitat attributes (Table 1) using Bayesian Model Averaging (same methodology as described above).

2.4.5. Burn-associated beetle assemblages and habitat relationship

Salvage logging is expected to generate major gradients in habitat attributes. We tested the effects of these attributes on beetle assemblages using permutational multivariate analysis of variance using distance matrices (ADONIS). The ADONIS procedure of the vegan package is analogous to the Anderson's (2001) PERMANOVA and can handle simultaneous analysis of multiple continuous attributes (Oksanen et al., 2010). We supplied raw data from burn-associated species for each year after salvage logging and used the Bray-Curtis method to generate a dissimilarity matrix. ADONIS examined how selected habitat attributes (Table 1) affected the variability in assemblages of burn-associated species, after accounting for all habitat attributes (type III ADONIS). This was done for each year. Habitat attributes with small or no support ($P > 0.1$) were not used in the analyses. To summarize ADONIS results, we produced ordinations for each year using redundancy analysis (RDA) that illustrated the relationships between influential habitat attributes (those significant following ADONIS results) and burn-associated beetles. We used RDA procedure in the vegan package for R, where species data were Hellinger transformed according to Legendre and Gallagher (2001).

3. Results

3.1. Abundance and species richness of burned versus girdled plots

A total of 13 843 specimens distributed amongst 133 species belonging to the eight studied families were identified: 11 680 specimens representing 115 species were caught in burned plots while 2 163 specimens distributed in 87 species were caught in girdled plots. Beetles were significantly more abundant ($F_{1, 44} = 11.55$, $P = 0.0014$) in burned plots (324.4 ± 16.0) than in girdled plots (216.3 ± 16.6), but no difference ($F_{1, 44} = 0.23$, $P = 0.6322$) was observed in average species richness between burned plots (34.9 ± 0.9) and girdled plots (33.9 ± 1.9).

3.2. Beetle assemblages in burned versus girdled plots

The ordination of BETADISPER's results (Figure 2; $F_{1, 44} = 11.38$; $N_{perm} = 999$; $P_{perm} = 0.002$) showed a clear distinction between assemblages in burned and girdled plots. A lower variability in burned plots assemblages was observed compared with the girdled plots, based on their average distance to group centroid, which were respectively of 0.29 versus 0.35.

3.3. Species associated with burned versus girdled plots

The species – habitat (burned versus girdled plots) associations analysis (Pearson's point-biserial correlation) identified 18 species, amongst 7 families, as associated with burns while 24 species, distributed in 3 families were associated with girdled plots (Table 2).

For each year after salvage logging, the burn-associated species were somewhat different. Respectively, 10, 11 and 15 species were identified as burn-associated species for years no.1, no.2 and no.3 after salvage logging. Two woodborers, *Arhopalus foveicollis* (Hald.) and *Monochamus scutllatus scutellatus* (Say), and one bark beetle, *Dryocoetes autographus* (Ratzburg), were associated with burned plots only for year no.1 after salvage logging. However, an increasing number of Elateridae species was associated with burned plots through time after salvage logging (Table 2). Seven species were found to be significantly associated with burned plots during each of the three years after salvage logging; these were *Acmeops pratensis* (Laicharteg), *Clypastraea fusca* Harold, *Agriotes limosus* (LeConte), *Ampedus quebecensis* W.J.Brown, *Sericus incongruus* (LeConte), *Corticaria dentigera* LeConte and *Sphaeriestes virescens* Randall. The strength of association (Phi coefficients) of these species with burned plots also varied through time. While the associations got stronger as time elapsed after fire and salvage logging for *Acmeops pratensis* and *Sericus incongruus*, it got weaker for *Clypastraea fusca*, *Agriotes limosus*, *Corticaria dentigera* and *Sphaeriestes virescens*. The salpingind *Sphaeriestes virescens* had the strongest overall coefficients of association with burned plots for all three years after salvage logging and was also the most abundant species overall. From the 42 species listed in Table 2, none was found only in burned plots whereas only the cerambycid *Pogonocherus penicillatus* was found exclusively in girdled plots. Only two species were found to be significantly associated with girdled plots during each of the three years after treatment: *Polygraphus rufipennis* (Kirby) and *Trypodendron lineatum* (Olivier), which are both scolytid. The cerambycid *Acmaeops proteus proteus* (Kirby) and the lathridiid *Enicmus tenuicornis* LeConte were associated with these plots on years no.1 and no.2, while the cerambycid *Tetropium* *cinnamopterum* Kirby and the scolytid *Dendroctonus valens* LeConte were associated only on year no. 1. Overall, Cerambycidae and Curculionidae were the two most important families associated with girdled plots, the former being mostly associated with this habitat over years no. 1 and 2 after treatment whereas the latter were mostly associated over years no.2 and no.3. This analysis did not point out significant associations for any buprestid beetles, even if out of the 11 buprestid species caught, 9 were only found in burned plots (Appendix A), including *Melanophila acuminata* (DeGeer).

3.4. Models relating abundance, species richness, species turnover and assemblages of burn-associated species to habitat attributes

In this section we summarize the effects of the most influential habitat attributes on the abundance, species richness, species turnover and assemblages of burn-associated species. In addition, we highlight the fact that less variables affected by salvage logging interacted with burn-associated species during year no.1 after salvage logging compared with years no.2 and no.3.

3.4.1. Mature coniferous trees (BSP.M, BSP-JPI.M and BFI.M)

The basal area of merchantable black spruce and jack pine snags contributed to overall species turnover between years no.1 and no.3 after salvage logging (Table 3c), and it affected beetle assemblages of years no.2 and no.3 after salvage logging (Table 4). The RDA biplot of year no.2 after salvage logging showed that the basal area of merchantable black spruce and jack pine snags at the 7 ha scale, and of black spruce at the 0.04 ha plot scale both were associated with the species gradient of the first axis, particularly with *Acmaeops pratensis* (Figure 3b). The observed gradient on 2nd axis (Figure 3b) was partly explained by the basal area of merchantable black spruce snags at the 0.04 ha scale (upper left of ordination) to which species such as the elaterid *Ampedus fusculus* (LeConte) seemed to be associated. The basal area of balsam fir positively affected the species richness of year no.1 after salvage logging (Table 3b), as well as the abundance of burn-associated species of year no.3 after salvage logging (Table 3a). Species turnover between years no.1 and no.3 were negatively affected by the basal area of balsam fir at the 7 ha scale (Table 3c).

3.4.2. Trees of non-merchantable dimensions (JPI.Y, BSP.Y, and Y.Stands)

Basal area of young jack pine snags at the 0.04 ha scale had a negative effect on species turnover between years no.1 and no.3 and between years no.2 and no.3 after salvage logging. Species assemblages of year no.2 after salvage logging were affected by the basal area of young jack pine snags at the 7 ha scale (Table 4), as observed by a positive association for species like *Agriotes limosus* (Figure 3b). Whereas, species turnover between years no.1 and no.3 after salvage logging were positively affected by the basal area of young black spruce snags at the 7 ha scale (Table 3c). Burn-associated species assemblages on year no.3 after salvage logging were partly explained by the basal area of young black spruce snags at the 0.04 ha scale (Table 4). This was illustrated by the RDA ordination of year no.3 after salvage logging; the 1st axis was mainly associated to the basal area of young black spruce snags at the 0.04 ha scale (Figure 3c), to which species such as the lathridiid *Corticaria dentigera* had a positive association. Finally, the area covered by young stands ($\leq$20 years) within the 7 ha scale had a positive effect on both abundance and species richness of burn-associated species in year no.3.

3.4.3. Down dead wood (JPI.DDW and BSP.DDW)

Down dead wood of black spruce negatively contributed to species turnover between years no.1 and no.3 after salvage logging, as well as between years no.2 and no.3 (Table 3c). This habitat attribute also contributed to beetle assemblages' structure of year no.3 after salvage logging (Table 4). The species distribution on the 2nd axis of the ordination (Figure 3c) showed that most of the burn-associated species of year no.3 after salvage logging were associated to down dead wood of black spruce (species in the upper part of the ordination) especially for species like the elaterid *Sericus incongruus*. In parallel, during year no.1 after salvage logging, the presence of down dead wood of jack pine took part in structuring the species assemblages (Table 4). The species gradient linked with down dead wood of jack pine might help explaining the effect that this attribute has on burn-associated assemblages of year no.1; even though the second axis of the ordination of year no.1 after salvage logging (Figure 3a) has a low percentage of explanation. It seems that the corylophid *Clypastraea fusca* was positively associated to it.

3.4.4. Burn severity (Brn.Sev) and distance to green forest (Dis.GF)

Species turnover between years no.1 and no.3 after salvage logging, as well as between years no.2 and no.3 were negatively affected by burn severity. Moreover, it positively contributed to both abundance and species richness of burn-associated species of year no.2 after salvage logging (Tables 3a, 3b). The variability of species assemblages between burned plots through year no.2 after salvage logging was partly explained by burn severity (Table 4). Indeed, the species distribution along the 1st axis of the RDA (Figure 3b) was strongly associated to burn severity; species such as *Acmaeops pratensis* was positively associated to burn severity, and some like *Limonius aeger* (LeConte) seemed to be negatively associated to it. The distance to continuous green forest (extent of the burns) positively influenced species turnover between years no.1 and no.2 (Table 3c), but negatively influenced the abundance of burn-associated species during year no.2 (Table 3a), and species richness on year no.3 after salvage logging (Table 3b). The 1st axis of the RDA biplot of year no.1 after salvage logging (Figure 3a) was strongly linked to the distance to green forest where *Thanasimus undatulus* (Say), *Arhopalus foveicollis* and *Acmaeops pratensis* seemed to be negatively associated to it.

3.4.5. Salvage area (Sal.Area)

The amount of salvaged area within the 7 ha scale had a negative influence on species turnover between years no.2 and no.3 after salvage logging (Table 3c).

4. Discussion

Postfire management more often results in the salvaging of merchantable dimension trees, regardless of the burn severity. Since these trees are a breeding and/or feeding substrate of predilection for many species, it is thus important to understand the effect of the withdrawal of such habitat on species and species assemblages that are closely associated to it.

4.1. Burned versus girdled plots

Our results showed that burned boreal forest yield higher abundance of flying saproxylic beetles and specific beetle assemblages when compared with stands submitted to a small gap dynamic perturbation, as emulated by tree girdling. However, species richness was similar after both types of perturbation. In mature black spruce forests, higher beetle abundance has also been reported in burned stands when compared with unburned ones but as opposed to our results, higher species richness was also reported in burned stands (Saint-Germain et al., 2004a; Moretti et al., 2010). This difference might be explained by the recent snags in the girdled plots, which are used by several saproxylic beetles, even if a small amount of snags was available (11 girdled trees).

Despite the absence of difference in species richness, burned plots showed specific beetle assemblages when compared to girdled plots. Other studies (Saint-Germain et al., 2004a; Moretti et al., 2010) reported similar results when comparing beetle assemblages from burned and unburned mature plots. Fungal flora has also been shown to differ between burned and unburned logs (Wikars, 2002), as well as bird communities in burned and unburned forests (Morissette et al., 2002). This indicates that postfire habitats are used by a high diversity of saproxylic species, probably because burns are an important source of dead wood in boreal forests (Siitonen, 2001; Drapeau et al., 2002; Nappi et al., 2004; Kennedy and Fontaine, 2009). The higher similarity in assemblages structure observed amongst burned plots might be explained by the widespread homogenisation generated by 1) the high fire severity, which killed at least 96 % of trees; 2) the removal of large diameter trees at the 7 ha scale and to the extent of salvage logging activities (Purdon et al., 2002; Lindenmayer and Ough, 2006; Schmiegelow et al., 2006; Lindenmayer et al., 2008). Our results also demonstrated that a small patch of only eleven girdled trees was enough to yield specific saproxylic assemblages, even if the girdling treatment was done few weeks before (year no.1).

4.2. Burn-associated species

Amongst the 133 species identified in our study, 18 were associated with burns and thus are thought to be more sensitive to a reduction in the availability of postfire habitats. Many of the burn-associated species identified in this study have been also found by Saint-Germain et al. (2004a) to be more abundant in burned than in unburned mature forest (see Table 2). However, by comparing burned and girdled plots, we identified species associated with burns versus another disturbance producing recently dead trees, like gap dynamic emulated by tree girdling. It allows discriminating saproxylic species associated with fire-killed trees from opportunistic species that may simply use an abundant resource suddenly available. A good example is *Acmaeops proteus proteus* (Kirby) that Saint-Germain et al. (2004a) found in higher abundance in burns, whilst we found it to be associated with girdled plots (Table 2). Therefore, *Acmaeops p. proteus* appears as an opportunistic saproxylic species, which is found in burns because it uses recently killed trees, but only a small patch of eleven girdled trees was suitable for this species. This seems to also be the case for the scolytid *Polygraphus rufipennis* (Table 2). None of the 18 burn-associated species identified in our analysis have been exclusively found in postfire habitats. This suggests that none depend on fire killed trees to complete its life cycle, but for some reason they have a stronger kinship with burns than the two species mentioned above. Burn-associated species identified in our study may thus also develop in unburned wood or forest. However, some hypothesized that the long-term survival of such species in the boreal forest may rely on recurrent fires (Wikars, 2002) which may permit build-up in burn-associated saproxylic species populations thus allowing species to persist until the next fire; though, this "pulse" hypothesis still need to be proven by further research addressing this specific question.

Trees killed by fire die almost instantly (like most trees in crown replacing fire) compared with other sources of mortality (like insect outbreaks or uprooting) were trees' physiological conditions decrease progressively before death. As trees killed by fire are generally in good health condition before fire event, they provide a fairly different substrate compared to other sources of recently killed trees (Ahnlund and Lindhe, 1992). Defensive mechanisms of trees attacked by insects are activated long time before death, which is not the case for burned trees. These postfire substrate conditions offer niches for species that cannot withstand the defence mechanisms of healthy trees, but thrive on weakened, dying, or dead hosts (secondary users) (Saint-Germain et al., 2004b); this might be the case for some burn-associated species we identified. The specific saproxylic fungal communities growing under the bark of fire-killed trees (Wikars, 2002) might also explain the association of fungivorous species like *Clypastraea fusca* and *Corticaria dentigera* to postfire habitats.

Species associated with burns do not only use early postfire habitats (Kennedy and Fontaine, 2009). Our results also show that different burn-associated species are found for different years after fire (Table 2). These differences are likely to result from temporal changes in the post-fire habitat (not documented in this study), making it more or less suitable for species (Smucker et al., 2005). For instance, the increase in the number of elaterid species associated with burns, or in their coefficients of association (e.g. *Sericus incongruus*; Table 2) with burns through time after salvage logging might be linked to a rise in the amount of down dead wood from falling snags (Boulanger and Sirois, 2006; Schwab et al., 2006; Angers, 2010), since many species of elaterids are known to be associated with decaying down dead wood (Thomas et al., 2009).

Species – habitat association analysis also brought some interesting information about species associated to girdled plots. In fact, such habitat containing recently killed unburned trees offers different habitat conditions and substrate that are less open, thus wetter and cooler, compared to burned plots. Indeed, the associated beetles were dominated by bark beetles in terms of number of species. Based on empirical work and literature, Wikars (2002) hypothesized that bark beetles could be less common in fire-scorched logs, thus more associated to unburned substratum, because the fungal flora found in burned logs (mostly ascomycete fungi, such as moulds of the genus *Trichoderma*) is detrimental to the symbiotic fungi mandatory for the development of some bark-beetles. Moreover, special conditions created by fire that are not produced by small gap dynamic seem to be necessary for many burn-associated species. This seems to be especially the case for species like the corylophid *Clypastraea fusca* that was caught on average 10.3 ± 1.3 specimens/plot in burned plots, while trapped only 0.7 ± 0.3 specimens/plot in girdled plots. The salpingid *Sphaeriestes virescens* was also caught more abundantly in burned plots (66.2 ± 3.6 specimens/plot) compared with girdled plots (6.6 ± 2.3 specimens/plot).

Even if no species of buprestid was found to be burn-associated due to the low numbers of catch, *Melanophila acuminata* was one of the nine species caught exclusively in burned plots. This is an holeoarctic species known for its adaptive traits to fire (Evans, 1966; Evans and Kuster, 1980; Schmitz et al., 2008) and as pyrophilous in Europe (Ahnlund and Lindhe, 1992; Wikars, 1997b). The low number of buprestid catches is thought to be due to the inefficacity of flight-interception trap to catch buprestids, or even because this family would be more abundant during the year of the fire (in our case 2005), which we did not inventoried. Though, these hypotheses would need to be investigated.

4.3. Salvage logging, habitat attributes and burn-associated species: temporal dynamics

We found that more habitat attributes affected by salvage logging contributed to explain the overall burn-associated beetles' assemblages' structure starting from year no.2 compared to those of year no.1 after salvage logging. Actually, three groups of habitat attributes mainly shaped burn-associated beetles assemblages through time after salvage logging. First, prefire forest conditions such as tree species composition was the main habitat attributes affecting burn-associated assemblages of year no.1 after salvage logging. Secondly, conditions generated by fire event such as the distance to the unburned forest, which is directly affected by the shape of the burned area, as well as burn severity both started to affect assemblages during years no.2 and no.3 after salvage logging. Thirdly, the effect of the amount of salvage logged area and the associated reduction of mature size coniferous snags (dbh > 9 cm); along with the indirect effect of salvage logging started to be felt only at year no.2 after salvage logging and lasted through year no.3. The indirect effects of the withdrawal of merchantable dimension trees by salvage logging are mainly considered to be a rise in the proportion of young stands and of non-merchantable dimension coniferous snags as available substrates, accompanied with a reduction in the input of down dead wood.

While studying the effects of postfire salvage logging on bird communities, Schmiegelow et al. (2006) obtained similar results, with both burn severity and prefire forest conditions generating variability that strongly influenced the postfire response of birds. Postfire salvage logging reduces this variability by removing important structural attributes of burned forests that underlie species' response (Schmiegelow et al., 2006).

4.3.1. Importance of prefire forest condition

The scarcity of balsam fir at the 7 ha scale in studied plots, compared to black spruce and jack pine (Table 1), is most likely due to the short fire cycle occurring in the western spruce – moss bioclimatic subdomain. Indeed, balsam fir abundance is known to generally increase with time after fire (Bouchard and Pothier, 2008; Bouchard et al., 2008). It may thus be linked to multiple characteristics of old-growth forest stands (e.g. abundance and diversity of dead wood, and of plant species colonizing micro-perturbation gaps) and indicative of habitat complexity which seems to support rich insect assemblages (Azeria et al., 2009a; Azeria et al., 2009b; Janssen et al., 2009). Even after fire, the presence of balsam fir in prefire forest composition had a similar effect on species richness of burn-associated beetles' species, as well as a positive effect on their abundance. This habitat component had a negative effect on species turnover throughout the whole study (between 2006 and 2008). This means that an increase in basal area of balsam fir in the forest mosaic would bring higher species richness and lower changes in the structure of burn-associated species assemblages. We can then infer that stand structure expressed by the presence of balsam fir offers suitable habitats which tend to last longer, even after salvage logging, than stands without balsam fir. While studying birds in the same general area and in some concomitant burns, Azeria et al. (in revision) also found a strong positive association with balsam fir for foliage insectivores.

4.3.2. Importance of fire severity and distance to unburned forest

Distance to burns edges seems to be an important factor in the colonization of the postfire habitat by beetles (Boulanger et al., 2010); it is thus not surprising that it is also an important factor explaining species turnovers of burn-associated beetles after salvage logging. Species turnover between years no.1 and no.2 after salvage logging were greater the further from burns edges; i.e. that being near the unburned continuous forest provides conditions allowing more structured (i.e. less changes through time) burn-associated beetles assemblages, and less stochastic colonization on the first year after salvage logging. During year no.2 after salvage logging, this habitat attribute had a negative influence on burn-associated species abundance as well as on species richness through year no.3, which suggests that species from the unburned matrix outside the burn persist to be colonizers of the burn even three years after salvage logging. Throughout the first three years after salvage logging, the distance from the plots center to the unburned forest, which is dependent of the burn's shape, is thus an important factor influencing burn-associated assemblages. Salvage logging should thus be done while preserving a maximum connectivity with the unburned matrix. Burn severity was also an important factor explaining assemblages of burn-associated beetles during year no.2, where it contributed positively to species richness and abundance of burn-associated species. Fewer changes in burn-associated beetles' assemblages were observed through the first three years after salvage logging with increasing fire severity. Consequently, areas of high burn severity close to burns edges would yield highest abundance and diversity of burn-associated beetles.

4.3.3. Temporal effect of postfire salvage logging

Our results mainly showed that burn-associated beetles responded more consistently to habitat attributes, and were more affected by salvage logging, both directly and indirectly, from year no.2. Indeed, burn-associated assemblages underwent changes linked to the reduction in the availability of mature coniferous trees and to a rise in the proportion of non-merchantable trees as an available breeding/feeding substrate. The amount of young stands (Y.Stands) present at the 7 ha scale, had a positive effect on both abundance and species richness of burn-associated beetles. Such habitats are known to yield high species richness of flying beetle in unburned forest (Janssen et al., 2009); in our case, these young stands increased habitat heterogeneity at the 7 ha scale, which could also increase species richness. During year no.2 after salvage logging, some species like the elaterids *Ampedus quebecensis*, *Pseudanostrirus triundulatus*, *Ampedus sp.*1 (prob. *nigrinus*) and *Ampedus fusculus* were positively associated with mature black spruce snags. Many elaterid species are known to be associated with down dead wood (Thomas et al., 2009) which is also illustrated by our results regarding the responses of burn-associated beetle assemblages of year no.3 after salvage logging (Figure 3c). Salvage logging, by removing snags of commercial dimensions and thus reducing inputs of down dead wood, could reduce habitat suitability for some burn-associated species.

4.4. Conclusion and management implications

The Canadian boreal fire regime has had impacts on the entomofauna, which in response has evolved burn-associated beetles species and specific beetle assemblages, as it has also been the case for the Swiss Alps fire regime (Moretti et al., 2010). In this study, a total of 18 species of beetles have been identified as burn-associated species, but we still need to look around in other post-disturbance habitats and other orders of organisms to refine our list of burn-associated species.

Because our study lasted three years after salvage logging, we could have uncover some of the effects that a second perturbation after fire has, since the main effects of salvage logging on burn-associated beetles only took place at year no.2. Thus, to detect meaningful biological response to a second disturbance after fire, studies should last more than two years post-disturbance (Smucker et al., 2005). Therefore, we can affirm that salvage logging had some effects on burn-associated beetle assemblages but there is still a need for further research to better understand and mitigate these effects, and determine whether they are in conflict with the objectives of biodiversity conservation.

The lack of pattern in beetle's response to postfire salvage logging in 2006 seems to be caused by the heterogeneity in prefire conditions, which is known to be one of the major source of noise in published wildlife data (Kennedy and Fontaine, 2009). This lack of pattern could also be due to the fact that beetles were still responding to fire event (first disturbance) when salvage logging (second disturbance) occurred, which might have brought even more noise in these restructuring beetle's assemblages. Besides, burn severity appeared as an important factor to consider when assessing the effects of salvage logging, since it was as important as the amount of residual snags in explaining burns-associated assemblages. Therefore, knowing the actual effects of fire on the habitat in terms of burned area, burn shape and severity would be essential in the design of salvage logging plans with respect to biodiversity and conservation objectives. Some have already made a strong argument for the need to incorporate burn severity into studies of wildlife response to fire (Smucker et al., 2005; Kotliar et al., 2007). We think there is a need for a common definition and assessment of fire severity, since these vary substantially across studies and institutions. By quantifying burn severity using dNBR, the most widely used remotely sensed measure of fire severity (Key and Benson, 2006), we think our results should be more readily comparable to others and usable by forest managers in designing salvage plans.

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Tables

Table 1. Codes, description and range of habitat attributes measured at the 0.04 ha scale and at the 7 ha scale

Habitat attributes		Range by scale	
Code	**Description**	**0.04 ha**	**7 ha**
BSP-JPI.M*	Basal area of Black spruce & Jack pine of dbh > 9 cm [m^2]	—	0 - 155.97
BSP.M*	Basal area of Black spruce of dbh > 9 cm [m^2]	0 - 4.73	—
BSP.Y*	Basal area of Black spruce of dbh ≤9 cm [m^2]	0 - 1.99	0 - 33.09
JPI.Y*	Basal area of Jack pine of dbh ≤9 cm [m^2]	0 - 1.18	0 - 21.05
Y.Stands*	Percentage of area covered by young stands 0 – 20 years [%]	—	0 - 84.98
DEC.M*	Basal area of deciduous trees (White birch and Trembling aspen) of dbh > 9 cm [m^2]	—	0 - 25.21
BFI.M*	Basal area of Balsam fir of dbh > 9 cm [m^2]	—	0 - 39.95
Sal.Area	Salvage area [ha]	—	0 - 5.68
Brn.Sev	Index of burn severity (mean) quantified as dNBR (scaled by 10^3)	—	97.35 - 570.56
Brn.Het	Index of burn heterogeneity (SD) computed from dNBR (scaled by 10^3)	—	66.31 - 642.33
BSP.DDW*	Down dead wood of Black spruce >5 cm [m^3/ha]	0 - 77.65	—
JPI.DDW*	Down dead wood of Jack pine >5 cm [m^3/ha]	0 - 137.06	—
Dis.GF*	Shortest distance to continuous unburned forest (extent of the burns) [km]	0.08 - 2.97	

*Square root transformed in models.

Table 2. Temporal species – habitat associations from Pearson's correlation (Phi)

Habitat	Families	Species	Phi coefficients of association			Mean catch per habitat		Total captures
			2006	2007	2008	Burned	Girdled	
Burned plots	Cerambycidae	*Acmaeops pratensis* (Laicharteg)[†]	0.326*	0.499**	0.518**	6.08	0.10	220
		Arhopalus foveicollis (Haldeman)	0.460**			1.78	0.20	66
		Monochamus scutellatus scutellatus (Say)	0.473**			2.78	0.70	107
	Cleridae	*Thanasimus undatulus* (Say)			0.432*	5.78	2.80	236
	Corylophidae	*Clypastraea fusca* Harold[†]	0.655***	0.457**	0.322*	10.31	0.70	378
	Curculionidae	*Dryocoetes autographus* (Ratzburg)	0.378*			5.19	3.90	226
		Xyleborus sayi (Hopkins)			0.444**	15.11	2.60	570
	Elateridae	*Agriotes limosus* (LeConte)[†]	0.604***	0.543***	0.518***	17.69	0.80	645
		Ampedus apicatus (Say)[†]		0.378*	0.386*	2.58	0.10	94
		Ampedus fusculus (LeConte)		0.482**	0.355*	3.47	0.40	129
		Ampedus pullus (Germar)			0.488*	3.72	0.60	140
		Ampedus quebecensis W.J.Brown	0.478**	0.283*	0.422*	2.97	0.10	108
		*Ampedus sp.*1 (prob. *nigrinus*)		0.340*	0.429*	5.14	0.40	189
		Limonius aeger (LeConte)			0.349*	1.22	0.10	45
		Pseudanostrirus triundulatus (Randall)[†]		0.306*	0.500**	50.72	12.70	1953
		Sericus incongruus (LeConte)[†]	0.466**	0.497**	0.549***	21.67	0.40	784
	Lathridiidae	*Corticaria dentigera* LeConte[†]	0.735***	0.474**	0.459*	42.25	9.00	1611
	Salpingidae	*Sphaeriestes virescens* Randall[†]	0.815***	0.770***	0.614***	66.17	6.60	2448
Girdled plots	Cerambycidae	*Acmaeops proteus proteus* (Kirby)[†]	0.540***	0.471***		13.89	44.70	947
		Asemum striatum (Linnaeus)		0.368*		0.17	1.00	16
		Monochamus mutator LeConte	0.378**		0.368*	0.19	2.20	29
		Pogonocherus penicillatus LeConte		0.402**		0	0.50	5
		Rhagium inquisitor (Linnaeus)		0.498**		1.08	3.10	70
		Tetropium cinnamopterum Kirby	0.546**			0.03	1.70	18
		Trachysida mutabilis (Newmman)		0.333*		0.08	0.20	5
	Curculionidae	*Crypturgus borealis* Swaine		0.508***	0.456***	0.19	7.10	78
		Dendroctonus rufipennis (Kirby)		0.359*		0.19	0.60	13
		Dendroctonus valens LeConte	0.333*			0.08	0.40	7
		Dryocoetes affaber (Mannerheim)		0.433**	0.533***	0.36	4.50	58
		Hylastes opacus Erichson			0.333*	0.03	0.20	3
		Hylastes porculus Erichson		0.329**	0.477***	0.50	15.40	172
		Hylurgops rugipennis (Mannerheim)			0.484***	0.44	3.20	48
		Ips pini (Say)		0.431**	0.446***	0.75	13.80	165
		Orthotomicus caelatus (Eichhoff)		0.461**		0.36	1.60	29
		Pissodes affinis Randall		0.333*		0.06	0.40	6
		Pissodes rotundatus LeConte	0.336*		0.368*	0.06	1.00	12
		Pityogenes plagiatus plagiatus (LeConte)		0.314*		0.06	0.30	5
		Polygraphus rufipennis (Kirby)[†]	0.719***	0.581***	0.626***	5.31	32.80	519
		Tripodendron lineatum (Olivier)	0.711***	0.423**	0.448***	1.00	8.30	119
	Lathridiidae	*Cortinicara gibbosa* (Herbst)		0.386*		1.56	3.00	86
		Enicmus tenuicornis LeConte	0.562**	0.557***		0.36	2.60	39
		*Lathridius sp.*1			0.359*	0.03	0.50	6

[†] Species found by St-Germain *et al.* to have higher abundance in burns than in unperturbed mature (80 years) forest. Significance level are indicated by stars (p : *** ≤0.001; ** ≤0.01; * ≤0.05). $\alpha = 0.05$.

Table 3. Averaged coefficients (Av.coef.) from multiple regression models based on the most supported habitat attributes from Bayesian Model Averaging (PP > 40)

Habitat attributes	2006 Av.coef. ± SE	PP	2007 Av.coef. ± SE	PP	2008 Av.coef. ± SE	PP
a. Abundance						
Landscape						
Dis.GF	-	9	-33.27 ± 14.87	**46**	-	8
7 ha scale						
BSP-JPI.M	-	7	-	7	-	14
BSP.Y	-	7	-	26	-	5
JPI.Y	-	7	-	8	-	18
Y.Stands	-	6	-	7	7.15 ± 2.69	**61**
DEC.M	-	17	-	7	-	25
BFI.M	-	31	-	9	14-20 ± 5-25	**44**
Sal.Area	-	5	-	26	-	36
Brn.Sev	-	6	8.42 ± 5.12	**53**	-	3
Brn.Het	-	23	-	36	-	5
0.04 ha scale						
BSP.M	-	6	-	7	-	11
BSP.Y	-	38	-	12	-	14
JPI.Y	-	8	-	6	-	8
BSP.DDW	-	5	-	6	-	5
JPI.DDW	-6.75 ± 1.68	**100**	-	6	-	3
R^2	0.323		0.190		0.272	
b. Richness						
Landscape						
Dis.GF	-	6	-	8	-3.07 ± 0.83	**93**
7 ha scale						
BSP-JPI.M	-	4	-	4	-	5
BSP.Y	-	5	-	17	-	7
JPI.Y	-	7	-	7	-	6
Y.Stands	-	7	-	4	0.24 ± 0.10	**59**
DEC.M	-	24	-	7	-	20
BFI.M	0.82 ± 0.31	**64**	-	6	-	8
Sal.Area	-	6	-	8	-	8
Brn.Sev	-	6	1.04 ± 0.40	**87**	-	4
Brn.Het	-	10	-	4	-	4
0.04 ha scale						
BSP.M	-	6	-	5	-	10
BSP.Y	-	34	-	9	-	5
JPI.Y	-	5	-	6	-	5
BSP.DDW	-	12	-	13	-	6
JPI.DDW	-	33	-	15	-	5
R^2	0.173		0.163		0.332	
c. Species turnover						
Landscape						
Dis.GF	0.16 ± 0.08	**50**	-	4	-	25
7 ha scale						
BSP-JPI.M	-	12	-	14	-0.03 ± 0.01	**65**
BSP.Y	-	5	-	21	0.03 ± 0.01	**48**
JPI.Y	-	16	-	7	-	11
Y.Stands	-	10	-	13	-	12
DEC.M	-	6	-	7	-	16
BFI.M	-	8	-	5	-0.06 ± 0.01	**57**
Sal.Area	-	20	-0.02 ± 0.01	**46**	-	18
Brn.Sev	-	5	-0.05 ± 0.02	**97**	-0.03 ± 0.02	**47**
Brn.Het	-	4	-	8	-	7
0.04 ha scale						
BSP.M	-	32	-	12	0.12 ± 0.04	**69**
BSP.Y	-	5	-	5	-	12
JPI.Y	-	7	-0.20 ± 0.05	**100**	-0.09 ± 0.05	**56**
BSP.DDW	-	37	-0.03 ± 0.01	**100**	-0.03 ± 0.01	**97**
JPI.DDW	-	5	-	6	-	14
R^2	0.106		0.544		0.582	

Table 4. Effects of habitat attributes on burn-associated beetle assemblages one, two and three years after salvage logging. The table shows output from ADONIS type III models, where significance tests are based on 1 000 permutations

	2006			2007			2008		
Habitat attributes	MS	*F*	R^2	MS	*F*	R^2	MS	*F*	R^2
Landscape									
Dis.GF	0.25	2.99	**0.072***	0.17	1.62	0.037	0.13	1.30	0.029
7 ha scale									
BSP-JPI.M	0.12	1.44	0.034	0.26	2.50	**0.057***	0.23	2.26	**0.050***
BSP.Y				0.09	0.88	0.020	0.21	2.06	0.046
JPI.Y				0.22	2.06	**0.047***	0.22	2.20	0.049
Y.Stands				0.13	1.21	0.028			
DEC.M							0.17	1.71	0.038
BFI.M	0.14	1.71	0.041				0.10	1.04	0.023
Sal.AREA				0.09	0.90	0.021	0.13	1.25	0.028
Brn.Sev				0.29	2.78	**0.064****	0.13	1.28	0.028
Brn.Het				0.21	2.00	0.046			
0.04 ha scale									
BSP.M				0.31	2.98	**0.068****			
BSP.Y							0.22	2.21	**0.049***
JPI.Y	0.02	0.27	0.006				0.10	1.02	0.023
BSP.DDW				0.20	1.95	0.045	0.36	3.60	**0.080****
JPI.DDW	0.24	2.88	**0.069***						
Total			0.222			0.433			0.443

Significance level are indicated by stars (p : *** ≤ 0.001; ** ≤ 0.01; * ≤ 0.05). $\alpha = 0.05$

Figures

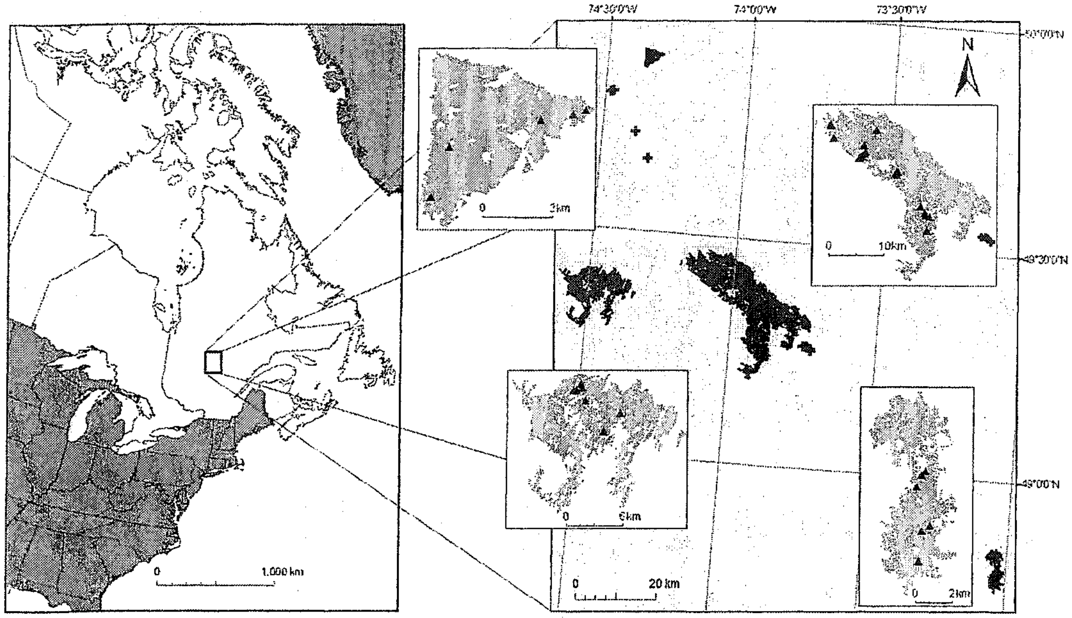

Figure 1. Study area and distribution of girdled plots (black crosses) and burned plots (black triangles) within the four studied burns of the Chibougamau region of Quebec, Canada.

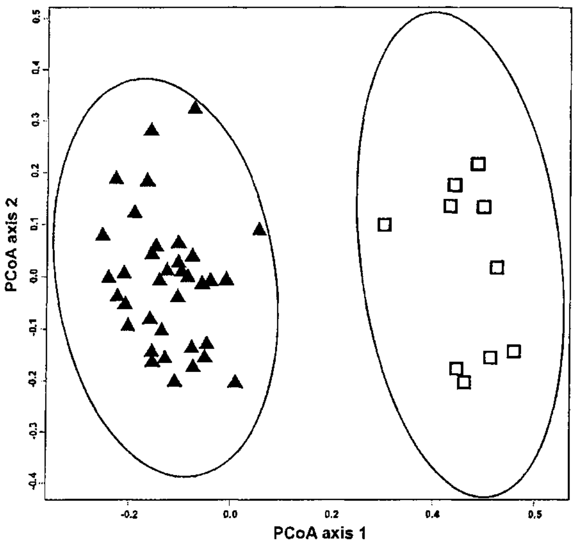

Figure 2. Ordination plot of the first two axis of a principal coordinate analysis (PCoA) using Bray-Curtis dissimilarity matrix from burned plots (filled triangles) and girdled plots (hollow squares). Ellipses represent 99 % of the standard deviation (S.D.). Statistical test comparing assemblages was done using BETADISPER procedure for R. $F_{1,44} = 11.38$; $N_{perm} = 999$; $P_{perm} = 0.002$

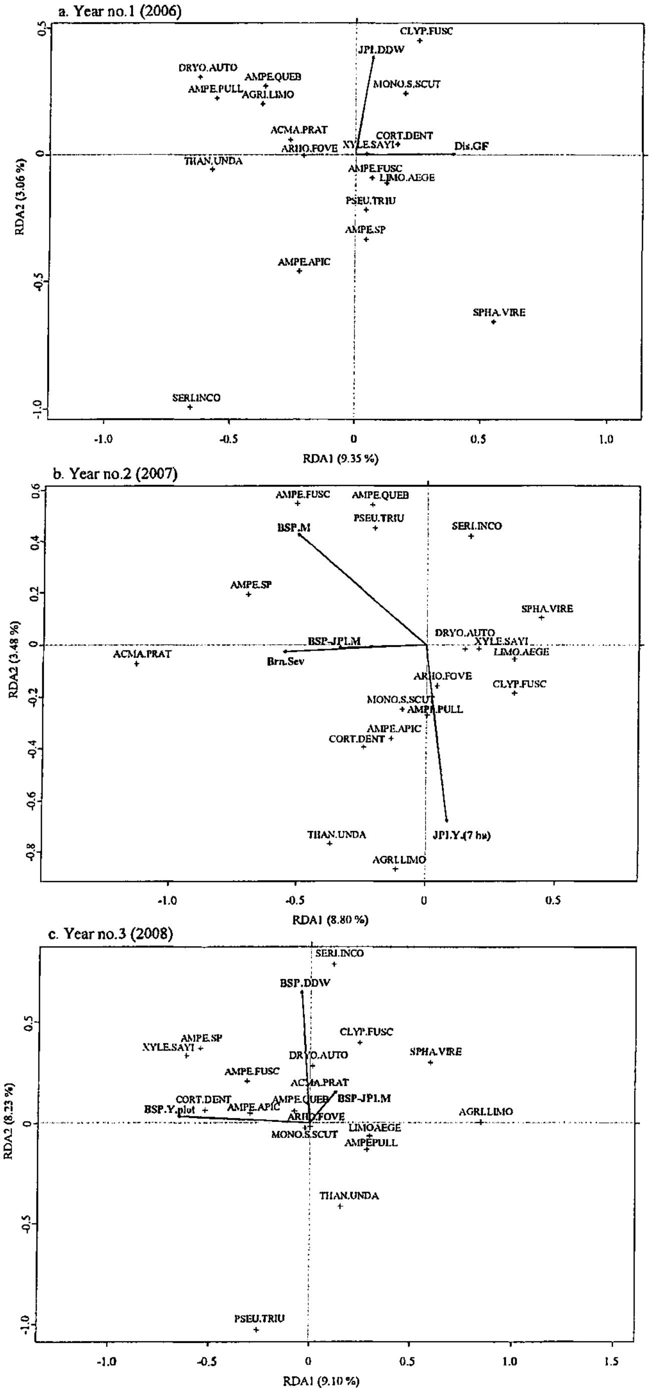

Figure 3. RDA biplot ordination using significant habitat attributes from ADONIS results (marked by arrows, for details see Table 1) for (a) year no.1 ($p = 0.01$, $R^2 = 12.41$ %), (b) year no.2 ($p = 0.01667$, $R^2 = 12.28$ %) and (c) year no.3 ($p = 0.005$, $R^2 = 17.33$) after salvage logging. Where species positions are marked with a cross and their names are represented by the first four letters of the genus followed by the first four letters of the species name (see Table 2 for full names).

Appendix

Appendix A. Species list and number of specimens captured by habitat for each year

		Burned			Girdled			
Famillies	Species	2006	2007	2008	2006	2007	2008	Total
Buprestidae	*Agrilus anxius* Gory	2	2	2	0	0	0	6
	Anthaxia inornata (Randall)	3	0	1	0	0	0	4
	Buprestis maculiventris Say	3	0	1	0	0	0	4
	Buprestis nutalli Kirby	1	0	0	0	0	0	1
	Chrysobothris femorata (Olivier)	0	0	1	0	0	0	1
	Cypriacis striata (Fabricius)	0	1	0	0	0	0	1
	Dicerca lugubris LeConte	1	0	0	0	1	0	2
	Dicerca tenebrica (Kirby)	1	2	0	0	0	0	3
	Dicerca tenebrosa (Kirby)	4	6	0	0	0	0	10
	Melanophila acuminata (DeGeer)	6	2	0	0	0	0	8
	Phaenops fulvoguttata (Harris)	2	0	0	2	0	0	4
Cerambycidae	*Acanthocinus pusillus* Kirby	2	0	0	0	0	0	2
	Acmaeopsoides rufulus (Haldeman)	2	0	0	0	0	0	2
	Acmaeops pratensis (Laicharteg)	39	106	74	1	0	0	220
	Acmaeops proteus proteus (Kirby)	283	111	106	311	117	19	947
	Arhopalus foveicollis (Haldeman)	59	4	1	1	0	1	66
	Asemum striatum (Linnaeus)	2	1	3	3	3	4	16
	Brachyleptura rubrica (Say)	0	0	1	0	0	0	1
	Evodinus monticola (Randall)	0	0	0	0	0	2	2
	Judolia montivagans montivagans (Couper)	0	1	0	0	0	1	2
	Lepturobosca chrysocoma (Kirby)	5	0	1	2	0	0	8
	Monochamus mutator LeConte	4	2	1	14	4	4	29
	Monochamus scutellatus scutellatus (Say)	88	8	4	4	1	2	107
	Neoclytus leucozonus leucozonus (Laporte & Gory)	1	0	0	0	0	0	1
	Pachyta lamed liturata Kirby	4	1	0	0	0	0	5
	Phymatodes dimidiatus (Kirby)	0	0	0	0	0	2	2
	Pogonocherus mixtus Haldeman	0	3	2	0	0	0	5
	Pogonocherus penicillatus LeConte	0	0	0	0	5	0	5
	Pronocera collaris collaris (Kirby)	1	0	1	0	0	0	2
	Pygoleptura nigrella nigrella (Say)	3	0	3	1	1	0	8
	Rhagium inquisitor (Linnaeus)	18	6	15	12	13	6	70
	Sachalinobia rugipennis (Newmman)	0	0	0	0	0	2	2
	Saperda candida candida Fall	0	0	0	0	1	0	1
	Stictoleptura canadensis canadensis (Olivier)	1	2	2	0	1	1	7
	Tetropium cinnamopterum Kirby	0	1	0	17	0	0	18
	Tetropium shwarzianum Casey	0	0	0	2	0	0	2
	Tetropium sp. 1	0	0	0	2	0	0	2
	Trachysida mutabilis (Newmman)	2	0	1	0	2	0	5
	Tragosoma depsarium (Linnaeus)	1	0	0	0	0	0	1
	Trigonarthris minnesotana (Casey)	2	0	0	0	0	0	2
	Xestoleptura tibialis (LeConte)	0	0	0	1	0	1	2
	Xylotrechus undulatus (Say)	2	0	3	1	1	0	7
Cleridae	*Thanasimus dubius* (Fabricius)	2	2	9	0	2	6	21
	Thanasimus undatulus (Say)	106	54	48	8	17	3	236
	Zenodosus sanguineus (Say)	0	0	0	0	1	0	1
Corylophidae	*Clypastrae fusca* Harold	194	116	61	1	1	5	378
	Clypastrae lugubra LeConte	3	0	0	0	0	0	3
Curculionidae	*Carphonotus testaceous* Casey	0	0	0	0	0	1	1
	Crypturgus borealis Swaine	1	3	3	1	28	42	78
	Dendroctonus punctatus LeConte	0	0	0	0	1	0	1
	Dendroctonus rufipennis (Kirby)	1	1	5	0	4	2	13
	Dendroctonus valens LeConte	0	0	3	2	0	2	7
	Dryocoetes affaber (Mannerheim)	7	3	3	2	20	23	58
	Dryocoetes autographus (Ratzburg)	58	94	35	4	23	12	226
	Dryocoetes betulae Hopkins	2	1	1	0	1	1	6
	Hylastes opacus Erichson	0	1	0	0	0	2	3
	Hylastes porculus Erichson	1	4	13	2	44	108	172
	Hylobius congener Dalla Torre,Schenkling,Marshal	36	1	14	2	2	17	72
	Hylurgops rugipennis (Mannerheim)	6	1	9	4	1	27	48
	Ips latidens (LeConte)	0	1	1	0	2	0	4
	Ips perroti Swaine	0	0	1	0	0	0	1
	Ips pini (Say)	9	1	17	9	11	118	165
	Magdalis hispoides LeConte	0	1	0	0	0	0	1
	Orthotomicus caelatus (Eichhoff)	4	1	8	0	7	9	29
	Pissodes affinis Randall	0	0	2	1	2	1	6
	Pissodes rotundatus LeConte	1	0	1	5	2	3	12

(Appendix A. Continued)		Burned			Girdled			
Famillies	Species	2006	2007	2008	2006	2007	2008	Total
	Pissodes strobi (Peck)	1	0	5	0	0	0	6
	Pityogenes plagiatus plagiatus (LeConte)	1	0	1	0	3	0	5
	Pityokteines sparsus (LeConte)	0	0	1	0	0	0	1
	Polygraphus rufipennis (Kirby)	31	48	112	46	152	130	519
	Procryphalus utahensis Hopkins	0	0	0	0	0	1	1
	*Pytyophtorus sp.*1	15	33	36	11	15	21	131
	Scolytus picea (Swaine)	0	4	0	0	0	0	4
	Tachyerges niger (Horn)	0	1	0	0	1	0	2
	Tripodendron lineatum (Olivier)	30	1	5	64	7	12	119
	Xyleborus sayi (Hopkins)	1	25	518	0	5	21	570
Elateridae	*Agriotella debilis* LeConte	0	0	0	1	0	1	2
	Agriotes fucosus (LeConte)	1	0	0	0	0	0	1
	Agriotes limosus (LeConte)	197	142	298	1	6	1	645
	Ampedus apicatus (Say)	43	33	17	0	1	0	94
	Ampedus deletus (LeConte)	1	0	1	0	0	0	2
	Ampedus evansi Brown	8	6	3	1	1	0	19
	Ampedus fusculus (LeConte)	5	62	58	0	1	3	129
	Ampedus laurentinus Brown	4	5	6	0	0	0	15
	Ampedus luctuosus (LeConte)	19	12	16	4	2	1	54
	Ampedus mixtus (Herbst)	5	12	37	1	1	4	60
	Ampedus pedalis Germar	3	2	0	0	0	0	5
	Ampedus pullus (Germar)	59	35	40	1	4	1	140
	Ampedus quebecensis Brown	47	46	14	0	1	0	108
	*Ampedus sp.*1 (prob. *nigrinus*)	16	67	102	1	0	3	189
	*Ampedus sp.*2	0	0	0	1	0	0	1
	Athous productus (Randall)	0	1	0	0	0	0	1
	Corymbitodes elongaticollis (Hamilton)	7	5	5	0	0	0	17
	Ctenicera falsifica (LeConte)	1	1	3	0	0	0	5
	Ctenicera kendalli (Kirby)	7	7	6	0	0	0	20
	*Dalopius sp.*1	2	0	0	0	0	0	2
	Danosoma brevicorne (LeConte)	0	0	0	1	0	1	2
	Denticollis denticornis (Kirby)	1	0	0	0	0	0	1
	Eanus decoratus (Mannerheim)	26	12	19	10	3	2	72
	Eanus estriatus (LeConte)	1	0	0	0	0	0	1
	Eanus maculipennis (Candèze)	2	0	0	0	1	0	3
	Hypnoidus bicolor (Eschscholtz)	0	1	0	0	0	0	1
	Limonius aeger (LeConte)	7	20	17	0	1	0	45
	Limonius pectoralis LeConte	0	2	7	0	0	0	9
	Liotrichus spinosus (LeConte)	6	20	55	2	4	7	94
	Melanotus castanipes (Paykull)	1	0	0	0	0	0	1
	Metanomus insidiosus (LeConte)	0	2	1	0	0	0	3
	Neohypdonus tumescens (LeConte)	1	0	4	0	0	0	5
	Nitidolimonius resplendens (Eschscholtz)	0	2	3	0	0	0	5
	Prosternon medianum (Germar)	13	18	25	2	0	1	59
	Pseudanostrirus propulus propulus (LeConte)	0	0	2	0	0	0	2
	Pseudanostrirus triundulatus (Randall)	50	280	1496	25	18	84	1953
	Selatosomus pulcher (LeConte)	0	1	0	0	0	0	1
	Selatosomus splendens (Ziegler)	0	0	0	1	0	0	1
	Sericus incongruus (LeConte)	233	252	295	2	2	0	784
	Setasomus aratus (LeConte)	0	0	1	0	0	0	1
	Setasomus nitidulus (LeConte)	0	3	7	1	1	0	12
	Sylvanelater mendax (LeConte)	0	1	0	0	0	1	2
Lathridiidae	*Cartodere constricta* (Gyllenhal)	80	28	7	14	10	5	144
	Corticaria brevicornis Fall	154	137	12	6	22	7	338
	Corticaria dentigera LeConte	1043	239	239	24	32	34	1611
	*Corticaria sp.*1	3	1	0	0	0	0	4
	*Corticaria sp.*2	5	1	1	0	0	3	10
	Cortinicara gibbosa (Herbst)	14	18	24	9	13	8	86
	Enicmus tenuicornis LeConte	6	2	5	12	13	1	39
	*Lathridius sp.*1	0	0	1	1	0	4	6
	Melanophthalma americana (Mannerheim)	0	0	1	0	0	0	1
	*Melanophthalma sp.*1	23	10	22	3	1	4	63
	*Melanophthalma sp.*2	0	0	0	1	0	0	1
	*sp.*1	2	0	0	0	0	0	2
	Stephostethus breviclavis (Fall)	2	0	1	2	1	0	6
Salpingidae	*Rhinosimus viridiaeneus* LeConte	2	0	18	0	0	5	25
	Sphaeriestes virescens Randall	1251	700	431	16	11	39	2448

2. Conclusion générale

Plusieurs auteurs rapportent que les forêts brûlées supportent une diversité unique de coléoptères saproxyliques comparativement à des forêts non-brûlées (Saint-Germain et al., 2004a; Moretti et al., 2010). Nos résultats comparant des forêts brûlées à d'autres non-brûlées, mais soumises à une dynamique de perturbations par petites trouées, tel qu'émulée par l'annelage d'une dizaine d'arbres vivants, confirment que les brûlis en forêt boréale supportent des assemblages spécifiques de coléoptères saproxyliques. Les espèces et assemblages qu'on y retrouve sont définis comme étant « associés au brûlis », ou simplement des espèces opportunistes comme *Acmaeops proteus proteus* (Kirby). Nos résultats démontrent aussi, que la coupe de récupération modifie les caractéristiques de l'habitat généré par le feu et que son impact se manifeste surtout après un délai d'une ou deux années sur les assemblages de coléoptères associés aux brûlis.

2.1 Diversité entomologique associée aux brûlis

Le régime de feu de la forêt boréale canadienne aurait façonné la faune entomologique en des assemblages de coléoptères spécifiques à cet habitat, au même titre que le régime de feu des Alpes Suisse (Moretti et al., 2010). En effet, nos travaux ont permis d'identifier 18 espèces de coléoptères associées aux brûlis parmi les huit familles de coléoptères étudiées. Bien qu'aucune de ces espèces ne soit exclusivement retrouvée dans les brûlis, il faut considérer qu'à l'échelle du paysage, les brûlis forment des habitats favorisant des assemblages d'espèces qui leurs sont inféodés et par conséquent ne sont ni retrouvés en peuplements matures non-brûlés (Saint-Germain et al., 2004a; Moretti et al., 2010), ni en peuplements non-brûlés contenants des chicots récents.

Les analyses d'associations espèces – habitats ont aussi apporté des informations intéressantes quant aux espèces associées aux sites contenant des arbres annelés. De tels habitats contenant du bois récemment mort, mais non-brûlé, offrent des conditions et un substrat différents ainsi qu'un milieu plus fermé, donc plus humide et plus frais que les sites brûlés, où l'écorce des arbres ne décolle pas aussi rapidement. En fait, une majorité d'espèces associées aux sites annelés étaient des scolytes, alors que peu d'entre elles étaient associés aux sites brûlés. Sur la base de ses propres observations et de la littérature, Wikars (2002) a émis l'hypothèse que les scolytes pourraient être moins communs dans les billots brûlés, donc plus associés a un substrat non-brûlé, parce que la flore fongique qui s'installe sur les billots brûlés (essentiellement des champignons ascomycètes, comme les moisissures du genre *Trichoderma*) est néfaste aux champignons symbiotiques transportés par certains scolytes et essentiels à leur développement. Conséquemment, les conditions spéciales créées par le feu ne sont pas produites par une dynamique de perturbations par petites trouées, mais elles semblent nécessaires au développement de plusieurs espèces associées aux brûlis. Un exemple d'une telle espèce pourrait être le Cerambycidae *Acmaeops pratensis* (Laicharting), une espèce holarctique, reconnue comme étant associé aux brûlis en Europe, où elle possède un statut d'espèce en danger sur les listes rouges (Moretti et al., 2010).

Il serait tout de même important d'investiguer d'autres groupes d'organismes dans d'autres milieux forestiers où l'on retrouve du bois mort récent (chablis, épidémies d'insectes, etc.), afin de raffiner notre liste d'espèces associées aux brûlis. Il est reconnu que le piège à impact multidirectionnel utilisé dans nos travaux est un outil efficace dans la capture de coléoptères saproxyliques volants (Okland, 1996; Saint-Germain et al., 2004a). Cependant, il est impossible avec un tel dispositif d'affirmer que toutes les espèces d'insectes capturées utilisaient vraiment le milieu inventorié pour se reproduire et compléter leur cycle vital. Plusieurs, surtout chez les moins abondantes, pourraient être des espèces touristes, n'étant que de passage dans le milieu étudié. La récolte et la mise en élevage de bûches (Saint-Germain et al., 2004b) provenant de chicots récents est un dispositif alternatif permettant de lier directement un spécimen au substrat qu'il utilise pour se développer. Cependant, ce type de dispositif récolte plusieurs spécimens au stade larvaire pour lesquels il y a peu de ressources taxonomiques. Ainsi, plusieurs spécimens restent non-identifiés. De plus, plusieurs espèces se développent lentement (ex. le Cerambycidae *Monochamus scutellatus scutellatus* (Say) nécessitant environ deux ans pour compléter son développement (Rose, 1957)), ce qui entraîne des délais importants dans l'obtention des résultats. Le dispositif d'encagement nécessite d'ailleurs de grands espaces à l'abri des intempéries, qui sont coûteux et rarement disponibles.

2.2 Effet temporel de la coupe de récupération et des attributs de l'habitat sur les espèces associées aux brûlis

Puisque notre étude s'est déroulée au cours des trois premières années suivant la coupe de récupération après feu, il nous a été possible d'identifier certains des effets d'une seconde perturbation après feu. En effet, la plupart de ces effets ne se sont manifestés qu'à partir de l'année no.2 après la coupe de récupération. En fait, afin de détecter une réponse biologiquement significative à une seconde perturbation après feu, les études devraient s'étaler sur plus de deux ans après perturbation (Smucker et al., 2005). Nous avons ainsi observé que la coupe de récupération, de par les changements qu'elle induit dans les proportions de tiges marchandes versus non-marchandes, a eu un effet négatif sur certaines espèces et ainsi sur la structure des assemblages de coléoptères associés aux brûlis (voir Figure 3b et c). Cependant, il y a toujours un besoin de recherches plus approfondies permettant de produire des modèles reliant chacune des espèces associées aux brûlis aux attributs de l'habitat affectés par la récupération. La compréhension de ces relations permettrait de mieux interpréter et mitiger les effets de la coupe de récupération et ainsi déterminer s'ils sont réellement en conflit avec les objectifs de maintient de la biodiversité.

L'absence de patrons de réponses quant à la récupération, de la part des coléoptères durant l'année no.1 (2006) immédiatement après la coupe de récupération, semble avoir été causé par l'hétérogénéité des conditions de l'habitat avant feu. Ce facteur est effectivement reconnu pour brouiller l'interprétation des résultats dans la plupart des travaux publiés sur la faune et la flore après feu (Kennedy et Fontaine, 2009). Cette absence de patron pourrait aussi être due au fait que les coléoptères réagissaient toujours à la perturbation du feu lorsque la coupe de récupération a eu lieu. Cela a pu entraîner une amplification de la stochasticité dans ces assemblages en restructuration. En effet, comparativement à l'année no.1, un plus grand nombre d'attributs de l'habitat ont contribué à expliquer la structure des assemblages de coléoptères associés aux brûlis à partir de l'année no.2 après la coupe de récupération. Essentiellement, trois groupes de facteurs environnementaux ont façonné les assemblages de coléoptères associés aux brûlis dans le temps après la coupe de récupération. D'abord, les conditions de la forêt avant feu, en termes de composition en essences, étaient les principaux attributs de l'habitat affectant les assemblages d'espèces associées aux brûlis de l'année no.1 après la coupe de récupération. Ensuite, les conditions générées par le feu, soit la distance à la forêt non-brûlée (directement influencée par la forme du brûlis) et la sévérité du feu dont les effets ne se font ressentir sur les assemblages d'espèces qu'aux années no.2 et no.3 après la coupe de récupération. Finalement, l'effet de la superficie du territoire récupérée et la réduction associée en chicots de conifères marchands (dhp > 9 cm), ainsi que les effets indirects de la coupe de récupération n'ont commencé à se faire sentir qu'à partir de l'année no.2 après la coupe de récupération et ont perduré jusqu'à l'année no.3. Les effets indirects du retrait des tiges marchandes par la récupération sont principalement : une augmentation relative dans la disponibilité de jeunes peuplements et de chicots de conifères aux dimensions non-commerciales (dhp ≤9 cm) en tant que substrat pour la reproduction et l'alimentation; accompagnée d'une réduction de l'apport en débris ligneux au sol).

L'étude de l'effet de la coupe de récupération après feu sur les communautés d'oiseaux, à produit des résultats similaires, où autant la sévérité du feu que les conditions de la forêt avant feu généraient une variabilité qui influençait grandement la réponse des espèces d'oiseaux après feu (Schmiegelow et al., 2006). En fait, la coupe de récupération réduit la variabilité naturelle générée par le feu et élimine des attributs structurels du brûlis qui sont à la source de la structure des communautés d'oiseaux (Schmiegelow et al., 2006).

2.3 Implications pour l'aménagement des brûlis et perspectives d'avenir

Puisque la sévérité du feu est un facteur important structurant les assemblages d'espèces associées aux brûlis, il est essentiel de la définir convenablement pour concevoir des plans de récupération optimaux, en particulier si l'on considère des objectifs en rapport avec la conservation de la biodiversité. Certains ont déjà 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 (Smucker et al., 2005; Kotliar et al., 2007). Nous pensons qu'il y a désormais un besoin grandissant pour une définition et pour une description commune de la sévérité du feu au Canada et même au niveau mondial, car celles-ci varient substantiellement à travers les études et les institutions. En utilisant le dNBR, la mesure par télédétection de la sévérité du feu la plus couramment utilisée (Key et Benson, 2006), nous pensons que nos résultats seront plus facilement comparables à d'autres et plus facilement utilisables par les aménagistes forestiers lors de la confection des plans de récupération.

Des résultats comme ceux de notre étude, combinés à une description cartographique de la sévérité du feu ainsi qu'à la couche des peuplements forestiers, deviennent un outil puissant dans la prédiction des points chauds (hot spots) à conserver pour la biodiversité. La précision d'une telle approche est par contre dépendante de la construction de modèles robustes reliant les espèces associées aux brûlis à leur milieu (Driscoll et al., 2010), ce qui restent d'ailleurs à être raffiné par de futures études. Ce type d'approche prévisionnelle permettrait d'identifier les points chauds pour la biodiversité, basée sur des modèles provenant d'un système d'information géographique (SIG) et pourrait être complétée par des informations en rapport à la régénération des essences forestières ainsi qu'aux contraintes opérationnelles lors de la réalisation de la coupe de récupération (pour détails voir Saint-Germain et Greene, 2009). L'intégration de telles informations dans un seul outil permettrait d'améliorer grandement l'efficacité de la coupe de récupération du point de vue de la conservation de la biodiversité.

Les plans quinquennaux d'aménagement devraient envisager l'avènement potentiel de perturbations majeures comme le feu et ainsi prévoir les grandes lignes décisionnelles quant à l'aménagement des zones perturbées. Ceci permettrait aux propriétaires de contrat d'approvisionnement et d'aménagement forestier (CAAF) de prévoir l'issue des activités d'aménagements post-perturbations, et ce avant que la perturbation ne se présente, plutôt que dans une atmosphère de « crise » suivant habituellement une perturbation majeure (Lindenmayer et al., 2008). L'approche par plan quinquennal serait d'autant plus intéressante, puisqu'elle permettrait aux aménagistes de refaire l'exercice de réflexion quant à l'aménagement des brûlis à tous les cinq ans. Cela leur permettrait de rester à jour par rapport à la recherche qui se fait dans le domaine ainsi qu'à l'affût des nouvelles technologies et considérations socio-économiques.

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