UNIVERSITÉ DU QUÉBEC À RIMOUSKI

COLONISATION INITIALE DES COLÉOPTÈRES SAPROXYLIQUES ET DÉCOMPOSITION DES DÉBRIS LIGNEUX GROSSIERS D'ÉPINETTE NOIRE APRÈS FEU EN MILIEU BORÉAL

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AVANT-PROPOS

Cette thèse s'articule autour de quatre chapitres principaux. Le premier chapitre concerne l'étude de l'importance des sources de colonisation et de l'habitat brûlé à différentes échelles spatiales sur la colonisation saproxylique l'année même du feu. Ce chapitre a été publié dans *Forest Ecology and Management* (260 : 1114-1123). Le deuxième chapitre s'intéresse surtout au patron spatial de colonisation l'année même du feu. Plus spécifiquement, nous y avons évalué à quelles échelles spatiales les communautés et certains taxons saproxyliques communs étaient spatialement corrélés et quels étaient les processus responsables de l'occurrence de ces patrons. Cette section de la thèse sera soumise pour publication dans *Landscape Ecology*. Dans le troisième chapitre, nous nous sommes concentrés sur les facteurs influençant la colonisation larvaire des arbres très récemment brûlés, soit un an après feu. De plus, l'importance de cette colonisation a été mise en relation avec l'abondance ou l'occurrence des adultes colonisateurs l'année précédente. Ce chapitre sera soumis pour publication dans *Environmental Entomology*. Finalement, dans le quatrième chapitre, l'impact de facteurs mesurés à l'échelle de l'arbre et du peuplement sur les taux de décomposition des débris ligneux postfeu ainsi que sur le taux de chute des chicots a été estimé. Nous souhaitons publier ce dernier chapitre dans *Canadian Journal of Forest Research*. Pour tous ces articles, je suis le principal auteur, ayant effectué l'essentiel de l'échantillonnage, des analyses et de la rédaction. Mes deux codirecteurs, les Drs Luc Sirois et Christian Hébert, en sont les coauteurs.

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Cette thèse a pour objet i) l'étude de la phase initiale de colonisation des débris ligneux d'épinettes noires (*Picea mariana* [Mill] B.S.P.) produits par le feu, par les coléoptères saproxyliques ainsi que l'étude ii) des facteurs régulant les taux de décomposition de ces débris ligneux dans le nord de la forêt boréale du Québec. Cette étude est la seule à ce jour traitant à la fois de la décomposition du bois et de la colonisation saproxylique dans un contexte postfeu. Entre autres, elle a mis à profit un dispositif d'échantillonnage entomologique installé très tôt après feu (7 jours). Ce dispositif ainsi que celui utilisé pour caractériser la décomposition de la matière ligneuse se sont étendus sur un large territoire ce qui a permis de couvrir l'essentiel de la variabilité des conditions postfeu ainsi que de considérer de multiples échelles spatiales. L'étude a ainsi mis en lumière l'importance de la sévérité du feu dans la structuration des patrons de colonisation. De plus, le patron de colonisation laisse présager que les capacités de dispersion des coléoptères saproxyliques colonisant les brulis récents sont très importantes. En plus d'influencer fortement le patron de colonisation des coléoptères saproxyliques, la sévérité du feu affecte aussi le processus de décomposition de la matière ligneuse.

Les caractéristiques de l'habitat brûlé ont influencé le patron de colonisation de façon très importante. Les attributs de l'habitat brûlé, plus particulièrement, la sévérité du feu, ont influencé ce patron à de multiples échelles spatiales et ce, à la fois pour les adultes colonisateurs et les néonates. De façon générale, les prédateurs et les xylophages adultes étaient plus abondants dans les paysages et les peuplements sévèrement brûlés alors que la sévérité du feu avait un impact opposé sur les mycophages. L'importance de la sévérité du feu devrait être une conséquence directe de l'impact de cette variable sur les propriétés nutritionnelles du substrat ligneux. En ce sens, une plus forte abondance des adultes xylophages dans les peuplements sévèrement brûlés est contre-intuitive. En effet, les néonates xylophages étaient plus abondantes dans les arbres faiblement brûlés, ces derniers favorisant la survie larvaire en maintenant un taux d'humidité subcorticale suffisant. Un tel comportement postfeu suggère une stratégie de colonisation non-optimale chez plusieurs espèces xylophages. Ce comportement pourrait être le résultat d'une pression évolutive qui aurait amené ces espèces à détecter et utiliser un substrat à l'apport beaucoup plus stable, en l'occurrence celui produit par sénescence naturelle en forêt verte, plutôt que celui résultant d'une perturbation survenant à des intervalles hautement variables dans le temps et l'espace. Se dirigeant vers le substrat brûlé en utilisant les mêmes volatiles que ceux émis par les arbres récemment morts en forêt non-brûlée, les adultes colonisateurs auraient majoritairement convergé vers les paysages contenant davantage de ces volatiles, soit ceux sévèrement brûlés. Malgré la non-optimalité de cette stratégie, l'utilisation des brulis demeurent une opportunité reproductive (plutôt que la panacée) pour les espèces xylophages considérant la très grande quantité de substrats qu'on y retrouve.

D'autre part, le processus de dispersion vers les habitats où la quantité de volatiles est élevée implique la prise en compte de caractéristiques environnementales à grandes échelles spatiales. Néanmoins, les caractéristiques de l'habitat brûlé mesurées à des échelles plus fines sont demeurées importantes afin de structurer le patron de colonisation. L'émigration des individus depuis des habitats-sources éloignés vers le substrat de reproduction ou d'alimentation a été la conséquence directe de ce patron spatial multi-échelles.

Par ailleurs, l'éloignement des sources de colonisation n'aurait eu que très peu d'impact sur la capacité des coléoptères saproxyliques adultes à atteindre l'habitat à coloniser. Seule l'abondance de quelques espèces majoritairement mycophages diminuait en fonction de la distance aux feux récents. L'absence d'effets négatifs de l'éloignement des sources de colonisation pourrait être conséquente aux très fortes capacités de dispersion présumées des espèces colonisatrices initiales.

En plus d'influencer la colonisation saproxylique, la sévérité du feu a eu un impact considérable sur les taux de décomposition de la matière ligneuse. De façon générale, ces taux étaient relativement bas (k = 0,013) lorsque comparés à ceux observés sur des taxons similaires et à l'intérieur d'écorégions comparables. La sévérité du feu a négativement influencé les taux de décomposition notamment en accélérant la perte d'humidité et la chute de l'écorce et en ralentissant la fragmentation des chicots. Les faibles taux de décomposition chez les arbres sévèrement brûlés pourraient aussi être conséquents à une action comminutive réduite des espèces xylophages.

Mots-clés : Feu de forêt, coléoptères saproxyliques, taux de décomposition, débris ligneux, *Picea mariana*, dispersion, patrons spatiaux, forêt boréale

ABSTRACT

In this thesis, I explored i) the initial colonization of post-fire black spruce (*Picea mariana* [Mill.] B.S.P) coarse woody debris (CWD) by saproxylic beetles and ii) the factors responsible of the decomposition rates of this woody substrate in the northern boreal forest of Québec. Up to date, this study is the first to concurrently study both of these processes in a post-fire context. It takes advantage of a unique sampling design where insect traps were put as soon as seven days after fire. This sampling design along with the one used to study the decomposition of CWD were established over large territories which allowed us to cover a great range of variability in post-fire conditions as well as to consider several spatial scales. This study outlined the importance of fire severity to shape the colonization pattern of saproxylic beetles. Moreover, these spatial patterns suppose that early post-fire saproxylic species have great dispersal abilities. In addition to colonization patterns, fire severity greatly affected the decomposition of CWD.

Burned habitat characteristics greatly affected the colonization pattern of saproxylic species. Among all predictors, fire severity had the greatest impact which was significant at several spatial scales for both adults and neonates. Overall, adult predators and xylophages were more abundant in severely burned stands and landscapes whereas fires severity had the opposite effect on mycophages. The importance of fire severity in this process must be directly related to the nutritional and reproductive quality of the substrate. In that sense, a higher abundance of xylophagous adults in severely burned landscape is a counterintuitive result. In fact, xylophagous neonates were most abundant in lightly burned trees, presumably as a result of higher moisture content in the subcortical tissus. Such result suggests a non-optimal colonization strategy for several xylophagous species. Even if speculative, this may the result of an evolutionary pressure that mostly pushed species to detect and use a more temporarily and spatially stable substrate, i.e. fresh CWD produced in unburned forests. When converging towards the burned patches, species may have used to same volatiles than those emitted by dead trees in green forests; consequently, adults immigrate mostly in severely burned landscapes where these volatiles should be more abundant. Despite this non-optimal strategy, we suggested that the use of burns represents a reproductive opportunity, rather than the panacea, for xylophagous species considering the great amount of available substrate.

Furthermore, the immigration towards severely burned landscape implies the perception of environmental characteristics at a large spatial scale. Nonetheless, burned habitat characteristics measured at the plot level were also very important to shape the colonization pattern. This multi-scale pattern was caused by dispersal from distant source habitats towards the burned substrate used for reproductive or feeding purpose.

On the other hand, distance to potential source habitats had very little or no negative effect on the ability of a saproxylic species to reach the habitat to colonize. The abundance of only few mycophagous species decreased as a function of distance to recent burns. The absence of such negative effect of distance to source habitats may be caused by the presumably great dispersal ability of most early saproxylic species.

In addition to colonization patterns, fire severity had a considerable impact on the decomposition rate of the woddy substrate. Overall, these rates ($k = 0.013$) were relatively low when compared to those observed for similar taxa in similar ecosystems. Fire severity had a strong negative effect on decomposition rates mostly by speeding bark shedding and moisture loss as well as by slowing the fragmentation of snags. Low decomposition rates in severely burned trees may also resulted from a reduced comminutive activity of xylophagous species.

INTRODUCTION GÉNÉRALE

L'importance des débris ligneux dans l'écosystème forestier

De façon générale, les débris ligneux constituent un élément fondamental des écosystèmes forestiers boréaux où ils remplissent d'importants rôles fonctionnels et structuraux (Harmon et al. 1986; Swift 1977a). La présence de débris ligneux au sol favorise l'établissement de nombreuses plantes vasculaires (Harmon et al. 1986). Les débris ligneux grossiers (DLG) représentent un habitat critique pour de nombreux taxons auto- et hétérotrophes saproxyliques (*sensu* Speight 1989) incluant bryophytes (Òdor et Standovar 2001), champignons (Renvall 1995), oiseaux nichant en cavité (Drapeau et al. 2002), amphibiens, reptiles, petits mammifères (Ecke et al., 2001) et insectes (Hammond 1996, Saint-Germain et al. 2004a; Boulanger et Sirois 2007). Ces espèces sont qualifiées de « saproxyliques » puisqu'elles dépendent des arbres morts, mourants ou moribonds ou d'autres espèces saproxyliques, afin de compléter au moins une partie de leur cycle vital (Speight 1989). En forêt boréale scandinave, on rapporte que 20 à 25% de l'entomofaune forestière pourrait être qualifiée de saproxylique (Siitonen 2001). La diminution drastique du volume de débris ligneux dans ces régions soumises à de fortes pressions anthropiques serait d'ailleurs le principal responsable de la précarité de 217 espèces saproxyliques (Rassi et al. 1992). Par conséquent, on porte récemment un intérêt particulier aux débris ligneux en tant que composante essentielle au maintien de la biodiversité dans les écosystèmes forestiers (Siitonen 2001; Grove 2002).

Le feu et les débris ligneux

Les feux constituent la principale forme de perturbation naturelle en milieu boréal (Rowe et Scotter 1973), brûlant en moyenne 2,8 millions d'ha par année au Canada (Stocks 2002). Ceux-ci jouent un rôle prépondérant dans la dynamique forestière (Payette 1992), la détermination des patrons de diversité végétale (Rowe et Scotter

1973; Heinselman 1981) et la distribution du carbone à l'intérieur de l'écosystème (Kasischke 2000). En forêt boréale, la récurrence périodique du feu constitue un élément essentiel de stabilité à long terme et de maintien de la biodiversité à l'échelle du paysage (McCullough et al. 1998). À l'instar de plusieurs perturbations naturelles en forêt boréale (Gromtsev 2002; Youngblood et Wickman 2002), les feux occasionnent une production considérable de nécromasse ligneuse (Tinker et Knight 2000). L'apport soudain et massif de débris ligneux après feu est reconnu pour affecter le budget local de carbone des écosystèmes boréaux soumis à l'action récurrente de ce type de perturbation. En effet, cette nécromasse constitue un important réservoir de carbone et de nutriments à moyen terme compte tenu du long temps de résidence de ce matériau à l'intérieur de l'écosystème boréal (Kasischke et Stocks 2000).

Les conditions environnementales régnant suite au passage d'un feu, quoique très variables, peuvent être particulièrement extrêmes lorsque comparées à celles, plus stables, régnant en forêt non-brûlée. En effet, le feu modifie profondément à la fois les états biotique et abiotique du milieu (Litton et Santelices 2003; Parmeter 1977). De plus, le brûlage induit des changements physicochimiques dans le bois mort, incluant au niveau du pH, de l'albédo et de la température (Shorohova et al. 2008). Qui plus est, plusieurs espèces d'arthropodes peuvent être extirpés temporairement des brulis en étant tués (Paquin et Coderre 1997) ou en se réfugiant à l'intérieur d'habitats non-brûlés limitrophes (Gandhi et al. 2001). Par conséquent, d'aucuns pourraient affirmer que les processus écologiques reliés à la décomposition de la matière ligneuse et de la colonisation par les espèces saproxyliques dans un contexte postfeu pourraient fortement différer de ceux prévalant en forêt non-brûlée.

Partie A - La colonisation postfeu des débris ligneux par les coléoptères saproxyliques

Les coléoptères constituent un des groupes d'insectes saproxyliques les plus abondants et diversifiés à coloniser les brulis (Boulanger et Sirois 2007; Saint-Germain et al. 2004a; Wikars 2002). La colonisation des débris ligneux s'effectue très peu de temps après feu, la plupart des espèces atteignant le brulis l'année même du feu (Boulanger et Sirois 2007). Parmi les colonisateurs initiaux, on retrouve surtout des espèces xylophages, mycophages et prédatrices (Muona and Rutanen 1994; Wikars 2002). Plusieurs de ces espèces sont reconnues comme étant de véritables pyrophiles (Evans 1966, Schmitz et al. 2002) puisqu'elles sont attirées activement par le bois brûlé durant une période très brève (Muona and Rutanen 1994; Hjältén et al. 2007).

Du « point de vue » des espèces saproxyliques, le feu convertit des peuplements contenant préalablement peu de ressources appropriées, en des peuplements où le substrat est abondant et disponible. Les patrons géographiques associés aux peuplements brûlés créent des régions spatialement définies et de haute qualité pour les espèces saproxyliques. Ces dernières atteignent ces peuplements depuis les régions limitrophes soit depuis i) la forêt non brûlée ou d'autres peuplements brûlés récemment (Saint-Germain et al. 2008). Ces deux derniers habitats peuvent être qualifiés d' « habitats-source » en opposition à l'habitat à coloniser, c.-à-d. le peuplement brûlé.

Habitats-sources vs qualité de l'habitat brûlé

Le succès de colonisation des espèces saproxyliques dépend à la fois de la qualité de l'habitat à coloniser ainsi que de la capacité des espèces provenant des habitats-sources à localiser et atteindre l'habitat brûlé (Bouget et Duelli 2004). Cette dernière devrait être inversement proportionnelle à l'isolement de cet habitat par rapport à l'habitat-source, énoncé repris dans plusieurs théories écologiques (ex. MacArthur et

Wilson 1967; Hubbell 2001). Récemment, davantage d'importance est accordée aux phénomènes de dispersion entre les communautés locales. Le patron de répartition ou d'abondance de telles métacommunautés peut ainsi être influencé par des phénomènes plus ou moins important de dispersion liant les communautés locales (Leibold et al. 2004; Cottenie 2005). Considérant que la colonisation des brulis implique nécessairement de la dispersion depuis des habitats-source, d'aucuns devraient ainsi affirmer que la dispersion devrait fortement influencer les patrons d'abondance des espèces saproxyliques après feu.

De façon évidente, l'échelle à laquelle un phénomène de ce genre est effectif dépend fortement des capacités de dispersion des espèces étudiées. Ainsi, il est généralement admis que les espèces saproxyliques colonisant très peu de temps suite au feu possèdent des capacités de vol leur permettant de se déplacer sur des distances considérables afin de se diriger vers le substrat nouvellement créé (Frost 1984; Schmitz et al. 2002; Allison et al. 2004). Par conséquent, la distribution spatiale de ces espèces saproxyliques ne devraient être affectée négativement que par l'isolement depuis des habitats-sources très éloignés.

Qui plus est, la qualité de l'habitat brûlé devrait influencer la colonisation des espèces saproxyliques en fonction de l'utilisation que celles-ci font du substrat. Plusieurs de ces espèces utilisent le substrat brûlé comme milieu reproductif et d'alimentation pour les larves, pour l'alimentation des adultes ou pour les deux (Muona et Rutanen 1994, Hanks 1999). Selon les espèces, la sévérité du feu ainsi que la dimension, la qualité nutritive, la position, l'ensoleillement et la disponibilité du substrat ligneux devrait être autant de facteurs susceptibles d'influencer l'abondance des adultes colonisateurs (Furniss 1965; Saint-Germain et al. 2004b,c; Hjalten et al. 2007). Chez les espèces xylophages plus particulièrement, les arbres possédant une écorce et un phloème plus épais augmenterait le taux de survie des larves de certaines espèces de longicorne (Peddle et al. 2002). Par ailleurs, les arbres de plus fort calibre seraient plus susceptibles d'être colonisés que ceux de plus petits diamètres (Saint-Germain et al. 2004b,c) alors que le taux d'humidité (Savely 1939; Saint-Germain et al. 2007a; Kelsey and Joseph 1999), l'âge et la vigueur de l'arbre avant feu pourrait aussi influencer la colonisation de diverses espèces xylophages (Saint-Germain et al. 2004b). Puisque ces exigences varient fortement d'une espèce à l'autre, les caractéristiques d'habitat sélectionnées par les diverses espèces saproxyliques devraient être sensiblement différentes.

Une colonisation multi-échelle

La colonisation des brulis par les espèces saproxyliques est souvent perçue comme étant un processus comportant de multiples étapes. Ce processus implique la dispersion des individus depuis des habitats-sources souvent très éloignés ainsi que la sélection de caractéristiques environnementales mesurées à diverses échelles spatiales (Økland et al. 1996; Holland et al. 2004; Saint-Germain et al. 2004c). En conséquence, des caractéristiques du paysage, du peuplement et du substrat ainsi que plusieurs déterminants biologiques de l'espèce peuvent inévitablement produire des patrons spatiaux de répartition relativement complexes chez les espèces saproxyliques. Les variables environnementales régissant la colonisation des espèces saproxyliques peuvent être elles-mêmes spatialement structurées à plusieurs échelles (Borcard et Legendre 1994; Jones et al 2008), causant ainsi de l'autocorrélation spatiale à diverses échelles dans la répartition des espèces (Addicott et al 1987; Cushman et McGarigal 2002). D'un autre côté, la dispersion limitée des individus contribue à la complexité de ces patrons; les espèces ne pouvant coloniser tous les habitats isolés auront plutôt tendance à être plus abondantes près des habitats-sources (Bjørnstad et al 1999; Trenham et al 2001; Bell 2001; Hubbell 2001). Évidemment, l'étendue spatiale de tels phénomènes dépend fortement des capacités de dispersion des espèces impliquées et de l'échelle à laquelle les observations sont effectuées. De plus, certaines espèces peuvent réagir à une caractéristique environnementale mesurée à une échelle donnée en plus d'une ou plusieurs autres mesurées à une échelle spatiale complètement différente (Wiens et Milne 1989;

Chust et al 2003). La dynamique des populations, la compétition intra- et interspécifiques, l'historique des perturbations sont autant de facteurs pouvant aussi engendrer une structure spatiale complexe dans la répartition des espèces (Borcard et Legendre 1994). La complexité de ces phénomènes est exacerbée par le fait que plusieurs de ces facteurs peuvent agir simultanément à des échelles spatiales multiples (Allen et Starr 1982). Ces déterminants peuvent être étroitement reliés entre eux et difficiles à séparer les uns des autres. De plus, l'importance de chacune des échelles spatiales peut varier d'un assemblage à l'autre (Holt 1996), voire d'une espèce à l'autre (Holland et al. 2004). En conséquence, la dissection de la structure spatiale de la répartition des espèces peut aider à identifier quels processus écologiques sont responsables du patron spatial observé (Addicott et al 1987; Borcard et al 2004). Ce travail de caractérisation du patron spatial de colonisation des espèces saproxyliques n'avait jamais été réalisé plus tôt.

Une quête optimale des adultes?

Selon la théorie de l'oviposition optimale (*optimal oviposition theory*), les adultes, *a fortiori* les femelles, devraient adopter un comportement tel qu'il maximiserait leur succès reproducteur (Jaenike 1978; Wajnberg et al. 2006) notamment en choisissant un hôte maximisant la performance des larves (Scheirs et DeBruyn 2002). Selon une stratégie comportementale optimale, la sélection de l'habitat par les adultes devrait donc refléter les besoins alimentaires des larves. Par conséquent, chez les espèces n'utilisant le substrat ligneux que comme milieu reproductif (entre autres, les espèces xylophages), on devrait s'attendre à ce que les variations d'abondance des adultes colonisant les brulis l'année même du feu aillent de pair avec les conditions environnementales influençant le succès reproducteur de ces espèces. Conséquemment, les conditions environnementales postfeu sélectionnées par les adultes colonisateurs devraient être sensiblement les mêmes que celles menant à une abondance plus importante des larves. Certains prétendent (Rausher 1979; Thompson 1988) cependant qu'un comportement non-optimal peut être utilisé lorsque les ressources sont surabondantes. Dans un contexte postfeu où la disponibilité du substrat de colonisation est plusieurs fois supérieure à celle rencontrée en forêt non-brûlée, d'aucuns pourraient s'attendre à ce qu'une telle stratégie non-optimale soit employée par les espèces colonisatrices initiales. Par contre, aucune étude à ce jour n'a été en mesure vérifier cette hypothèse chez les insectes xylophages dans un contexte postfeu.

Partie B – La décomposition du bois après feu

Facteurs influençant la décomposition de la matière ligneuse

La décomposition de la matière ligneuse comprend à la fois le catabolisme fongique, le lessivage des éléments organiques et minéraux de même que la fragmentation du substrat (Swift 1977b). Cependant, c'est essentiellement par la dégradation fongique des parois cellulaires végétales qu'est perdue, par respiration, la majorité de la masse ligneuse (Renvall 1995; Boddy et Watkinson, 1995). Par conséquent, les taux de décomposition de la matrice ligneuse résultent essentiellement de l'action des champignons et des facteurs qui régissent leur colonisation et leur croissance.

La qualité du substrat influence directement la décomposition de la matrice ligneuse en conditionnant partiellement le succès de colonisation (Sippola et Renvall 2001; Siitonen et al. 2005) et l'activité détritique des champignons, laquelle détermine le taux de décomposition (Harmon et al. 1986; Laiho et Prescott 2004). À l'instar de la décomposition des autres composantes de la matière organique, la décomposition du bois mort est essentiellement fonction de la température et de l'humidité du substrat (Chambers et al. 2000; Progar et al. 2000; Yatskov et al. 2003; Gough et al. 2007). L'humidité limite fréquemment la décomposition de la nécromasse ligneuse (Laiho et Prescott 1999; Wang et al. 2002) puisque les basidiomycètes saproxyliques ne peuvent se développer qu'à l'intérieur de taux d'humidité situés entre 30 et 160 % (Erickson et al. 1985; Harmon et al. 1986). Par conséquent, on observe de façon générale une tendance vers de faibles taux de décomposition aux hautes latitudes

(Chambers et al. 2000) et altitudes (Brown et al. 1998) ou encore à l'intérieur d'environnements trop secs (Erickson et al. 1985) ou trop humides (Progar et al. 2000). En forêt boréale, une faible température moyenne annuelle ainsi qu'une courte saison de croissance réduisent d'autant les activités des espèces hétérotrophes ce qui mène à de faibles taux de décomposition (Trofymow et al. 2002; Wang et al. 2002; Boulanger et Sirois 2006). Qui plus est, la variation des conditions de température et d'humidité à l'échelle locale, notamment de l'exposition solaire, du drainage, de l'orientation et la force de la pente (c.f. Laiho et Prescott 2004; Harmon et al. 1986) influencent la température et l'humidité du substrat et ainsi les taux de décomposition. À l'échelle du substrat, le diamètre ainsi que la position verticale du débris ligneux auraient aussi une forte influence sur les taux de décomposition. Une telle variation des taux de décomposition de la matière ligneuse en fonction des conditions environnementales est susceptible d'avoir un impact majeur sur la caractérisation du cyclage du carbone (Wang et al. 2002).

Influence du feu sur la décomposition ?

La très grande majorité des études portant sur la décomposition du bois mort se sont déroulées à l'intérieur de peuplements forestiers non-brûlés. Tels que mentionné précédemment, les conditions micro-environnementales régnant suite au feu sont susceptibles d'être excessivement différentes de celles prévalant en forêt non-brûlée (Parmeter 1977). Les conditions postfeu seraient à même d'influencer fortement la décomposition de la matière ligneuse puisqu'elles influenceraient considérablement la température et les conditions d'humidité du bois mort. Bien que les effets du feu sur ce processus ne soient que partiellement connus, certains auteurs (Boulanger et Sirois 2006; Angers 2010) ont enregistré de très faibles taux de décomposition chez les arbres tuées par le feu. Ainsi, le feu peut réduire la vitesse de décomposition en exposant davantage les débris ligneux aux radiations solaires et au vent suite à la disparition de la canopée, ce qui pourrait avoir un effet direct sur la perte d'humidité. De plus, les arbres brûlés auraient tendance à demeurer en position verticale pour une plus longue période ainsi qu'à perdre leur couvert cortical plus rapidement ce qui ralentirait d'autant le processus de décomposition (Boulanger et Sirois 2006; Angers et al. 2010). Évidemment, d'aucuns pourraient s'attendre à ce que les conditions postfeu (ex. : ouverture de la canopée, carbonisation, température, humidité, etc.) varient fortement en fonction de la sévérité du feu. En conséquence, les variations de ces conditions pourraient influencer de manière importante les taux de décomposition des débris ligneux produits par le feu.

Un lien avec les insectes colonisateurs?

Les insectes saproxyliques entretiennent une position stratégique en tant que régulateur des flux de matière et d'énergie dans les écosystèmes forestiers (Ausmus 1977). En effet, plusieurs espèces sont impliquées dans la dégradation du substrat ligneux et le cyclage subséquent des éléments nutritifs en fournissant un accès aux champignons saproxyliques ou en dispersant les propagules fongiques. Les insectes saproxyliques peuvent faciliter la colonisation fongique en créant des conditions microenvironnementales favorables à la germination et la croissance des champignons à l'intérieur du substrat (Edmonds and Eglitis 1989). Plusieurs espèces de longicornes (Coleoptera : Cerambycidae) et de scolytes (Coleoptera : Curculionidae [Scolytinae]) pénètrent le bois à l'état larvaire, offrant ainsi des conditions favorables à la croissance microbienne en augmentant le taux d'humidité du substrat ligneux (Zhong et Schowalter 1989).

Certains insectes saproxyliques peuvent servir de vecteurs passifs ou actifs de champignons saproxyliques. La vectorisation passive de propagules fongiques fut observée chez certaines espèces xylophages (e.g. Buprestidae, Cerambycidae) (Garcia et Morrell 1999) où l'inoculation s'effectue lors de l'oviposition des femelles. D'autres groupes de coléoptères saproxyliques entretiennent des associations très spécifiques avec certains champignons saproxyliques. Plusieurs espèces de scolytes (Curculionidae, Scolytinae) et de *Tetropium* spp. (Cerambycidae) vectorisent activement certaines espèces appartenant aux genres

Ophiostoma, *Leptographium*, *Ceratocystiopsis* et *Ceratocystis* (Haberken et al., 2002; Jacobs et al. 2003; Six et Bentz, 2003; Kim et al. 2005). La colonisation entomologique des débris ligneux est donc susceptible d'influencer la colonisation fongique et conséquemment des taux de décomposition du substrat ligneux (Zhong et Schowalter 1989; Edmonds and Eglitis 1989).

Approches méthodologiques employées dans la thèse

L'aire d'étude

L'aire d'étude se situe dans le nord de la forêt boréale du Québec, dans la région de la Baie James. Cette région appartient au sous-domaine bioclimatique de la pessière à lichens (Rowe et Scotter 1973). Le climat y est de type bas-subarctique avec une température moyenne annuelle de -3,6 °C, les temperatures moyennes de janvier et de juillet étant respectivement de -25 et 13 °C. Les precipitations moyennes annuelles s'élèvent à 637 mm, 40% d'entre elles tombant sous forme de neige (Environnement Canada 1993). Des peuplements équiens d'épinettes noires (*Picea mariana* [Mill.] B.S.P.) et de pins gris (*Pinus banksiana* Lamb.) occupent la majorité des sites mésiques. Des peuplements inéquiens dominés par l'épinette noire se retrouvent dans les dépressions et les sites où la paludification est importante. Les feux de forêts constituent la principale forme de perturbation naturelle avec un cycle de récurrence d'environ 100 ans en site mésique (Payette et al. 1989; Parisien et Sirois 2003, Héon et al. en préparation).

Ce territoire constitue une région de choix pour l'étude des processus écologiques liés aux débris ligneux produits après feu considérant la fréquence élevée des feux, leurs très grandes superficies ainsi que leur relative accessibilité. De plus, cette région est pratiquement exempte d'activités anthropiques et ses impacts sur le milieu forestier sont minimes. Par conséquent, cette région offrait un cadre unique pour l'étude de la variabilité des processus liés au bois mort en forêt naturelle tout en considérant plusieurs échelles spatiales. L'inclusion de plus grandes échelles spatiales est essentielle afin de mieux interpréter le processus de colonisation par les espèces saproxyliques après feu (Holland et al. 2004; Saint-Germain et al. 2007b). De même, l'utilisation de grands territoires d'étude est primordiale afin de capter l'essentiel de la variabilité associée aux conditions postfeu et ainsi à la décomposition des arbres brûlés.

Processus de colonisation entomologique

Pour les trois premiers chapitres, cette étude a pour avantage unique d'utiliser des données entomologiques concernant la totalité de la diversité saproxylique récoltée l'année même d'un feu de forêt. Très peu d'études ont investigué les processus de colonisation de la matière ligneuse par les insectes. De plus, peu d'entre elles se sont concentrées sur la totalité de la biodiversité des coléoptères saproxyliques (Saint-Germain et al. 2004a; Hjältén et al. 2007), *a fortiori* immédiatement après feu (Boulanger et Sirois 2007) dans un cadre spatialement explicite. Qui plus est, pour des raisons logistiques évidentes, la plupart des patrons de colonisation sont fréquemment interprétés à partir de données de diversité et d'abondance récoltées un an après feu. Pourtant, de récentes observations tendent à démontrer que la très grande majorité de la colonisation initiale s'effectue très peu de temps après feu, soit durant la saison même où survient le feu (Wikars 2002; Boulanger et Sirois 2007). La plupart des mesures de l'impact immédiat du feu sur les communautés saproxyliques a été effectuée suite à des brûlages dirigés, opérations couvrant souvent de petites superficies (quelques dizaines d'hectares tout au plus) ce qui ne permet pas d'évaluer le processus de colonisation à des échelles spatiales beaucoup plus grandes. Ainsi, cette étude met à profit un dispositif d'échantillonnage (voir figure 1.1) installé aussi tôt que 7 jours après le début d'un feu de forêt de grande superficie (76 183 ha). Le nombre de sites échantillonnés (n=66) ainsi que l'accessibilité de ce feu sur plus de 25 km de part et d'autre de la route de la Baie James a ainsi permis de caractériser le processus de colonisation à l'intérieur de conditions postfeu variées et ce, tout en considérant plusieurs échelles spatiales distinctes.

Approches pour caractériser la colonisation de l'entomofaune saproxylique

Dans le cadre de cette thèse, nous étions intéressés à la fois aux processus de colonisation des espèces saproxyliques au stade adulte mais aussi au stade larvaire en ce qui concerne les xylophages. Par conséquent, deux dispositifs d'échantillonnage dictincts ont été employés afin de capturés respectivement les adultes colonisateurs ainsi que les néonates émergentes. Dans le premier cas, des pièges à impacts disposés sur les troncs brûlés quelques jours suivant le feu (*trunk-window traps sensu* Kaila 1993) ont été utilisés. Ce type de piège est reconnu pour être très efficace afin de caractériser l'entomofaune saproxylique (Kaila 1993) bien qu'il agisse à une échelle spatiale plus grossière que celle de l'arbre (Wikars et al. 2005; Saint-Germain et al. 2006). D'un autre côté, les néonates ont été récoltées suite à l'élevage de sections troncales récoltées 1 an après la perturbation. Bien que cette technique ne permette l'obtention d'un grand nombre de spécimens, elle possède tout de même l'avantage de caractériser les facteurs influençant l'occurrence ou l'abondance des espèces xylophages à l'échelle de l'arbre (Saint-Germain et al. 2006). L'utilisation conjointe de ces deux techniques d'échantillonnage permet sans contredit de caractériser de manière plus précise l'entomofaune saproxylique colonisant les brulis (Boulanger et Sirois 2007).

Qualité de l'habitat brûlé, habitats-sources et limitations

Tout au long des trois premiers chapitres, les analyses reposent essentiellement sur l'identification des facteurs environnementaux influençant l'abondance ou l'occurrence des espèces saproxyliques à l'intérieur des peuplements brûlés. Ces facteurs environnementaux ont principalement été classés en deux catégories distinctes à savoir ceux référant à la qualité de l'habitat brûlé et ceux faisant référence aux habitats-sources. La qualité de l'habitat brûlé concerne principalement des variables correspondant à la disponibilité, la dimension (chapitres 1 à 3) et différentes caractéristiques subcorticales (chapitre 3 seulement) du substrat ainsi qu'à la sévérité du feu mesurée à diverses échelles spatiales (arbre, peuplement, paysage) (chapitres 1 à 3; Savely 1939; Furniss 1965; Martikainen et al. 2000; Peddle et al. 2002; Similä et al. 2003; Bouget and Duelli 2004; Saint-Germain et al. 2004b,c; Jonsell et al. 2007).

Tel que mentionné précédemment, la distance aux habitats-sources est fortement susceptible d'influencer le patron de colonisation des espèces saproxyliques. Les chicots et les débris au sol récemment produits peuvent constituer des « pouponnières » d'individus saproxyliques pour le substrat brûlé nouvellement créé. Ces substrats-sources peuvent se situer i) à l'intérieur d'autres peuplements récemment brûlés, ii) en forêt non-brûlée (e.g. produits par élagage ou sénescence naturelle, chablis, maladies, épidémies, etc.) ou iii) à l'intérieur même du peuplement brûlé. Par conséquent, nous avons considéré les chicots et les débris au sol non-brûlés et récemment produits à l'intérieur du peuplement brûlé comme source locale potentielle. Aux plus grandes échelles spatiales, il aurait évidemment été impossible de mesurer la quantité de substrat source pouvant potentiellement influencer la colonisation des espèces saproxyliques. Afin de pallier à cette situation, nous avons plutôt utilisé plusieurs variables référant à la quantité de forêts non-brûlées à l'intérieur de rayons de dimensions multiples ainsi qu'à la distance minimale à divers peuplements-sources potentiels (récemment brûlés ou non).

Certaines limitations sont conséquentes à l'utilisation de telles variables. La distribution spatiale du volume de substrat ligneux devrait être fortement hétérogène d'un peuplement-source à l'autre, celle-ci pouvant être dépendante de l'âge et la densité des peuplements (Siitonen 2001) ou de phénomènes stochastiques (e.g. chablis). De plus, ces variables ne permettent pas de couvrir l'ensemble des habitats-sources potentiels, certains pouvant se trouver au-delà des distances considérées dans la présente étude. Néanmoins, nous sommes confiants que ces variables permettent tout de même de caractériser une part non-négligeable de l'influence de la matrice forestière et des peuplements récemment brûlés (du moins, à l'intérieur des échelles spatiales considérées) sur la colonisation initiale.

Utilisation de l'analyse en coordonnées principales de matrice de voisinage afin de caractériser le patron spatial de colonisation (chapitre 2)

Parmi les méthodes estimant l'importance de la spatialisation des processus écologiques, nous avons choisi l'analyse en coordonnées principales de matrice de voisinage (CPMV). Cette méthode appartient aux analyses spatiales basées sur l'utilisation de vecteurs propres (Griffith et Peres-Neto 2006). L'analyse CPMV repose sur une matrice tronquée retenant la distance géographique entre les sites voisins. Dans cette matrice, les distances plus importantes que celle reliant les points voisins les plus éloignés sont remplacées par des valeurs égales à quatre fois cette distance-seuil (Borcard et Legendre 2002). Par la suite, une analyse en coordonnées principales est effectuée sur cette matrice tronquée. À la suite de cette analyse, les vecteurs propres positifs et non-nuls sont conservés, ceux-ci constituant les variables CPMV. Ces variables représentent des « vagues » orthogonales dont les longueurs d'onde se distribuent parmi toutes les échelles spatiales résultant du dispositif d'échantillonnage (Brind'Amour et al. 2005; Jones et al. 2008). Il a été démontré que cette méthode permettait une caractérisation beaucoup plus précise des patrons spatiaux complexes que l'analyse de tendance de surface (*trend surface analysis*) (Borcard et al. 2004; Jones et al. 2008). Puisque les variables CPMV sont complètement orthogonales, il est aussi possible de décomposer l'importance de chaque échelle spatiale distincte sur un processus écologique donné. Cette technique pouvait donc être d'une aide considérable afin de décomposer la structure spatiale complexe de la colonisation saproxylique.

Partitionnement de la variation (chapitres 1 et 2)

À l'intérieur des chapitres 1 et 2, nous voulions caractériser l'importance de plusieurs groupes de variables sur la variation totale de communautés ou d'espèces distinctes (chapitre 1) ou sur le patron spatial de ces taxons (chapitre 2). Ce paramètre peut se mesurer par le pourcentage de la variation totale expliquée (R^2,

R^2_a et leurs équivalents multivariés $R^2_{Y|X}$ et $R^2_{Y|Xadj}$) par les variables incluses dans les groupes respectifs. Cette proportion peut être qualifiée de « marginale » (*sensu* Cushman et McGarigal 2002) puisqu'une partie de celle-ci peut aussi être expliquée de façon concomitante par un ou plusieurs autres groupes de variables. En effet, il est pratiquement impossible que les groupes de variables utilisées dans les analyses soient parfaitement orthogonaux. L'ubiquité de la collinéarité entre les variables environnementales implique qu'une proportion de la variation totale peut être expliquée simultanément par plusieurs groupes de variables (on parle alors de variation « partagée »). L'importance de cette proportion ainsi que de celle ne pouvant être attribuée exclusivement qu'à un groupe de variables donné (variation « indépendante » *sensu* Cushman et McGarigal 2002) peuvent être déterminées par partitionnement de la variation (Borcard et al. 1992; Anderson et Gribble 1998; Cushman et McGarigal 2002). Dans un contexte où les déterminants du patron de colonisation de l'entomofaune saproxylique risquent d'être hautement collinéaires (e.g. distance par rapport aux habitats-sources et sévérité du feu), l'utilisation du partitionnement de la variation permettait de disséquer la proportion de la variation expliquée par chacun de ces groupes de déterminants.

Approches utilisées pour l'étude des taux de décomposition de la matière ligneuse après feu

Le dernier chapitre met à profit l'utilisation d'une région de 428 121 ha qui a brûlé en 1989 près de Radisson, Baie James, Québec (voir figure 4.1). À l'instar des trois premiers chapitres, l'utilisation d'une telle superficie brûlée permet la caractérisation du processus de décomposition du bois en fonction de multiples conditions environnementales postfeu. Jusqu'à maintenant, une seule étude récente (Angers 2010) a étudié l'impact de la sévérité du feu sur le processus de décomposition du bois mort. Cette étude s'est concentrée sur les variations du taux de chute des chicots après feu alors qu'aucune étude ne s'est penchée sur les taux de minéralisation, i.e. de perte de densité des débris ligneux produits par le feu. L'immense région brûlée en 1989 offrait donc une opportunité unique afin d'étudier les variations de ce processus.

Mesure des taux de décomposition de la nécromasse ligneuse

La décomposition des débris ligneux concerne à la fois la fragmentation et la minéralisation de la nécromasse (Swift 1977a; Harmon et al. 1986). Dans cette étude, nous avons considéré que les pertes par fragmentation étaient négligeables si bien qu'elles n'ont pas été incluses dans les analyses. En conséquence, seules les pertes de masse obtenues par minéralisation ont été considérées. Au cours du processus de décomposition, la matrice ligneuse perd de la masse en fonction du temps à mesure que les composés organiques complexes (lignine, cellulose, hémicellulose) sont i) dégradés par l'activité enzymatique des champignons saproxyliques ou ii) perdus par lessivage (Harmon et al. 1986). En considérant que les pertes par fragmentation sont négligeables au début du processus de décomposition, cette perte de masse se traduit essentiellement par une diminution progressive de la densité (en $g.cm^{-3}$) du substrat. Dans cette étude, nous avons caractérisé l'importance de la décomposition des débris ligneux comme étant la proportion de la masse initiale perdue depuis la perturbation, i.e. depuis 1989.

Estimation de la densité initiale

Les données de densité initiale utilisée afin d'estimer les taux de décomposition du bois mort sont fréquemment obtenues à partir de données théoriques de densité anhydre (voir Jessome 1977) ou encore à partir de valeurs moyennes obtenues sur des individus vivants (Boulanger et Sirois 2006). Ces méthodes suggèrent que la densité spécifique avant perturbation est relativement constante d'un individu à l'autre. Par contre, la densité interindividuelle de nombreuses espèces, notamment celle de l'épinette noire, peut être fortement variable et serait fortement liée au taux de croissance (Zobel et van Buijtenen 1989; Zhang 1995). Conséquemment, nous avons construit un modèle prédictif de la densité du bois avant perturbation en utilisant des données de densité et de taux de croissance provenant d'arbres vivants échantillonnés dans l'aire d'étude. Bien que cette technique permette de réduire le biais associé à l'estimation de la densité initiale du bois, elle n'a été que très peu utilisée lors d'études concernant les taux de décomposition de la nécromasse ligneuse (Naesset 1999, Mäkinen et al. 2006).

Choix du modèle afin d'exprimer la constante de décomposition k

Les pertes de densité sont généralement rapportées sour forme d'une constante de décomposition (k ou k_m lorsqu'il s'agit exclusivement de taux de minéralisation), laquelle exprime la proportion de la densité de bois perdue à chaque année. Cette diminution peut se traduire en fonction du temps après la mort de l'arbre (t) suivant un modèle négatif exponentiel (Olsen 1963) :
(1) $Yt = Y_0.e^{-km.t}$
où Y_0 et Y_t représentent respectivement la densité initiale du bois ainsi que celle au moment de l'échantillonnage. Bien que ce modèle soit fréquemment utilisé dans la littérature, certains rapportent que les pertes de densité peuvent s'effectuer selon un modèle sigmoide incluant un temps de délai (*lag-time model*) ou de manière linéaire en fonction du temps (voir Harmon et al. 1986 pour plus de détails). Dans notre cas, il était virtuellement impossible de déterminer quel modèle de décomposition était le plus approprié (i.e. qui pouvait le mieux s'ajuster aux données de pertes de densité en fonction du temps) considérant que nous n'avions que les données de décomposition provenant d'un point temporel unique, soit 17 ans après feu. Dans un souci d'uniformisation par rapport à la littérature, nous avons tout de même décidé d'exprimer les taux de décomposition obtenus selon un modèle négatif exponentiel.

Structure de la thèse et liens entre les chapitres

Cette thèse avait ainsi pour objectifs principaux d'étudier le processus de colonisation des espèces saproxyliques associées à l'épinette noire (*Picea mariana* [Mill.] B.S.P.) l'année même du feu (Partie A) ainsi que de déterminer quels sont les facteurs importants régulant la décomposition des débris ligneux d'épinette noire produits par le feu (Partie B). Dans la première partie, nous voulions déterminer l'importance des sources de colonisation et de l'habitat brûlé à différentes échelles spatiales sur la colonisation saproxylique l'année même du feu (Chapitre I). Ces facteurs étaient à même d'être à l'origine de patrons d'autocorrélation spatiale (*sensu lato*) dans l'abondance des adultes l'année même du feu. En conséquence, nous voulions évaluer à quelles échelles spatiales étaient spatialement structurées les communautés saproxyliques et quels étaient les processus responsables de l'occurrence de ces patrons (Chapitre II). Après avoir identifiés les facteurs influençant les adultes colonisateurs, nous nous sommes concentrés sur ceux influençant la colonisation larvaire subséquente des arbres très récemment brûlés. L'importance de cette colonisation a été mise en relation avec l'occurrence des adultes colonisateurs afin de vérifier si la colonisation par les adultes s'effectuait de manière optimale (Chapitre III).

Tels que mentionné précédemment, la colonisation saproxylique initiale est susceptible d'influencer la décomposition subséquente des débris ligneux (Edmond et Eglitis 1989, Zhong et Schowalter 1989). Dans la deuxième partie, nous avons donc évalué l'impact de facteurs mesurés à l'échelle de l'arbre et du peuplement sur les taux de décomposition des débris ligneux produits après feu (Chapitre IV). Bien que l'influence causale de l'entomofaune saproxylique sur les taux de décomposition n'ait pu être vérifiée à l'intérieur de cette thèse, les résultats obtenus dans la première partie ont été utiles dans l'interprétation du processus de décomposition de la matière ligneuse après feu.

CHAPITRE PREMIER

DISTRIBUTION OF SAPROXYLIC BEETLES IN A RECENTLY BURNT LANDSCAPE OF THE NORTHERN BOREAL FOREST OF QUÉBEC

1.1 Résumé

Cette étude évalue l'importance de la qualité de l'habitat brûlé et de la dispersion présumée depuis des habitats sources spécifiques sur la répartition des coléoptères saproxyliques l'année même du feu. L'analyse concerne la faune entomologique saproxylique des peuplements d'épinettes noires (*Picea mariana* [Mill] B.S.P.) du nord de la forêt boréale du Québec. La distribution des espèces colonisatrices était principalement influencée par les caractéristiques de l'environnement brûlé à l'échelle de la parcelle (0,04 ha), particulièrement la sévérité du feu, suggérant que ces carcatéristiques environnementales jouent un rôle très important à très fine échelle spatiale. Quelques xylophages et la plupart des prédateurs étaient plus abondants dans les peuplements sévèrement brûlés alors que cet attribut avait un effet opposé sur plusieurs espèces mycophages. L'abondance des arbres nouvellement brûlés pouvant servir de substrat de reproduction n'avait que très peu d'influence positive sur la répartition de ces groupes fonctionnels. La grande majorité des espèces colonisatrices initiales étaient faiblement associées à la distance depuis les forêts non-brûlées ou d'autres forêts récemment brûlées, toutes deux pouvant servir d'habitats sources potentiels. Ces variables étaient d'ailleurs d'une importance moindre que celles associées aux caractéristiques de l'habitat brûlé. Les arbres morts déjà présents avant feu, lesquels pouvaient aussi servir de substrat source, n'ont pratiquement eu aucune influence sur l'abondance locale des espèces colonisatrices. Plusieurs espèces, la plupart étant pyrophiles, étaient plus abondantes à mesure que l'on s'éloignait des peuplements non-brûlés. Cette relation contre-intuitive pourrait refléter le fait que la dispersion des insectes vers le paysage brûlé, très peu de temps après feu, pourrait être affectée par la quantité de volatiles émis depuis les peuplements sévèrement brûlés; ceux-ci devraient être plus abondants à mesure que la distance de puis les forêts non-brûlées augmentent.

1.2 Abstract

This study evaluated the importance of burned habitat characteristics as well as the likely dispersal from specific habitats in the distribution of saproxylic beetles the same year as a fire occurred, in burned black spruce stands (*Picea mariana* [Mill] B.S.P.) in the northern boreal forest of Québec. The distribution of early post-fire saproxylic species was mainly driven by burned habitat attributes at the plot-scale (0.04 ha), especially fire severity, suggesting that the effect of environment attributes can act at a relatively fine scale. Some xylophagous and most predaceous species were more abundant in severely burned stands whereas fire severity had the opposite effect on several common mycophagous species. The amount of newly fire-killed trees that could be used as breeding substrates in the burned stands had only a weak positive influence on these functional groups. The great majority of early saproxylic species were weakly associated with the distance from unburned forests or other recently burned patches that could act as potential "source-habitats". Indeed, these variables were of lesser importance than the attributes of the burned habitat. Woody debris that were already present in plots before the fire, potentially serving as local of source-populations for early colonizers, had virtually no influence on the local abundance of species. Many saproxylic species, including some true pyrophilous, clearly showed higher abundance as distance from unburned stands increased. This unexpected relation may reflect that dispersal of insects toward the burnt landscape very shortly after fire could be driven by the higher amount of volatiles released by severely burned forests, which are more likely as distance from unburned forest increased.

Keywords : Boreal forest, fire, saproxylic beetles, dispersal, burned habitat

1.3 Introduction

Stand-replacing wildfires constitute the most important natural disturbance in northern boreal forests of Canada (Rowe and Scotter 1973). Fire shapes both landscape and floristic diversities (Payette 1992) and influences the carbon flux in boreal forest ecosystems (Kasischke 2000). Wildfires transform most trees into woody detritus all at once (Tinker and Knight 2000). This dead wood represents a critical habitat for a tremendous diversity of heterotrophic taxa, particularly insects (Siitonen 2001). These species are known as "saproxylic" as they 'depend for at least part of their life cycle upon dead or dying wood of moribund or dead trees, or upon wood-inhabiting fungi, or upon the presence of other saproxylic species' (Speight 1989).

Beetles are among the most diverse and abundant saproxylic insects that colonize burned forests (Boulanger and Sirois 2007; Saint-Germain et al. 2004a; Wikars 2002). Early colonizing saproxylic beetles include mostly xylophagous, mycophagous and predaceous species (Muona and Rutanen 1994; Wikars 2002). Several species are considered truly pyrophilous (Evans 1966, Schmitz et al. 2002) as they are actively attracted to scorched wood during a brief post-fire period (Hjältén et al. 2007; Muona and Rutanen 1994). Colonization occurs shortly after tree death with most species arriving during the year of the fire (Boulanger and Sirois 2007).

The initial colonization of a burned forest by saproxylic species can be considered as the onset of a patch dynamic process (Amarasekare and Possingham 2001) that drives the turnover of the saproxylic community (Boulanger and Sirois 2007). Fire readily converts poorly suitable patches that have few resources for saproxylic species to highly suitable ones, characterized by abundant resources that become available for colonization by early successional saproxylic species. The geographical patterns associated with burned areas produce spatially defined patches whose attributes at various spatial scales likely influence the local abundance of colonizing species.

Successful colonization by saproxylic species depends on both the local habitat quality and the ability of species living in "source" habitats to reach these newly generated habitats (Bouget and Duelli 2004). Potential source habitats may include woody debris located in unburned forests in the surroundings, other recently burned stands (Saint-Germain et al. 2008) or in the burned habitat itself, as one cannot exclude that fire does not kill all organisms (Ulyshen et al. 2010). Large distance from source habitats or reduced local populations before fire may negatively affect the probability of a species to be collected in a suitable habitat. The resulting spatial patterns of colonizing saproxylic insects will strongly depend on both the dispersal ability of the species involved as well as the capacity of a given source habitat to provide individuals to the burned patch. Indeed, it is generally assumed that early colonizer saproxylic species have great dispersal and detection capacities (Bouget 2005; Byers 2000) considering the ephemeral and unpredictable suitability of the burned substrate. Several are known to be attracted by smoke (Frost 1984), infrared (Schmitz et al. 2002) or volatile organic compounds released by freshly fire-killed trees or use kairomones emitted by their prey (Allison et al. 2004) sometimes at great distances (Franklin et al. 2000; Turchin and Thoeney 1993). For example, experimental studies in flight mills revealed that many of these species are capable of flying up to several tens of kilometres (Atkins 1961; Jactel and Gaillard 1991). This differs from late successional saproxylics which colonize more stable habitats such as old-growth forests and therefore have limited dispersal capacities (Jonsson 2002).

The colonization process of saproxylic species may also be influenced by the quality of the habitat to be colonized (Hjältén et al. 2007; Saint-Germain et al. 2004a). Abundance of either larvae or adults may vary with respect to fire severity, woody debris size and availability, moisture content, nutrient quality, position and sun exposure (Boulanger and Sirois 2007; Cerezke 1977; Saint-Germain et al. 2004a, 2004c). For instance, severely burned trees are less colonized by several species, as for small diameter trees (Saint-Germain et al. 2004b, 2004c). Abundance may be further influenced by attributes, either related to source or burned habitats, measured at several spatial scales, in addition to tree and stand characteristics (Boulanger et al., submitted; Gibb et al. 2006; Holland et al. 2004; Økland et al. 1996; Southwood 1977). As colonizing species may exhibit different substrate preferences, saproxylic beetle assemblages may also differ according to burned habitat characteristics (Johansson et al. 2007).

Studies addressing the colonization process of saproxylic beetles after fire are scarce, particularly concerning unmanaged forests. Few studies have investigated the entire diversity of insects with an emphasis on saproxylic species (Hjältén et al. 2007; Saint-Germain et al. 2004a) immediately following fire (Boulanger and Sirois 2007) and in a spatially explicit framework. Moreover, colonization patterns are frequently interpreted from abundance and diversity data collected one year after fire (Saint-Germain et al. 2004a) while most species colonize the burned trees during the season of fire occurrence (Boulanger and Sirois 2007; Wikars 2002). The rare measurements of immediate fire impact on saproxylic beetle colonization were conducted after prescribed burning that did not allow landscape-scale appraisals of the colonization process (e.g. Hjältén et al. 2007; Toivanen and Kotiaho 2007; Wikars 2002) . The integration of larger spatial scales is thought to be essential in order to better interpret the colonization process of saproxylic beetles (Holland et al. 2004; Saint-Germain et al. 2007a).

In the northern boreal forest, fires exceeding 10 000 ha are frequent (Stocks et al. 2002). For instance, during the summer of 2005, several lightning-ignited fires burned 232 914 ha of mostly mature black spruce (*Picea mariana* [Mill] B.S.P.) forests in the James Bay area. Since this territory is almost a pristine forest ecosystem, it offers a unique opportunity to study post-fire ecological processes in an unmanaged forest context. Our study examines the colonization process in burned forests by post-fire saproxylic beetles from the onset of the post-fire period in the northern boreal forest. More specifically, we estimated the relative importance of the burned habitat attributes at two spatial scales (at the plot-level and in a 250 m radius) as well as the effects of the amount and qualities of pre-fire coarse woody debris and the distance to potential and specific source habitats on i) the structure of saproxylic functional groups (predators, xylophages and mycophages) and ii) the abundance of the most common species.

1.4 Methods

1.4.1 Study area

The study area is located in the northern boreal forest in the James Bay area, Canada (Figure 1). This area belongs to the lichen woodland ecosystem (Rowe and Scotter 1973). The landscape is characterized by a low altitude (100-200 m) plateau divided by lowlands (Stockwell et al. 1968). The climate is low-subarctic with a mean annual air temperature of –3.6°C with daily averages of –25 and 13°C in January and July respectively. Annual precipitation averages 637 mm, 40% of which falls as snow (Environment Canada 1993). Forests grow on all non-edaphically limited sites and are composed of even-aged stands of black spruce and jack pine (*Pinus banksiana* Lamb.) on mesic sites, whereas open, uneven-aged stands dominated by black spruce are found on paludified sites in the lowlands. Wildfires are the most important natural disturbance in the region with a recurrence cycle of approximately 100 years (Parisien and Sirois 2003).

1.4.2 Sampling design

Study plots were established in two different burned areas (northern and southern areas) located within a 76 183 ha territory that burned between May 29 and June 9, 2005 (Figure 1). Fire was ignited by lightning and burned mostly mature (80-150 years old) and old-growth (>150 years old) black spruce stands. This fire was essentially a crown fire even though scorching severity was highly heterogeneous throughout the burned area. Two patches that burned in 2002 were located within 25 km of the 2005 burned area (Figure 1.1).

Sixty-six plots were systematically established at 500 m intervals, perpendicular to each side of the two main roads in this area (Figure 1). In each plot, one trunk-window trap (TWT), known for its efficacy to sample saproxylic coleoptera (Kaila 1993), was set up within 7 days after the onset of the fire, as soon as the area was secured by authorities. Traps were operated from June 5 to August 3 and were emptied twice during this period.

Coleoptera were sorted in the laboratory and identified at the species level except for difficult taxa that were identified to higher taxonomic levels. Species were grouped into five functional groups based on their feeding habits (e.g. xylophagous, mycophagous, predaceous, saprophagous and others, see Appendix A1) according to the available literature and expert advice. Species clearly not associated with dead wood (e.g. Silphidae, some Elateridae, Scarabeidae) were discarded from the analyses. Voucher specimens are kept at the Canadian Forest Service in Québec City and at the Université du Québec à Rimouski.

1.4.3 Description of the forest in the study plots

In each site, a circular 400 m^2 plot centered on the trap was established and the diameter at stump height (DSH, i.e. 30 cm above root collar) was measured on every living and burned tree $\geq$10 cm. The DSH of all living and burned saplings (2-10 cm) was also recorded in a 100 m^2 circular plot also centered on the trap. Fire severity on all stems ($Fire_{tree}$, 0 to 4) that were alive before fire (>2 cm of DSH) was assessed as the portion of charred bark on the tree trunk. A site fire severity index ($Fire_{site}$, 0 to 4) was computed for each plot as follows:

$$(1)\quad Fire_{site} = (\Sigma\,(Fire_{tree} * Bas\_Area_{tree}))/Bas\_Area_{site}$$

with Bas_Area_{tree} being the basal area of the tree in m^2 and Bas_Area_{site} the total basal area in the plot in m^2. The volume of all logs with diameter > 5 cm and the total basal area of snags with DSH > 5 cm that were already present in the stands before fire were determined in four additional 100 m^2 circular plots located 50 m apart from the central plot. The diameter at both ends and the length of logs were measured. Log volume was estimated as a cone or a truncated cone if the main axis was broken. The decomposition stage was determined according to the five decay classes proposed by Hayden et al. (1995) and only for unburned logs and snags because it was difficult to determine the decay classes of highly charred debris.

At the landscape scale, fire severity and the importance of sources (unburned stands and 2002 burned areas) around the sampled plots were assessed from Landsat 5 TM satellite images taken after fire in July 2005. We chose the Normalized Burn Ratio (NBR) as the image derived index because it showed the highest correlation (Pearson r=0.68) with the site fire severity index ($Fire_{site}$). A regression model predicting NBR as a function of $Fire_{stn}$ was developed to assign a fire severity class to each pixel (unburned, lightly, moderately, or severely burned). Only coniferous stands (burned or unburned) were considered in the analyses.

1.4.4 Data analysis

1.4.4.1 Variables included in analyses

Environmental variables included in the study were classified in four sets, i.e. "the local- and nearby burned habitat quality", "the pre-fire coarse woody debris (CWD)" and "the distance to specific source habitats" (Table 1.1). In addition to fire severity, local and nearby burned habitat quality was assessed according to the size and abundance of burned trees at the respective scales. As several authors have pointed out that substrate availability (Bouget and Duelli 2004; Martikainen et al. 2000; Similä et al. 2003) as well as tree diameter (Jonsell et al. 2007; Saint-Germain et al. 2004b, 2004c) may influence colonization by saproxylic beetles, we included the total basal area and the mean diameter of trees with DSH > 10 cm as variables associated with burned wood. Fire severity measured in the plot (equation 1) was also included in this set. At the nearby scale, we included an estimate of fire severity in a 250 m radius around the trap by averaging fire severity of all pixels within this spatial extent. We further computed an index (*Dens250m*) assessing the relative density of the forest that burned by using the EOSD classification (Beaubien et al. 1999). Values from 1 to 3 were given to each pixel dominated by coniferous forest according to forest cover before fire (tree bog or fen or tree cover: 10-25% = 1; 26-60% = 2; cover > 60 % = 3). The sum of values for all pixels within 250 m around the plot center (*Dens250m*) was included as an index of forest density in the nearby burned habitat quality set. We did not use a larger radius in this set in order to avoid buffer overlapping between sites and thus respect their spatial independence (Holland et al. 2004).

Two other sets of variables were used to estimate the effect of pre-fire CWD and the distance to other potential source habitats on the colonization pattern of saproxylic species. CWD present before fire may provide individuals for the newly fire-killed trees; therefore, we included the total volume of logs and basal area of snags (burned and unburned) in this set. Furthermore, since many early post-fire colonizers, e.g. wood-feeders, do not use heavily decayed woody debris (Saint-Germain et al. 2007b), only unburned snags and logs belonging to decay classes 1 and 2 were considered as additional variables. In the fourth set, we included the distance to the 2002 burned areas, to the fire edge and to the nearest 10 ha of unburned forests in order to assess the potential effect of dispersal from these habitats.

1.4.4.2 Effects of environmental variables on the saproxylic community

Canonical redundancy analyses (RDA) were used to assess the effects of environmental variables on the ordination of the saproxylic community. Analyses were performed separately on the xylophagous, mycophagous and predaceous functional groups as these may be significantly associated with different sets of environmental variables. Several saproxylic species are known for their non-linear response to fire severity; such effects were thus assessed by adding a polynomial term in analyses (Jones et al. 2008). Because representing the polynomial term of a given variable may result in strong distortion of the ordination space, plot-level and nearby fire severity was expressed using dummy variables (Fire1 and Fire1_250: <2.5; Fire2 and Fire2_250m = 2.5-3.5) in ordination. Significant ($P<0.05$) variables of each type were assessed by forward selection after 9999 unconstrained Monte Carlo permutations. In order to downweight rarely caught species in the analyses, singletons were excluded and abundance of species were Hellinger-transformed (Legendre and Gallagher 2001).

The proportion of the variation in species assemblages of each saproxylic functional group explained by each combinations of set of variables (Table 1.1) was assessed by variation partitioning (Borcard et al. 1992). First, the significant variables belonging to each of the four sets of variables were identified as above by means of forward selection in separate RDA. This procedure was applied separately for each functional group. In contrast to the graphical representation of RDA, partitioning analyses were performed using local and nearby fire severity as a continuous variable and by including their respective quadratic term. Variation partitioning was then performed with these significant variables to assess the importance of variation explained by each set as well as the one shared between one or several sets. The independent explained variance of a given set was estimated separately from the variation explained without considering confounding effects of other sets (marginal effect *sensu* Cushman and McGarigal 2002). Significance of testable partitions was evaluated by 999 Monte Carlo permutations under the reduced model. The proportion ($R^2_{Y|Xadj}$) of variance explained was adjusted for the number of variables (*p*) and sampling effort (*n*) (Peres-Neto et al. 2006).

1.4.4.3 Specific responses

We computed specific analyses on common (> 150 individuals of total abundance) xylophagous (*Acmaeops proteus proteus*, *Arhopalus foveicollis*, *Hylobius congener* and *Monochamus scutellatus scutellatus*), mycophagous (*Atomaria* sp., *Caenoscelis* sp., *Cartodere constrictus*, *Corticaria dentigera*, *Corticaria* sp. 2 and *Clypastraea fusca*) and predaceous (*Sericoda obsoleta*, *Sphaeriestes virescens* and *Thanasimus undatulus nubilus*) species. Most of these species have already been reported to be favoured by conditions generated by fire (St-Germain et al. 2004a; Boulanger and Sirois 2007).We developed and tested 31 biologically plausible models of regression to evaluate the relationships between the abundance of these taxa and several variables associated with the four sets of variables identified earlier (see Appendix A2). Some model included fire severity and its quadratic term to assess any curvilinear relationship with beetle abundance. The most parsimonious models for each species were selected according to the corrected Akaike's Information Criterion (AIC_c). Multimodel averaging was used when the AIC_c weight of the top-ranking model was lower than 0.90 (Burnham and Anderson 2002). All species abundances were log+1 transformed prior to analysis to reduce overdispersion.

All regression analyses were performed using R 2.9.2. (R Development Core Team 2010) whereas multimodel averaging of model parameters was assessed using the *AICcmodavg* package (v1.06, Mazerolle 2009) in R. The *packfor* library (Dray 2007) in R was used for forward stepwise selection of variables in RDA computed on each functional group as well as for forward selection in each set of variable used in partitioning analyses. These latter analyses were performed using the *vartpart* function in the *vegan* package (v1.11-5) and the *anova* function in the *stats* package in R.

1.5 Results

A total of 14 850 beetles belonging to at least 159 taxa were collected during the sampling period. Among these, 14 746 individuals belonging to at least 139 species were classified as saproxylic (either obligate or at least facultative) (Appendix A1). Predators (55 spp.) was the most diversified feeding guild followed by xylophagous (41 spp.) and mycophagous (30 spp.) taxa. The 13 most abundant saproxylic taxa made up 93.7% of total saproxylic catches. Sixty-nine (49.6%) saproxylic taxa were singletons or doubletons (Appendix A1).

1.5.1 Community analyses

Variables included in RDA explained 21.4%, 23.4% and 36.7% of variation among assemblages of the xylophagous, mycophagous and predators functional groups, respectively (figure 1.2). Selected variables were mostly related to fire severity measured at the plot or at the nearby scales, as well as to the amount and size of fire-killed trees at these spatial scales. Distance to the 2002 burned patches was also significant for every functional group whereas a significant portion of the xylophage variation was related to the distance to large (>10ha) unburned patches. Pre-fire CWD was not retained for any saproxylic assemblages.

Axis one (12.1 %, P<0.001) of the xylophage ordination (figure 1.2a) mostly depicted a gradient of fire severity with lightly burned plots including small diameter trees and low density of burned forest at the nearby scale located at the left-side of the graph. The abundance of many species, particularly *Arhopalus foveicollis*, *Gnathacmaeops pratensis, M. s. scutellatus* and *Pachyta lamed*, was positively related to the fire severity, the amount and size of fire-killed trees, and the distance to >10ha unburned patches. At the opposite, several bark beetle species were associated with lightly burned stands. The abundance of *Acmaeops p. proteus* and *Oxypteris acuminata* were associated to moderately burned stands and positively related to the distance to the 2002 fires on the second axis (8.4%, $P<0.001$) whereas *Hylobius congener* and *Dryocoetes autographus* showed the opposite trend.

The great majority of the variation in species composition of the mycophage functional group was explained on the first axis (23.5%, $P<0.001$) by plot-level fire severity and by the distance to the 2002 burned patches (figure 1.2b). Indeed, the great majority of mycophagous species were associated to lightly burned stands located close to the 2002 burned patches.

A similar gradient was depicted on the first axis (30.9%, $P<0.001$) of the predator's ordination analysis (figure 2c), although most taxa had opposite trends compared to mycophages. The second axis (8.9 %, $P<0.001$) mostly depicted a gradient in size and amount of fire-killed trees at the plot-level with few species (*Heterothops minor*, *Oxypoda amica*, *Sericoda obsoleta* and *Sphaeriestes virescens*) being negatively related to these attributes.

1.5.2 Variation partitioning

The marginal and independent effects of the plot-level variables were highly significant ($P < 0.001$) and explained the highest amount of variation for all functional groups (figure 1.3). Marginal effects of nearby burned habitat were also important, especially for predators and mycophagous species. Nevertheless, a higher portion of the variation explained by this set was shared with other sets of variables. Distance to other habitats was of a lesser importance and was highest for mycophagous taxa ($R^2_{Y|Xadj} = 0.116$, $P<0.001$). However, much of the variation explained by these attributes was shared with other groups so their independent effects was low ($R^2_{Y|Xadj} \leq 0.038$), although significant ($P<0.05$) for all functional groups. Marginal effects of pre-fire CWD was rather low, though significant ($P<0.001$); however the unique contribution of this set was not significant for mycophagous and predaceous functional groups and was virtually nil ($R^2_{Y|Xadj} = 0.013$, $P<0.05$) for xylophagous species.

1.5.3 Specific responses

In all cases, the top-ranking models showed AIC_c weights rather low (<0.90), indicating that other models also received a certain level of support (Appendix A3). Most top-ranking models included variables measured at the plot-level and/or distance to other habitats. Noteworthy, no model with $\Delta AICc < 4$ included pre-fire CWD characteristics.

1.5.3.1 Xylophagous species

Fire severity at the plot- and/or nearby spatial scale was included in high ranking models for most xylophagous species (Appendix A3). Models including size and amount of burned substrates at both spatial scales received the highest level of support (wt = .397) for *M. s. scutellatus*. Other models adding fire severity at one or both spatial scales also received a relatively high level of support (wt = 0.100-.279) for this species. Indeed, a majority of xylophagous species was significantly ($P<0.05$) and positively related to the diameter of the tree holding the trap (table 2). *Acmaeops p. proteus* and *M. s. scutellatus* were more common in moderately burned plots whereas the abundance of *H. congener* was positively related to fire severity at this scale (Appendix A4). Even if variables measured at the nearby scale were included in top-ranking models, only *Dens250* had a significant positive ($P<0.05$) effect on *M. s. scutellatus* after multi-model averaging (table 1.2). Moreover, except for *M. s. scutellatus*, several top-ranking models included the distance to other habitats. Both *A. foveicollis* and *H. congener* were more abundant ($P<0.01$) with increasing distance to large unburned patches. The latter species was negatively influenced by the distance to the 2002 fires whereas *A. p. proteus* showed the opposite trend (table 1.2).

1.5.3.2 Mycophagous species

Top-ranking models included fire severity at the nearby and/or at the plot scale for *Corticaria* sp.2, *Caenoscelis* sp. and *C. fusca* (Appendix A3). However, fire severity at the plot scale was only significant for the latter two taxa, both being most abundant in moderately burned plots although *C. fusca* was also rather abundant in lightly burned plots (table 1.2, Appendix A4). In addition to fire severity, variables associated with substrate size and amount at both the plot and nearby scales were included in top-ranking models of *Corticaria* sp.2. These latter attributes were also included in models for *Atomaria* sp., *C. constrictus* and *C. dentigera* (Appendix A3). Indeed, the total basal area in the plot had a significant ($P<0.05$) positive effect on *Atomaria* sp. and *Corticaria* sp.2 although density of burned forest in a 250 m radius had the opposite effect for this latter species and *C. constrictus* (table 1.2). Variables related to distance to other habitats were included either alone or in addition to attributes of substrate size and amount in the most parsimonious models for *C. constrictus*, *Atomaria* sp. and *C. dentigera*. The two latter species were indeed negatively ($P<0.05$) affected by the distance to the 2002 burned patches (table 1.2).

1.5.2.3 Predators

Models including fire severity and size and amounts of fire-killed trees at both the plot and nearby scales altogether received high levels of support for all common predaceous species. Model including only these variables was by far the most parsimonious for *S. obsoleta* (wt = .803, Appendix A3). Abundance of common predators was positively related to fire severity at the plot- and nearby-scales except for *S. virescens* for which it was not significant (table 1.2).

1.6 Discussion

To our knowledge, this study is the first to appraise the distribution of saproxylic species in burned patches the same year as the fire in a spatially explicit framework. Several taxa captured in our study are recognized as truly pyrophilous (*Oxypteris acuminata* and *Sericoda* spp.) while others are clearly associated to fire (e.g. *Corticaria* spp, *Sphaeriestes* spp.,*Clypastraea fusca, Monochamus s. scutellatus*) (Dajoz 1998; Lundberg 1984; Wikars 1997). Fire attraction habits of the very common species *H. congener*, *A. foveicollis* and *T. u. nubilus* are less known although they were already reported in great numbers after fire (Boulanger and Sirois 2007; Saint-Germain et al. 2004a). Saproxylic assemblages were influenced by various environmental attributes measured at several spatial scales. Moreover, our results showed that environmental attributes associated with the burned habitat, especially at the plot scale, were of greater importance than distance to potential source habitats. Furthermore, local pre-fire CWD had very weak influence on the abundance of most early colonizers.

1.6.1 Effect of burned habitat quality

Saproxylic functional groups appeared to be mainly driven by the quality of the burned habitat measured at the plot scale suggesting that environmental control can act at a relatively fine scale. Saproxylic species may respond to habitat characteristics measured at spatial scales up to few hundreds or thousands metres (Boulanger et al., submitted; Holland et al. 2004; Økland et al. 1996). However, this study suggests that the influence of the burned habitat at the nearby scale (250 m) was less important than at the plot scale. High dispersal capacities probably allowed most colonizers to reach and resolve fine-grained habitats. Nevertheless, this does not ruled out the potential effects of other habitat characteristics measured at coarser spatial scales than those assessed in the present study (Boulanger et al., submitted).

Among plot-scale attributes, fire severity was the most important one for predicting early post-fire saproxylic species abundance. Saproxylic communities were clearly different along the whole fire severity gradient. Effect of fire severity on saproxylic species is relatively well-known for several xylophagous species but less so for other functional groups. Attraction of *M. s. scutellatus*, *A. p. proteus* and phloem feeders, including scolytids, to moderately-lightly burned stands was already noticed in previous studies (Cerezke 1977; Saint-Germain et al. 2004b, 2004c). Black spruce has a thin bark and its insulating property may be affected by fire severity that may reduce moisture content. Consequently, lightly burned trees are less likely to experience extreme temperatures and may keep higher moisture content in the subcortical area where these beetles are actively feeding (Furniss 1965; Peddle et al. 2002; Savely 1939). Negative effect of fire severity on the inner bark moisture content may also explain the lower abundance of mycophagous species, including the most common ascomycete feeders, in severely burned stands. Depleted moisture content in severely burned trees may affect the subsequent ascomycete colonization success (Boddy and Rayner 1988; Harmon et al. 1986).

The positive effect of fire severity on predaceous species is surprising. Many predators, including *T. undatulus nubilus* and *S. virescens*, were more common in severely burned patches where associated preys (e.g. bark beetles) are nonetheless much less common. Likewise, many xylophagous species were actually more abundant as distance to unburned forests increases, that is where severely burned stands were more likely to occur. Furthermore, although it was favoured by moderate fire severity at the plot-scale, *A. p. proteus* was more abundant away from the 2002 fires, i.e. in the northern and more severely burned area. As a result, several xylophagous species actually oriented themselves towards areas which appear as suboptimal considering their reproduction requirements, larvae being more abundant in lightly or moderately burned trees (Saint-Germain et al. 2004b, 2004c, Boulanger et al., submitted). It should be noticed that, since sampling was performed very soon after fire, individuals were actively dispersing and as such, they may not automatically be considered as "true" colonists. Consequently, their abundance in burned sites may not necessarily reflect the subsequent use of the substrate (Boulanger et al., submitted). Species may have therefore orient themselves to areas where volatiles were more abundant despite of being first attracted to the optimal habitat (Boulanger et al., submitted). Such higher amount of volatiles may occur in severely burned areas (Kelsey and Joseph 1999, 2003) or away from unburned habitats. Yet, such pattern is not consistent for all functional groups. While predaceous and xylophagous beetles that are known to use volatiles as attractive cues followed this pattern, mycophagous species did not. Even though several authors (Fäldt et al. 1999; Guevera et al. 2000; Jonsell and Nordlander 1995; Jonsson et al. 1997) suggested that some mycophagous associated with bracket fungi may orient by using host volatiles or pheromones, no studies have assessed the role of post-fire volatiles in the dispersal of mycophagous species.

Most saproxylic species were not positively influenced by the abundance of breeding substrates in burned stands but many of them were more common in traps attached to larger diameter trees. Large trees may have been more attractive as larvae of these species are thought to benefit from physical characteristics (higher moisture content and bark insulating properties, thicker phloem) of such trees (Saint-Germain et al. 2004b, 2004c). Even though the trunk-window trap is not recognized as a substrate-specific collecting method (Saint-Germain et al. 2006; Wikars et al. 2005), this result may reflect the importance of tree diameter as visual cues for landing decision (Campbell and Borden 2009).

1.6.2 Potential effect of dispersal from other habitats

The matrix of green forest is generally assumed to be the most important source of individuals for colonizing burned patches (Saint-Germain et al. 2008). Most species captured in our study may reproduce in or use dead wood produced in unburned forest (Saint-Germain et al. 2007b). Emigration from these habitats is thus a likely phenomenon as many early colonizers are known as opportunistic that may benefit from the "competition-free" environment provided by the recently burned patches (Holliday 1991). In this study, distance to the green matrix did not have any detrimental effect on the abundance of most saproxylic species. One may argue that dispersal from other habitats than the green matrix, e.g. other recent burns that host high volumes of freshly killed trees (Boulanger and Sirois 2006), may also affect the local abundance of saproxylic species after fire. Again, most predators and xylophagous species did not show any negative relation with the distance to recently burned stands, whereas mycophagous species, including the common *Atomaria* sp. and C. *dentigera*, showed the opposite. Negative effect of distance to the green matrix may have been overlooked since these habitats were located much closer from plots (0 – 2.1 km) compared to the other recent fires (4.8 – 23.8 km).

If one assumes that unburned forests or recently burned patches were a significant source of saproxylics, these results should be explained by the high dispersal capacities that allowed most early colonizers to reach any colonisable habitats within the burned patch. Yet, caution must be taken when assessing the relative importance of distance to other habitats as this group of variables was rather collinear with other burn's attributes. For example, lightly burned habitats were more likely to be close to unburned forests whereas habitats located farthest from the 2002 fires were also the most severely burned. In addition, other landscape characteristics not considered in this study (e.g. edge effect, landscape or patch complexity, etc.) may have affected the distribution patterns of saproxylic species (Boulanger et al., submitted; Holland et al. 2004; Wiens and Milne 1989). Dispersal of surviving individuals from sources located in the vicinity of the sampling points (e.g. lightly burned woody debris or dead wood located in small unburned patches enclosed within the burn) cannot be excluded at this point since epigeic arthropods may survive to low severity burns (Ahlgren 1974; Paquin and Coderre 1997, Wikars and Schimell 2001). Ulyshen et al. (2010) recently reported that saproxylic beetles may survived to prescribed, low intensity fires. However, the volume of local pre-fire CWD and low fire severity at the nearby scale did not have such positive effect on the local abundance of saproxylic species. Survivorship, especially for subcortical species, after wildfires which are likely to be more intense, is still unknown. Considering the scarcity of data on the survivorship of saproxylic species after a burn, the relative importance of the various source habitats in the post-fire colonization of burned patch by saproxylics remains to be elucidated.

Forests in the study area are pristine ecosystems subject to large and frequent wildfires (Payette 1992; Rowe and Scotter 1973; Stocks et al. 2002). In this context, the amount and availability of dead wood is probably spatially and temporarily rather stable at the regional scale which may lead to the maintenance of very high populations of saproxylic beetles (McCullough et al 1998). This contrast with ecosystems that have been under intensive management over a long period of time and where many species are now threatened (Siitonen 2001). Such high regional pool of individuals in the present study may have overwhelmed any effect of dispersal from specific source habitat as well as the effect of the amount of pre-disturbance CWD.

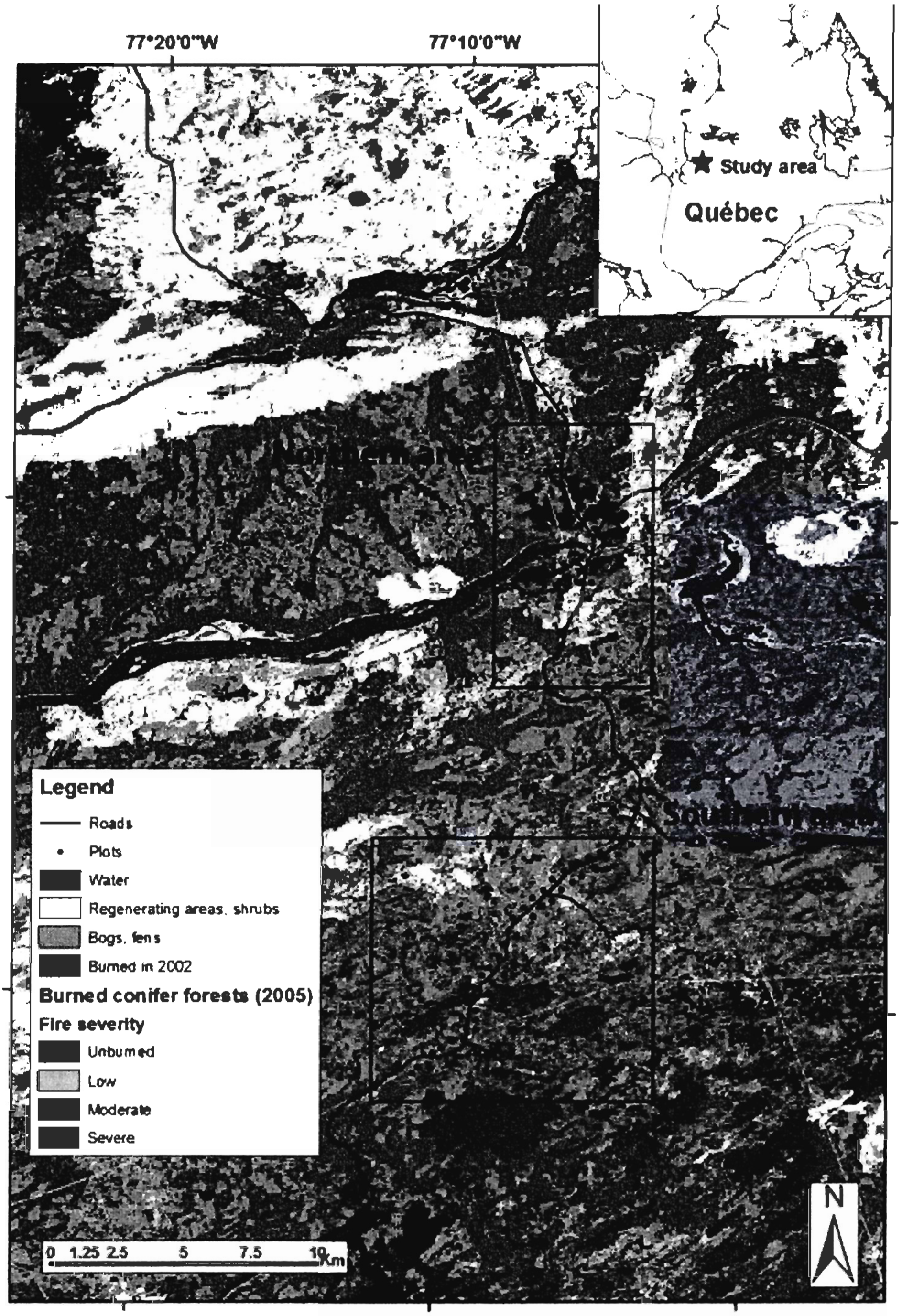

Figure 1.1. Study area and distribution of sampling sites with respect to fire severity in the 2005 burned coniferous forests in Northern Quebec. Fire severity was determined according to NBR Index from Landsat TM5 satellite images.

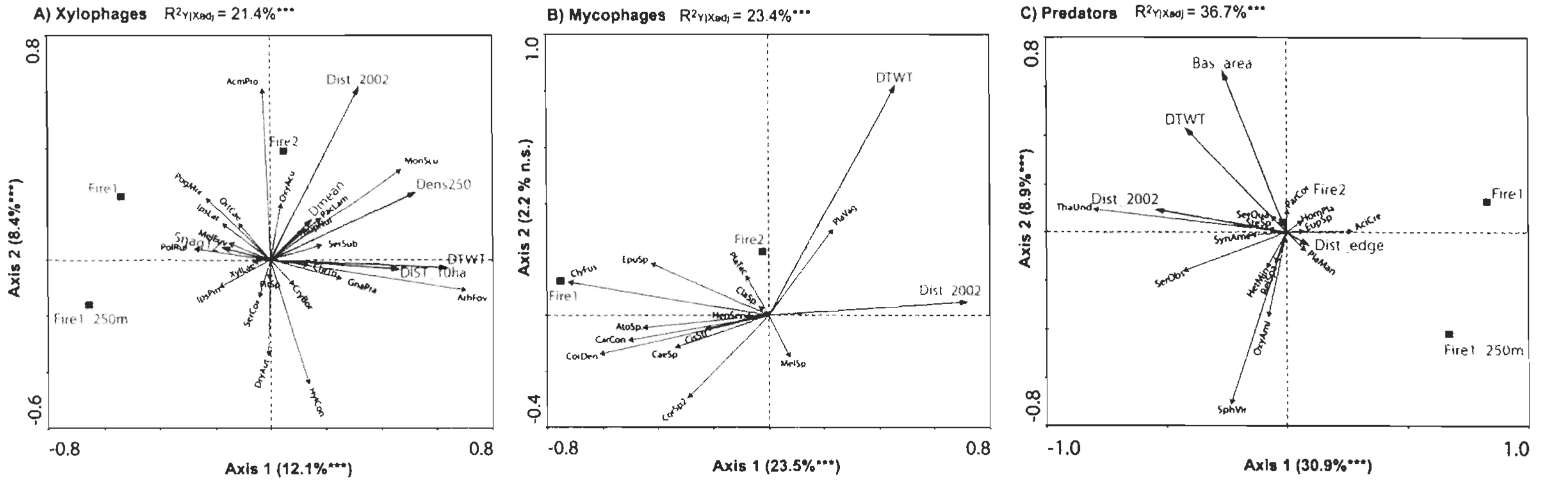

Figure 1.2. Ordination of the a) xylophagous, b) mycophagous and c) predaceous functional groups by canonical redundancy analyses (RDA) using significant variables. Only species with ≥5 individuals are shown. See supplementary material A for species name abbreviations. Bas_area : Total tree basal area; Dens250: Burned forest density index in a 250 m radius; Dist_2002: Minimum distance to the 2002 fire patches; Dist_10ha: Minimum distance to unburned conifer-dominated forest >10 ha; Dist_edge : Minimum distance to the nearest extreme edge of the 2005 fire patch; Dmean : Mean diameter of trees in the plot; DTWT : Diameter at stump height of the tree on which the trap was attached; Fire1: Low fire severity measured in the plot (dummy); Fire2: Moderate fire severity measured in the plot (dummy); Fire1_250: Low fire severity measured in a 250m radius (dummy); Fire2_250: Moderate fire severity measured in a 250m radius (dummy); Snag12: Basal area of unburned snags (>5 cm of diameter) of decay classes 1 and 2.

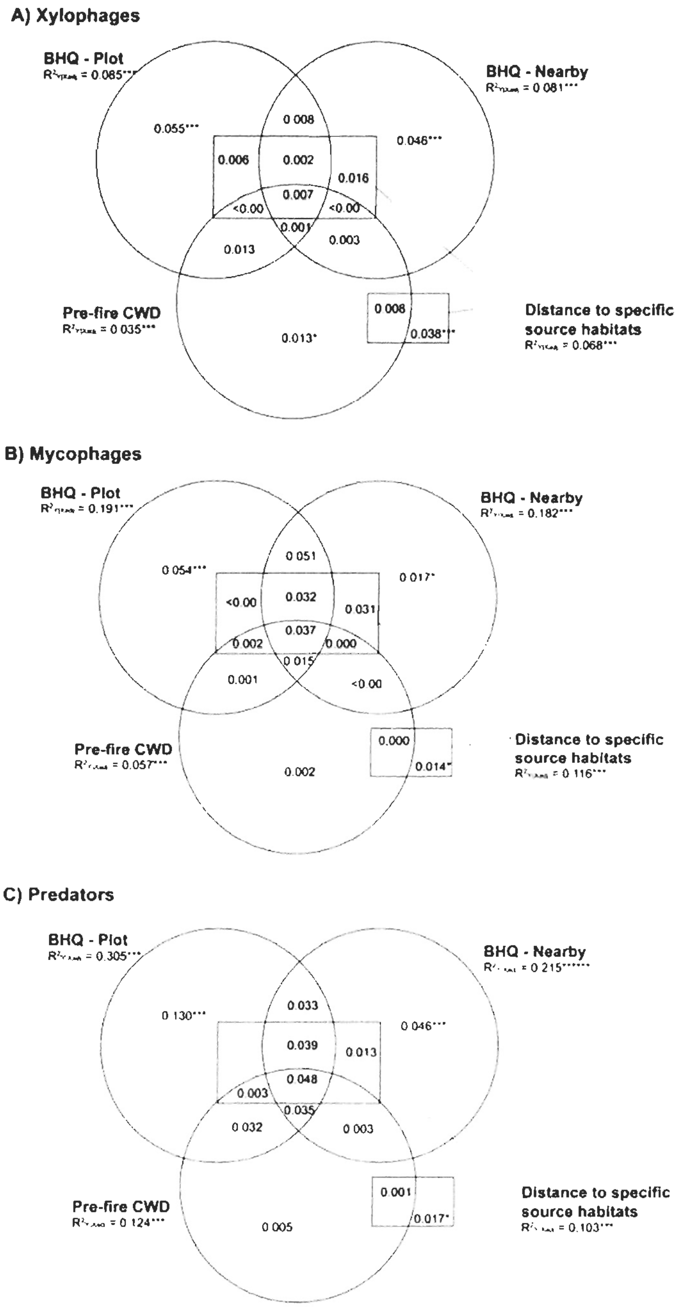

Figure 1.3. Venn diagrams representing the independent and the shared variation explained ($R^2_{Y|Xadj}$) by burned habitat quality (BHQ) variables at the plot and nearby scale, pre-fire coarse woody debris (CWD) and by the distance to other habitats. Analyses were performed separately for a) xylophagous, b) mycophagus and c) predaceous species. *: $P<0.05$; **: $P<0.01$; ***: $P=0.001$ after 999 Monte Carlo permutations on reduced models.

Table 1.1 Description of the variables used in the present study.

Variable	Set	Description	Mean	Range
Dtwt	BHQ[1] - Plot	Diameter at stump height (DHS) of the tree on which the trap was attached (cm)	15.0	10.1-24.6
Dmean	BHQ - Plot	Mean diameter (cm) of burned trees > 10 cm of DSH	13.5	11.1-20.2
Bas_area	BHQ - Plot	Total tree basal area ($m^2.ha^{-1}$)	19.0	3.5-54.9
Fire_plot	BHQ - Plot	Fire severity measured in the plot	3.09	1.21-4
Fire_250	BHQ - Nearby	Fire severity measured in a 250 m radius centered on the trap	2.49	0.64-3.91
Dens_250	BHQ - Nearby	Burned forest density index in a 250 m radius centered on the trap	359.4	22-830
Log12	Pre-fire CWD	Volume ($m^3.ha^{-1}$) of unburned downed CWD (>5 cm of diameter) of decay classes 1 and 2	0.2	0-2.5
Snag12	Pre-fire CWD	Basal area ($m^2.ha^{-1}$) of unburned snags (>5 cm of diameter) of decay classes 1 and 2	0.2	0-3.6
All_snags	Pre-fire CWD	Basal area ($m^2.ha^{-1}$) of all snags (>5 cm of diameter)	2.10	0-6.95
All_logs	Pre-fire CWD	Volume ($m^3.ha^{-1}$) of all downed CWD (>5 cm of diameter)	13.1	0-52.0
Dist_edge	Distance to specific source habitats	Minimum distance to the nearest extreme edge of the 2005 fire patch (m)	571	2-2067
Dist_2002	Distance to specific source	Minimum distance to the 2002 fire patches (m)	13930	4814-23788

Variable	Set	Description	Mean	Range
	habitats			
Dist_10ha	Distance to specific source habitats	Minimum distance to unburned conifer-dominated forest >10 ha (m)	661	35-2002

1. Burned habitat quality

Table 1.2. Effects of environmental variables to predict the abundance of 13 common saproxylic beetle taxa in burned black spruce stands of the northern boreal forest of Québec. Multimodel averaging was used for all species since the weight of the top-ranking models was always below 0.90.

[a]+++,--- : P<0.001, ++, -- : P<0.01, +,- : P<0.05

		Burned habitat quality								**iii) Pre-fire CWD**				**iv) Distance to other habitats**		
		i) Plot					**ii) Nearby**									
	Species	**Dtwt**	**Fire**	**$Fire^2$**	**Dmean**	**Bas_area**	**Fire250**	**$Fire250^2$**	**Dens250**	**Snag12**	**Log12**	**All_snags**	**All_logs**	**Dist_10ha**	**Dist_edge**	**Dist_2002**
Xylophagous	*Acmaeops p. proteus*			--												+++
	Arhopalus foveicollis	+++												++		
	Hylobius congener	+	+++	-										++		--
	Monochamus s. scutellatus	+++		--					+							

		Burned habitat quality								iii) Pre-fire CWD				iv) Distance to other habitats		
		i) Plot					ii) Nearby									
	Species	**Dtwt**	**Fire**	**Fire^2**	**Dmean**	**Bas_area**	**Fire250**	**Fire250^2**	**Dens250**	**Snag12**	**Log12**	**All_snags**	**All_logs**	**Dist_10ha**	**Dist_edge**	**Dist_2002**
Mycophagous	*Atomaria sp.*					+										--
	Caenoscelis sp.			-												
	Cartodere constrictus								--							
	Clypastraea fusca			-												
	Corticaria dentigera	-													+	-
	Corticaria sp.2	--				+++	++		---							
Pr	*Sericoda obsoleta*	+	+				++		--							

	Burned habitat quality								iii) Pre-fire CWD				iv) Distance to other habitats		
	i) Plot					ii) Nearby									
Species	Dtwt	Fire	$Fire^2$	Dmean	Bas_area	Fire250	$Fire250^2$	Dens250	Snag12	Log12	All_snags	All_logs	Dist_10ha	Dist_edge	Dist_2002
Sphaeriestes virescens		+++			-										+
Thanasimus undatulus		+++				++									

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CHAPITRE 2

SPATIAL PATTERNS OF SAPROXYLIC BEETLES SHORTLY AFTER FIRE IN THE NORTHERN BOREAL FOREST

2.1 Résumé

Nous avons analysé le patron spatial des espèces de coléoptères xylophages, mycophages et prédatrices saproxyliques colonisant les brulis l'année même du feu dans le nord de la forêt boréale. En utilisant le partitionnement de la variation ainsi que l'analyse CPMV, nous avons identifié quels déterminants (caractéristiques environnementales des parcelles structurées dans l'espace, caractéristiques environnementales mesurées à une échelle plus grossière que la parcelle ou la dispersion depuis les habitats-sources) étaient plus à même de causer de l'autocorrélation spatiale à une échelle donnée. Pour la plupart des taxons, l'autocorrélation spatiale était importante à très grande échelle (selon un gradient géographique X/Y), ainsi qu'aux grandes (2650 m) et moyennes (1325m) échelles spatiales. Ces patrons spatiaux étaient fortement reliés à la distance depuis les habitats-sources ainsi qu'aux caractéristiques de l'habitat brûlé mesurées à une échelle plus grossière que celle de la parcelle. Les limitations de dispersion plus importantes chez les mycophages ont vraisemblablement causé une distribution agglomérée près des habitats-sources à très grande échelle. Néanmoins, l'abondance de plusieurs espèces xylophages et prédatrices à très grande et grande échelles augmentait à mesure que la distance depuis les habitats-sources était plus importante. Par conséquent, il serait surprenant que la dispersion des espèces xylophages et prédatrices soit limitée par la distance aux habitats-sources, du moins à l'intérieur des échelles spatiales considérées dans la présente étude. Ces espèces ont été attirées davantage vers les forêts sévèrement brûlées à très grande et grande échelles alors que les espèces mycophages suivaient un patron opposé. Bien que les patrons d'autocorrélation spatiale expliquent une portion significative de la variation des espèces considérées, les effets indépendants des caractéristiques mesurées à l'échelle de la parcelle étaient aussi importants particulièrement pour les espèces xylophages et prédatrices. Ceci suggère que la colonisation des coléoptères saproxyliques après feu est fortement contrôlée par des caractéristiques environnementales effectives à de multiples échelles spatiales.

2.2 Abstract

In this study, we analyzed the spatial pattern of xylophagous, mycophagous and predaceous species of saproxylic beetles the same year as the fire in a northern boreal forest. Using variation partitioning and PCNM analysis, we identified which processes (spatially structured environmental attributes measured at the plot or larger than the plot-level, or dispersal from specific source-habitats) caused spatial patterns at a given spatial scale. For most taxa, spatial patterns were most important at the very large scale, whereas large (2650 m) and medium (1325 m) spatial scales patterns, although significant, were much less important. Spatial patterns at most scales were strongly related to distance to specific source-habitat variables and burned habitat attributes measured at the given scale. Clumped distribution near source-habitats at the very large spatial scales suggests limited dispersal for mycophagous species. However, strong colinearity between attributes related to distance to potential source habitats and to the burned habitat makes difficult to disentangle which of these attributes were important. Moreover, abundance at very large and/or large scales increased with distance to specific source-habitats for many species which make dubious any negative effect of dispersal limitation at the scales encompassed within the present study. Predators and xylophagous species were attracted to severely burned forests at the very large and large spatial scales whereas mycophagous species were more common in lightly burned landscape at the very large scale. Though spatially correlated patterns were significant for most species, environmental control of plot-level attributes were also very important, especially for predaceous and xylophagous taxa. Hence, although the initial dispersal pattern may be influenced by large scale habitat characteristics, this suggests that final habitat selection of saproxylic beetles is done by using fine-grained habitat attributes.

2.3 Introduction

Ecological systems may exhibit a hierarchy of spatial organisation levels (Allen and Starr 1982, Kotliar and Wiens 1990, Wiens 1989). This hierarchy may result from various factors that rely on species or environmental determinants (Lichstein et al. 2002). A direct effect of these factors is the spatial structuring of species distribution (Peres-Neto and Legendre 2010). Among others, climate, past events (Rettie and Messier 2000), species dispersal ability (Turchin and Thoeny 1993, Franklin et al. 2000) and grain size perception of the environment (Chust et al. 2003) are well known determinants that may cause spatial structures in species distribution. These factors may act simultaneously across a range of spatial scales (Allen and Starr 1982) that blur the response of a community to factors operating at a single scale (Cushman and McGarigal 2002).

The environmental variables influencing species abundance are often spatially structured at a number of scales, a phenomenon known as spatial dependency (Legendre et al. 1993, Borcard and Legendre 1994, Jones et al. 2008) therefore resulting in patchy species distributions in the landscape (Addicott et al. 1987, Cushman and McGarigal 2002). On the other side, spatial patterns may arise from various species-specific characteristics such as dispersal abilities, perception of the environment as well as population dynamics (Borcard and Legendre 1994). Species with limited dispersal abilities might not be able to colonize every remote patch of suitable habitats in a given landscape. In general, most species will colonize nearby suitable habitats thus producing clumped spatial patterns, sometimes disregarding the spatial distribution of environmental variables (Bell 2001, Hubbell 2001). As a result, dispersal limitation is often viewed as one of the most important ecological process that causes spatial autocorrelation (Bjørnstad et al. 1999, Trenham et al. 2001) when compared to environmental factors.

In addition, species may respond to environmental variables at different spatial scales (Wiens and Milne 1989, Chust et al. 2003). The scale at which species respond may vary according to its trophic level (Holt 1996, but see Chust et al. 2004 and Holland et al. 2004). Species that are highly mobile should perceive their environment at a coarser scale (Suarez-Seone et al. 2002, Hirao et al. 2008) whereas those occurring in ephemeral habitats should respond to environmental characteristics at large spatial scales since they need to disperse farther to find their resources (Southwood 1977).

Complex spatial patterns that are displayed at multiple scales may be the result of various closely intermingled determinants (Borcard et al. 2004). As a result, dissecting the spatial structure of species abundance can help to assess which ecological processes may generate the observed spatial patterns (Addicott et al. 1987, Borcard et al. 2004). Even though plenty of studies have focused on the spatial structures of species or assemblages in a given ecological context, very few studies have assessed the spatial hierarchy of underlying patterns.

In boreal forests, fire generates spatially defined patches, sometimes of considerable size (>100 000 ha). For many early seral species, these new habitats may be considered as "opportunity-habitats" toward which individuals may converge from distant external sources (Saint-Germain et al. 2008, Boulanger et al. 2010). Among the newly generated substrates, burned trees, are widely used by numerous saproxylic species (i.e. "species that depend on dead or dying trees or other saproxylic species for at least a part of their life cycle" [Speight 1989]), especially beetles (Wikars 2002, Saint-Germain et al. 2004a, Boulanger and Sirois 2007). The post-fire colonization of burned trees by beetles starts readily after fire (Wikars 2002, Boulanger and Sirois 2007). This process involves dispersal from source-habitats and is thought to involve the selection of burned environment attributes displayed at various spatial scales. As a result, landscape, stand and substrate characteristics as well as species determinants likely produce complex spatial patterns in the species abundance. The colonization of the mosaic of variously suitable habitats in a burned landscape by saproxylic beetles represents a unique opportunity to decipher the spatial structure of underlying processes that drive species abundance.

During the summer of 2005, several lightning-ignited fires burned 232 914 ha of mostly mature black spruce (*Picea mariana* [Mill] B.S.P.) forests in the James Bay area, in northern Québec. In a previous analysis (Boulanger et al., 2010), we evaluated the importance of various source- and burned habitat attributes in order to explain the local abundance of saproxylic species. The present analysis focused on the spatial patterns of colonizing saproxylic species immediately after fire. In particular, we wanted to identify at which scales specific saproxylic taxa belonging to contrasting functional groups were spatially structured and which processes could generate these patterns.

2.4 Methods

2.4.1 Study Area

The study area is located in the northern boreal forest of James Bay, Canada (Chap. 1, figure 1.1) in the lichen woodland forest region (Rowe and Scotter 1973). The climate is low-subarctic with a mean annual air temperature of –3.6°C while January and July average –25 and 13°C respectively. Annual precipitation averages 637 mm, 40 % of which falls as snow (Environment Canada 1993). Even-aged black spruce (*Picea mariana* B.S.P. [Mill.]) and jack pine (*Pinus banksiana* Lamb.) forests occupy every suitable sites except rocky outcrops. Uneven-aged stands dominated by black spruce are found on paludified sites on the lowlands, intermingled with extensive bogs and fens. Wildfire is the most important natural disturbance in this area with an average recurrence cycle of approximately 100 years (Parisien and

Sirois 2003). There is no fire control in this region except in the immediate vicinity of municipalities and hydroelectric facilities.

2.4.2 Beetle sampling and characterisation of the study plots

Sixty-six plots of 0.04 ha were established within a 76 483 ha (52°00 N, 78°00 W) patch that burned between May 29th and June 9th 2005 (Chap. 1, figure 1.1). Sampling was conducted in two defined areas (hereafter referred to as northern and southern areas) within the burned patch considering logistic constrains. Plots were systematically located by pairs every 500 m along the two major roads crossing the burned area. In each plot, beetles were sampled using one trunk-window trap made of a 10 x 30 cm Lexan^{TM} translucent plate. The trap was attached perpendicularly at breast height (1.3 m) on the trunk of a burned black spruce located at the center of each study-plot. Traps were fixed within seven days after the onset of fire and were operated from June 5th to August 3rd 2005. Plots were georeferenced and included in a geographical information system.

Diameter and abundance of burned trees >10cm of diameter at stump height (DSH) was recorded in the plot. Same measurements were taken on smaller stems (2-10 cm of DSH) in a 0.01 ha plot centered on the TWT (Appendix B.1). Fire severity on all stems ($Fire_{tree}$) that were alive before fire (>2 cm of DSH) was assessed as the portion of charred bark on their trunk (0: unburned; 1: burned but still with green foliage; 2: dead, <33% charred; 3: dead, 34-66 % charred; 4: dead, >67 % charred). A plot-scale fire severity index ($Fire_{site}$, 0 to 4) was computed for each plot as follows:

$$(2)\quad Fire_{site} = (\Sigma\,(Fire_{tree} * Bas\_Area_{tree}))/Bas\_Area_{site}$$

with Bas_Area_{tree} being the basal area of the tree and Bas_Area_{site} the total basal area in the plot. The volume of logs > 5cm at the largest end and the total basal area of snags of >5cm of DSH that were present before the fire were evaluated in the central

100 m^2 plot and in four additional 100 m^2 plots located 50 m apart from the trap. The diameter at both ends and the length of logs were measured. Log volume was estimated as a cone or a truncated cone if the main axis was broken. The decomposition stage was determined according to the five decay classes proposed by Hayden et al (1995) and only for unburned CWD because it was difficult to determine decay classes of highly charred logs and snags.

Fire severity was also estimated at the landscape scale from Landsat 5 TM satellite images taken after fire, in July 2005. According to the Normalized Burn Ratio (Epting et al 2005), each pixel of coniferous stands (burned or unburned) was classified as either unburned, lightly, moderately, or severely burned (see Chapter 1 for more details). Large (>10ha) unburned coniferous stands were delineated using these data.

Beetles were sorted and identification was completed at the species level with the exception of some difficult taxa (e.g. Cryptophagidae, Lathridiidae, Aleocharinae) that were identified at higher taxonomic levels. Trophic guild (e.g. xylophage, mycophage, predator, saprophage, other) of each coleopteran species was attributed according to the available literature and expert advices. Species clearly not associated with dead wood (e.g. Silphidae, some Elateridae, Scarabeidae) were discarded from the analyses.

2.4.3 Statistical analyses

We restricted our analyses to common (>150 individuals) saproxylic taxa. These included four xylophages, six mycophages and three predators (Appendix B2) making up 93.7 % of total saproxylic individuals collected in the present study. Our analyses were carried out in four steps. 1) First, we determine at which scale(s) the saproxylic taxa were spatially correlated. Then, 2) we assessed the importance of three sets of environmental variables (i. plot-level, ii. coarser-scales environmental variables of the burned patch and iii. specific external source habitats) that may explain the spatial patterns identified in (1). Moreover 3), we evaluated the proportion of the spatial pattern identified in (1) that was not explained by these three sets of environmental variables. Finally (4), we assessed the proportion of the species abundance that relied on environmental variables that were not spatially correlated.

The Principal Coordinates of Neighboring Matrices approach (PCNM, Borcard and Legendre 2002) was used to estimate the importance of spatial patterns (see Appendix B3 for details). PCNM variables were produced for the two areas (northern and southern) separately. Among the 45 PCNM variables produced, 23 were retained since others were not spatially correlated according to the Moran's Index. Final PCNM variables were classified as either large- (1983 to 3305 m, mean=2644m), medium- (1322 m) or small-scale (661 m) (Appendix B3).

Step 1) For common saproxylic taxa, significant XY coordinates were retained by forward selection in regression analyses. Residuals from these analyses were computed and used in regression analyses to select significant PCNM variables by forward selection. As PCNM variables are completely orthogonal, we estimated the proportion of the spatial variation in species abundance residuals that was explained by significant PCNM variables at the corresponding spatial scale.

Step 2) Three different sets of environmental variables were tested in order to evaluate their role in the spatial pattern of saproxylic species (Appendix B4). The first set (P) included variables associated with the plot-level attributes of burned stands as these were likely to be spatially structured themselves (Appendix B4). Habitat selection may be done at a larger-scale (e.g. selection of severely burned landscape), disregarding spatial patterns identified from the first set. Hence, the second set of environmental variables (B) included the amounts of coniferous forests burned at various severities (light, moderate and severe) that were measured in buffers of radii corresponding to each spatial scale investigated (650, 1300 and 2650 m, Appendix B4). Finally, we considered a set of variables (SH) associated with peripheral patches considered as external source habitats (Appendix B4) to evaluate the importance of species dispersal from these habitats in the observed spatial patterns. These habitats include dead wood from where saproxylic beetles could emigrate from and then converge toward the burned forests. Different variables associated with unburned stands and recently burned stands in the vicinity of the 2005 burn were included in this set.

In each set, we identified variables that were best related to the spatial patterns recognized previously in step 1. Submodels were built using linear combinations of the significant spatial variables pertaining to a given scale (Brind'Amour et al. 2005). Submodels were computed by adding the value of significant spatial variables together, using their standardized regression coefficients as weights (Borcard et al. 2002). We then ran forward stepwise multiple regression analyses to evaluate which environmental variables were best correlated with each submodel. As the 2002 fire patches were located outside the 2005 burn, minimum distance to one of these recent burns was only tested in spatial trend submodels. Prior to analyses, variables were standardized to be of equal mean (=0) and variance (=1). Forward selection was repeated separately for environmental variables associated with each of the three sets and at every significant spatial scale identified from PCNM variables. Variables measured in buffers (burned or unburned forests) were only included in models of the appropriate scale determined by PCNM variables (Appendix B1) whereas all buffer variables were tested for trend submodels. The importance of each set of variables in the given spatial pattern was evaluated by variation partitioning (Borcard et al. 1992) (Appendix B5) in order to take into account any confounding effects due to collinear variables belonging to different sets. Positive or negative effect of environmental variables retained at each spatial scale was investigated. This was conducted by using species submodels values which were interpreted in the light of the standardized coefficients of significant environmental variables that were best modelled by spatial variables.

Steps 3 and 4) Spatial patterns may arise from e.g. intra- or inter-specific competition, dispersal from unknown sources, past site history or neutral dynamics (Borcard and Legendre 1994, Cottenie 2005, Jones et al. 2008). On the other hand, environmental variables can generate undetectable spatial patterns, especially if i) environmental control proceed from very small grained variables, at the plot-scale, and ii) if these environmental attributes are not spatially structured themselves. These two proportions were estimated using variation partitioning (Appendix B5). We first identified the environmental variables in the three different sets that significantly explained the abundance of each saproxylic taxa by means of forward selection in respective regression analyses. Variation partitioning was then performed between significant environmental and spatial variables identified previously. Only independent effects of these two types of variables were considered.

PCNM were produced using the program *SpaceMaker2* (Borcard and Legendre 2004). Abundance of each taxa was log (x+1) transformed prior to regression analyses to reduce overdispersion. For every variation partitioning analyses, significance of testable partitions was evaluated by 9999 Monte Carlo permutations. Adjusted-R^2 ($R^2_{Y|Xadj}$) was used to measure the strength of these proportions (Peres-Neto et al. 2006). Partitioning analyses were performed using the *vartpart* function in the *vegan* package (v1.11-5) and the *anova* function in the *stats* package in R 2.8.0 (R Development Core Team 2008). Forward selection of significant spatial and environmental variables was performed using the *packfor* (v.0.0-7) (Dray et al. 2007) package in R v2.8.0. Significant variables were retained after 9999 Monte Carlo permutations. The latter package was also used for forward selection of environmental variables in spatial submodels.

2.5 Results

A total of 14 746 saproxylic beetles belonging to at least 139 species were collected throughout the study. Predators (55 spp.) were the most diversified feeding guild followed by xylophagous (41 spp.) and mycophagous (30 spp.) taxa. Extensive results on saproxylic diversity can be found in Chapter 1.

2.5.1 Objective 1: Spatialization of the colonization

The variation in taxa abundance explained ($R^2_{Y|Xadj}$) by spatial variables for the three common predator taxa was always >.20 as for all Lathridiidae (figure 2.1). Indeed, *C. dentigera* showed the highest variance explained by spatial variables ($R^2_{Y|Xadj}$=.488). At the opposite, three out of four xylophagous taxa showed rather low spatial structure ($R^2_{Y|Xadj} < .15$) (figure 2.1). Spatial patterns noticed for most saproxylic taxa were predominantly explained by a linear or planar spatial trend and by large and medium scale PCNM variables (figure 2.2). Spatial patterns explained by XY coordinates were significant for 11 out of 13 taxa while all predators and three mycophagous taxa showed significant medium scale patterns. Large spatial scale patterns were also important for three mycophagous taxa (figure 2.2). Small scale patterns were significant ($P<.05$) for two xylophagous (*M. scutellatus* and *A. foveicolis*) and two mycophagous taxa but remained low ($R^2_{Y|Xadj} < .07$) except for *C. dentigera* ($R^2_{Y|Xadj} = .156$).

2.5.2 Objective 2: Variation partitioning of spatial patterns

a) Linear and planar trends. Six taxa, including all predaceous species, showed a significant west-east linear spatial trend while three mycophagous taxa and *Monochamus scutellatus* were significantly correlated with the south-north linear trend (figure 2.3, Table 2.1). Only *C. dentigera* abundance was best explained by a planar spatial trend. Most of the spatial variation resulting from these trends may be explained by collinear effects of buffer and source habitats although independent effects of both sets of variables were significant in all cases (figure 2.3). Buffer independent effects were particularly important ($R^2_{Y|Xadj} = .255$, $P<.001$) to explain the spatial trend of *C. dentigera* which was strongly linked with the amount of moderately burned patches in the 2650 m radii scale. All spatial trends were highly correlated with the distance to the 2002 fire patches and the abundance of severely burned forest measured in a 2650 m radius (Table 2.1). Values of both of these variables increased from west to east and from south to north. Abundance of all xylophagous and predaceous species were highest in plots located farther from the 2002 fire patches and in severely burned areas whereas it was the opposite for all mycophagous taxa except *Corticaria* sp.2 (Table 2.1). Along the south to north trend, the abundance of *M. scutellatus* increased concurrently with the mean diameter of burned trees as opposed to mycophagous taxa (Table 2.1).

b) Large scale patterns. Significant large scale patterns may mostly be explained by collinear source habitat and buffer variables except for *Clypastrea fusca* for which it was only explained by source habitats characteristics (Figure 2.3). Independent effects of all three sets of variables were significant although independent effects of plot attributes were negligible ($R^2_{Y|Xadj} <.05$). Large scale abundance of *C. fusca* was inversely related to the amount of unburned forests in a 2650 m radius (Table 2.1). All other taxa showed clumped large scale patterns associated to increasing distance to unburned patches of >10 ha or avoidance of areas with lightly burned forests (Table 2.1).

c) Medium scale patterns. Patterns at this scale were quite variable among saproxylic taxa (Figure 2.3, Table 2.1). Abundance of *Sericoda obsoleta* and *Sphaeriestes virescens* decreased with either the total basal area or the number of burned stems between 2 and 5 cm of DHS. *S. virescens* also avoided plots burned at low severity (Table 2.1). Mycophagous taxa showed medium scales patterns resulting mostly from independent effects of potential source habitat and burned habitat buffer variables (figure 2.3). *C. dentigera* and *Caenoscelis* sp were less abundant in medium scaled areas with high amount of unburned forests and, to a lower extent, with high amount of moderately burned forests (Table 2.1). The abundance of *Caenoscelis* sp. decreased as distance to >10 ha unburned patches and fire edges increased. Distance to fire edge had similar effects for *C. fusca*. At the opposite, increasing distance to fire edges had a positive effect for *H. congener* and *T. u. nubilus,* although variation explained by source habitats at this scale for the latter species was relatively low ($R^2_{Y|Xadj} < .05$, figure 2.3). Indeed, variation explained at the medium scale for *C. fusca, H. congener* and *T. u. nubilus* was rather low ($R^2_{Y|Xadj} < .065$).

d) Small scale patterns. Small scale patterns were poorly explained by environmental variables (figure 2.3). No environmental variable was significantly related to these patterns for both *Corticaria* species. Patterns at this scale for xylophagous species *A. foveicollis* and *M. scutellatus* were weakly ($R^2_{Y|Xadj} < .065$, figure 2.3d) and negatively correlated with local fire severity and mean diameter of burned trees, respectively (Table 2.1).

2.5.3 Objective 3: Unexplained spatial patterns

Independent effect of spatial variables, i.e. spatial patterns unexplained by variables included in models, were very low for studied saproxylic taxa (Figure 2.4). Such spatial patterns were significant for *Caenoscelis* sp. *C. dentigera, M. scutellatus* and *Atomaria* sp., although unexplained variation for the latter two species was low ($R^2_{Y|Xadj} < .057$).

2.5.4 Objective 4: Independent effects of environmental attributes vs spatial patterns

A great proportion of variation was attributed to effects of environmental variables that were independent of spatial patterns for most common taxa (figure 2.4). This proportion was particularly important for predaceous and xylophagous taxa. The variation of most common mycophagous taxa was spatially structured since independent effects of environmental variables were only significant for *C. constrictus*.

2.6 Discussion

This study is the first to document the spatial structure of saproxylic beetle abundance after fire. We identified major spatial structures at scales >~650m with patterns occurring at most spatial scales investigated. The great majority of species, disregarding their functional group, were mainly spatially correlated at the very large scale, mostly according to a south-north gradient. Spatial structures at finer scales were consistent among functional groups as all showed significant spatial patterns at both the medium and fine scales. Yet, effects of plot-scale environmental variables, i.e. those that were not spatially structured, should not be neglected for most saproxylic taxa. This suggests that the post-fire colonization of saproxylic beetles is a process mostly driven by factors operating at great spatial scales although very fine scale attributes should be considered.

2.6.1 Effect of dispersal from potential source habitats

Even though partitioning analyses gave high importance to the predictors associated with these potential sources, it rather appeared that negative effect of increasing distance from these potential sources was noticed only for few species. Indeed, increasing distance from the 2002 burned patches negatively affected the abundance of four out of six mycophagous taxa along the geographic trend. Potential dispersal from unburned forests did not affect the spatial pattern of most saproxylic taxa. It has been suggested that the forest matrix may act as an important source of recruitment for post-fire saproxylic species (Saint-Germain et al. 2008). However, since the studied area is characterized by a rather short fire cycle that produces a patchy pattern of recently burned areas within the forest matrix (Parisien and Sirois 2003), recently burned areas are suspected to significantly contribute as source habitats for newly burned habitats (Boulanger et al. 2010). Indeed, spatial patterns observed for mycophagous species may result from their lower dispersal capacities

(Ranius and Hedin 2001, Jonsson 2002) compared with predaceous and xylophagous taxa.

If one assumes that unburned forests and recent burns are important sources of individuals for the burned patches, the absence of negative effect of distance to potential source habitats for the majority of species should be the result of their great abilities to disperse and their capacities to localize the focal habitat. Indeed, species abundance should decrease with distance from source habitats (Turchin and Thoeny 1993, Franklin et al. 2000), depending on species' dispersal ability. The absence of such patterns, especially for predaceous and xylophagous species, suggests that the spatial extent of the current study was not large enough to capture spatial patterns driven by dispersal limitation from these specific source habitats. It is generally assumed that early colonizers have very high dispersal capacities in order to reach distant and transient resources. Many saproxylic species evolved remarkable dispersal and habitat detection capabilities to head towards burned forests (Frost 1984, Schmitz et al. 2002, Allison et al. 2004). Mark-recapture studies reported travel distances of > 2000 m for bark beetles (Turchin and Thoeny 1993, Franklin et al. 2000) whereas experimental studies revealed that some of these species performed flights up to several tens of kilometres (Atkins 1961, Jactel and Gaillard 1991) although such information is lacking for most species. In the lack of further knowledge on dispersal capacities for most saproxylic species, one may hypothesize that they are able to disperse over similar ranges.

However, one must be cautious when interpreting dispersal from potential source habitats. Very large scale patterns (> 2650 m) resulting from isolation from large (>10 ha) unburned forests have not been recorded since these habitats were always located at shorter distances (maximum = 2067 m). Furthermore, unburned forests or recently burned patches are likely to be a subset of all source habitats that may provide individuals to the newly burned patches. Dispersal of surviving individuals from unknown sources located in the vicinity of the sampling sites (e.g. lightly burned woody debris or other dead wood enclosed within the burn) cannot be excluded at this point since epigeous (Ahlgren 1974, Paquin and Coderre 1997, Wikars and Schimell 2001) and saproxylic (Ulyshen et al. 2010) arthropods may survive to low severity burns. Such dispersal from unknown sources may explain the higher proportion of the spatial variation that was not explained by attributes included in models for few mycophagous species. Nonetheless, this situation is rather unlikely for other species, especially xylophagous, as the amount of local and suitable CWD in this area was not shown to positively influence the studied species (Boulanger et al. 2010).

2.6.2 Effect of multi-scale burned habitat characteristics

A great portion of the spatial pattern, especially at the largest scales, was explained by burned habitat characteristics. However, there is strong collinearity between source-habitat and buffer variables at the very large and large scales. In such context, it may be difficult to disentangle the importance of source and burned habitat variables. Lightly burned habitats were more likely to be close to unburned forests whereas habitats located farthest from the 2002 fires were also the most severely burned. Indeed, is the very large scale abundance of mycophagous species mostly driven by i) dispersal limitations from the 2002 fires , ii) or because lightly burned habitats were more common close to these burns iii) or because of a mix of both ? Even though it may be difficult to conclude which process was more important at this scale for mycophagous species, many relationships related to source habitat attributes identified for other species or at other spatial scales were biologically dubious. For example, the very large, large and/or medium scales abundance of many species, including most xylophagous and predaceous species, actually increased along with distance to the unburned matrix or with distance to the 2002 fires which opposed to the concept of dispersal limitations. Consequently, disregarding these relations puts high importance on burned habitat attributes to shape the spatial pattern of early colonizers.

Two alternative views can be invoked to explain how the burned habitat attributes caused the spatial patterns noticed in this study. The first holds that the spatial pattern is caused by insect's perception of its environment at a coarser grain-size (Roland and Taylor 1997, Chust et al. 2003, 2004). Alternatively, insect abundance inside the burned patch may rely on plot-scale burned habitat characteristics that are themselves spatially structured at the respective scales (Borcard et al. 1992). In this study, buffer variables explained much more variation of the spatial patterns at most spatial scales than spatially structured burned habitat attributes measured at the plot scale. Environmental variables at large scales are likely to be important as species that are highly mobile should perceive their environment at a coarser scale (Wiens 1992, Suarez-Seone and Baudry 2002, Hirao et al. 2008). Moreover, saproxylic beetles may be influenced by habitat attributes measured at scale larger than the plot level (e.g. Økland et al. 1996, Holland et al. 2004). In this case, buffer variables, mostly at greater scales, shaped the spatial pattern of most saproxylic taxa.

Nonetheless, local, plot-level attributes strongly influenced the spatial patterns, especially for predaceous and xylophagous taxa, as suggested by their important independent effects. In a concurrent study, we showed that local plot-level fire severity was the most important variable to predict the abundance of saproxylic beetles (Boulanger et al. 2010). Hence, although the initial dispersal pattern may be influenced by large scale habitat characteristics, this indicates that saproxylic species have the ability to resolve fine-grained habitats.

Such hierarchical selection of burned habitat attributes may be the result of a multi-scale dynamic caused by the emigration of individuals from distant source habitats. According to this hypothesis, insects would be first attracted from external source habitat towards more attractive landscapes. Indeed, many wood-feeders were shown to orient themselves to the suitable substrates at a relatively large spatial scale (Saint-Germain et al. 2007). As most species are suspected to use volatiles emitted by dead trees in order to locate the focal habitat, high concentration of post-fire volatiles should be more attractive (Kelsey and Joseph 1999, Pureswaran et al.

2004). One may argue that severely burned areas, may release larger amounts of these attractants (Kelsey and Joseph 2003) than areas intermingled with lightly burned and unburned forests. This should explain why several xylophagous and predaceous taxa that are known to use specific cues to locate potential hosts (Allison et al. 2004) were attracted to severely burned stands at the very large scales. Likewise, many species, disregarding the functional group, were more common at the large and/or very large spatial scales as the distance to the unburned matrix increased or as the amount of lightly burned habitats decreased. Fine scale high quality habitats within the burned patch can be subsequently selected as dispersing individuals are heading towards the burned substrates for oviposition or feeding purposes (Saint-Germain et al. 2006).

2.7 Conclusions

Deciphering the spatial structures of saproxylic beetles provided valuable insights to understand the underlying processes which drive the post-fire colonization. Indeed, it suggested that the post-fire colonization of burned trees is markedly different from the colonization of CWD in unburned forests (Økland et al. 1996, Saint-Germain et al. 2007) even though both involve determinants that occur at multiple spatial scales (this study; Holland et al. 2004). The post-fire colonization implies processes that take place at much larger spatial scales, primarily considering the necessary long-range dispersal of species in this particular context. Consequently, further studies on the colonization dynamic of saproxylic beetles after fire should include very large spatial scales, e.g. several tens of km, in order to appreciate the whole process.

Table 2.1. Variables from the different sets tested that were significantly correlated with the spatial submodels of saproxylic taxa and their respective standardized coefficients. Results are shown separately for every spatial scale tested in the present study. The sign of coefficients was adapted to reflect changes in species abundance at the given scale. See appendix 1 for variable name and description. *: P<0.05; **: P<0.01; ***: P<0.001 after 9999 Monte Carlo permutations.

Sets	**Variables**	**Taxa**										
A) Linear and/or planar trends												
		A. p. proteus	*A. foveicollis*	*Corticaria* sp.2	*S. obsoleta*	*S. virescens*	*T. u. nubilus*	*Atomaria* sp.	*C. constrictus*	*C. fusca*	*M. s. scutellatus*	*C. dentigera*
Plot-level	Fire1			-.344**					.258*		-.258*	
	Dmean			.275*					-.482***		.482***	-.455***
Buffers	BurnResLiS			-.204					.233***		-	

Sets	Variables	Taxa			
	BurnResLiM	-.473**		.233***	
	BurnResMoM	.432***	-.146***		
	BurnResSevM	-.463**		.146***	
	BurnResLiL	-.294*		-	
	BurnResMoL		.355***	.355***	-
	BurnResSevL	.859***	-.770***		.595***
					-
					.688***
				.770***	.727***
Source habitats	Dist_2002	.913***	-.930***	.930***	-
	UnbL	-.248***	-.207***	.207***	.564***
					-
					.580***

B) Large scale

Sets	Variables	Taxa			
		C. constrictus	*Corticaria* sp.2	*Cl. fusca*	*H. congener*
Plot-level	Nd25	.354**	.297*		.297*
	Fire1		-.242*		-.242*
Buffers	BurnResLiL	-.739***	-.837**		-.837**
	BurnResSevL	-.209*	-.223**		-.223**
Source habitats	Dist_10ha	.665***	.795***		.795***
	UnbL	-.193*		-	
	Dist_edge			.543***	
				-.366**	

C) Medium scale

Sets	Variables	Taxa						
		H. congener	*Caenoscelis* sp.	*C. fusca*	*C. dentigera*	*S. obsoleta*	*S. virescens*	*T. u. nubilus*
Plot-level	Bas_area		.276*				-	
	Fire1						.343**	
	Nd25		-.265*		-		-	
	Nd510				.405***	- .287*	.310**	
Buffers	BurnResMoM	-.323**	-.346**		- .467***			
Source habitats	UnbM		-.764***		-.621**			
	Dist_10ha		-.510**		-.379			
	Dist_edge	.521***	-.258*	-.253*				.253*

D) Small scale

Sets	**Variables**	**Taxa**			
		A. foveicolis	*M. s. scutellatus*	*C. dentigera*	*Corticaria* sp.2
Plot-level	Fire1	-.249*		None	
	Dmean		-.252*		
Buffers		None	None	None	None
Source habitats		None	None	None	None

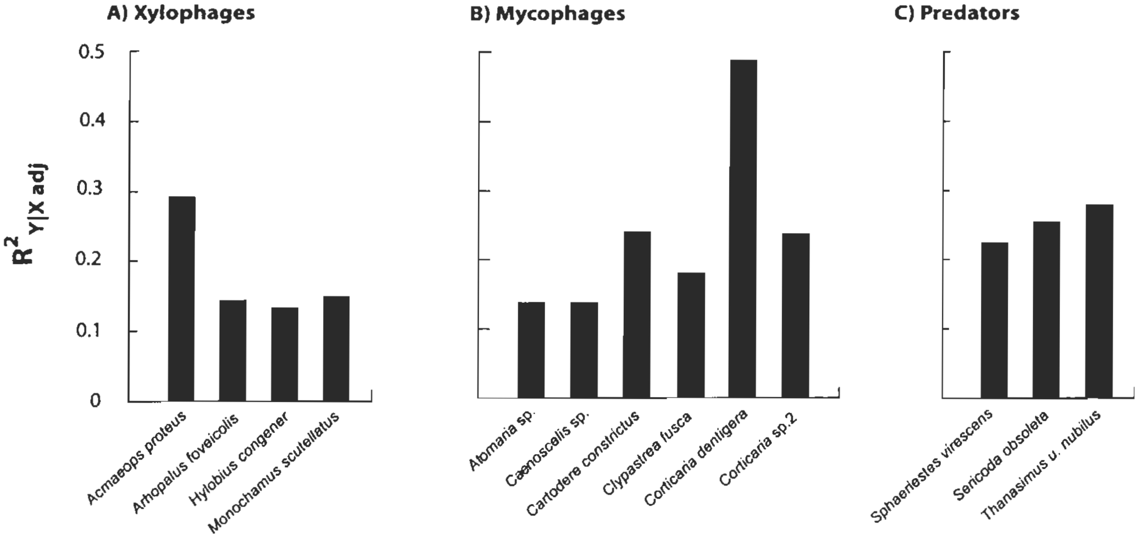

Figure 2.1. Variation ($R^2_{Y|Xadj}$) of species distribution explained by significant spatial variables.

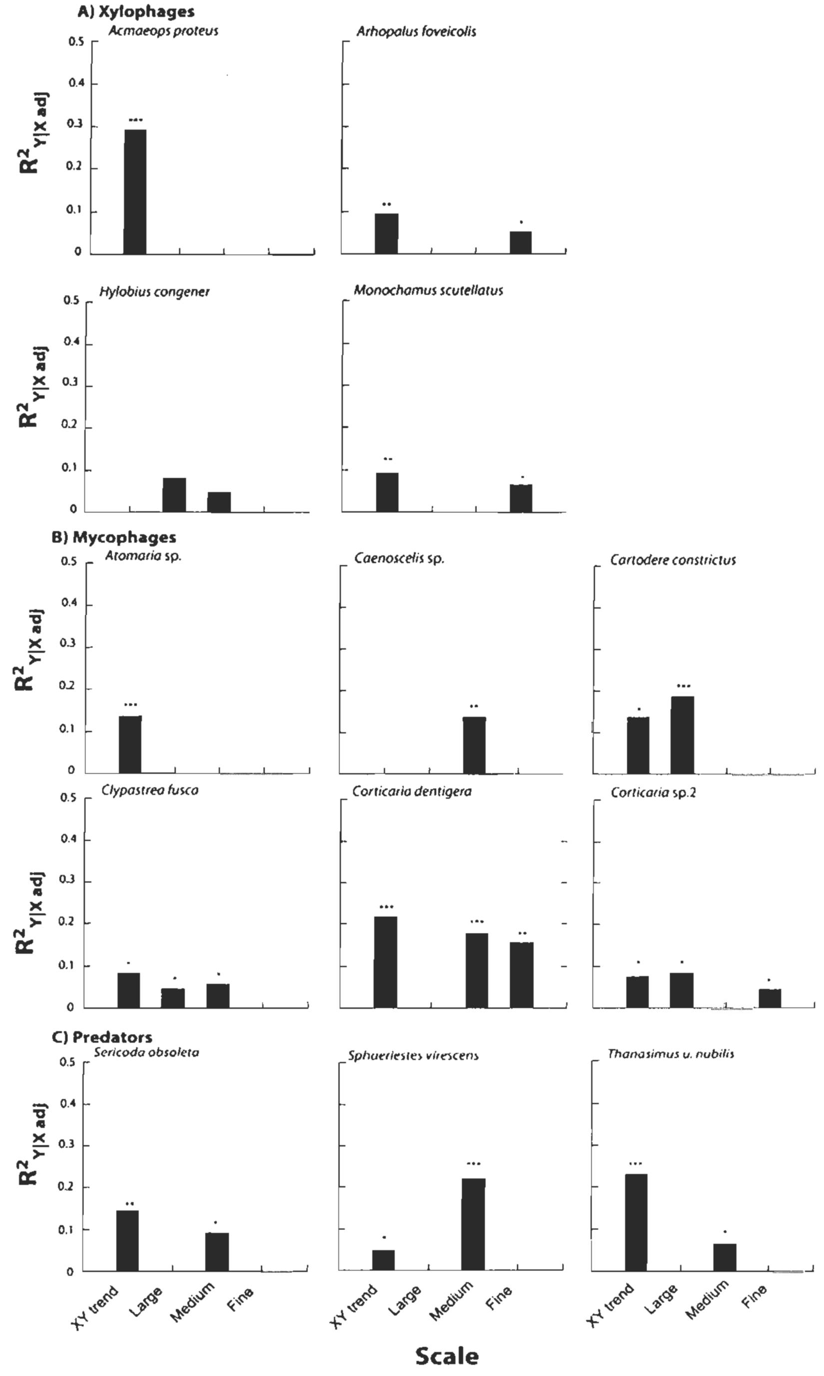

Figure 2.2. Total spatially autocorrelated variation ($R^2_{Y|Xadj}$) decomposed according to each spatial scale investigated for either common saproxylic taxa or trophic guilds. *: $P<0.05$; **: $P<0.01$; ***: $P=0.001$ after 999 Monte Carlo permutations.

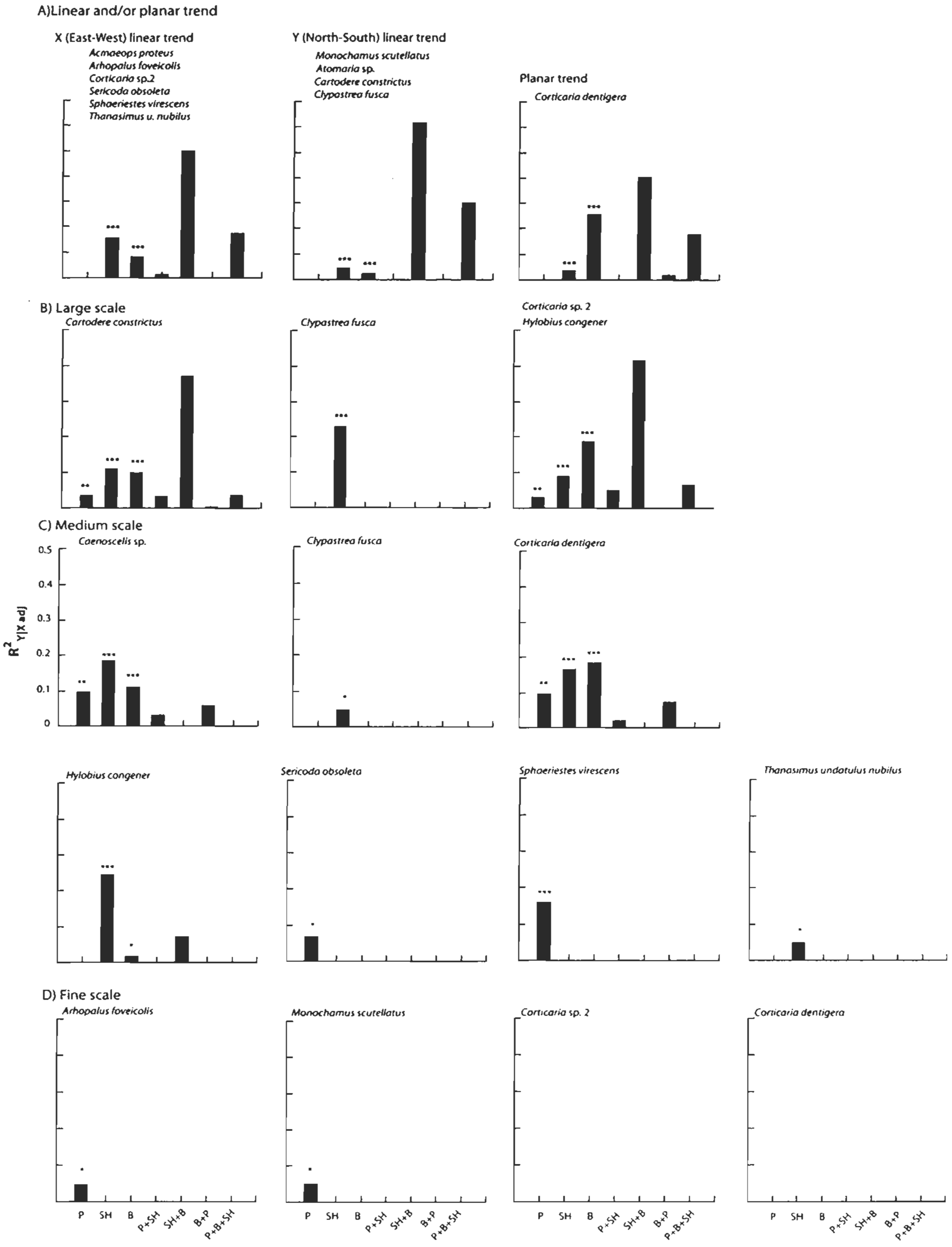
A)Linear and/or planar trend
X (East-West) linear trend
Acmaeops proteus
Arhopalus foveicolis
Corticaria sp.2
Sericoda obsoleta
Sphaeriestes virescens
Thanasimus u. nubilus
Y (North-South) linear trend
Monochamus scutellatus
Atomaria sp.
Cartodere constrictus
Clypastrea fusca
Planar trend
Corticaria dentigera
B) Large scale
Cartodere constrictus
Clypastrea fusca
Corticaria sp. 2
Hylobius congener
C) Medium scale
Caenoscelis sp.
Clypastrea fusca
Corticaria dentigera
0.5
0.4
0.3
0.2
0.1
0
$R^2_{Y|X\ adj}$
Hylobius congener
Sericoda obsoleta
Sphaeriestes virescens
Thanasimus undatulus nubilus
D) Fine scale
Arhopalus foveicolis
Monochamus scutellatus
Corticaria sp. 2
Corticaria dentigera
P
SH
B
P+SH
SH+B
B+P
P+B+SH

Figure 2.3 (previous page). Partition of the spatially structured variation ($R^2_{Y|Xadj}$) of common saproxylic taxa explained by spatial variables according to the three sets of predictors used in this study, i.e. from environmental variables measured in the plots (P), burned habitat attributes measured in either 650, 1300 or 2650m buffer radius (B) and dispersal from specific source habitats (SH) or a combination of two or all sets of variables. Results are shown for every spatial scale separately. *: $P<0.05$; **: $P<0.01$; ***: $P=0.001$ after 999 Monte Carlo permutations on testable partitions.

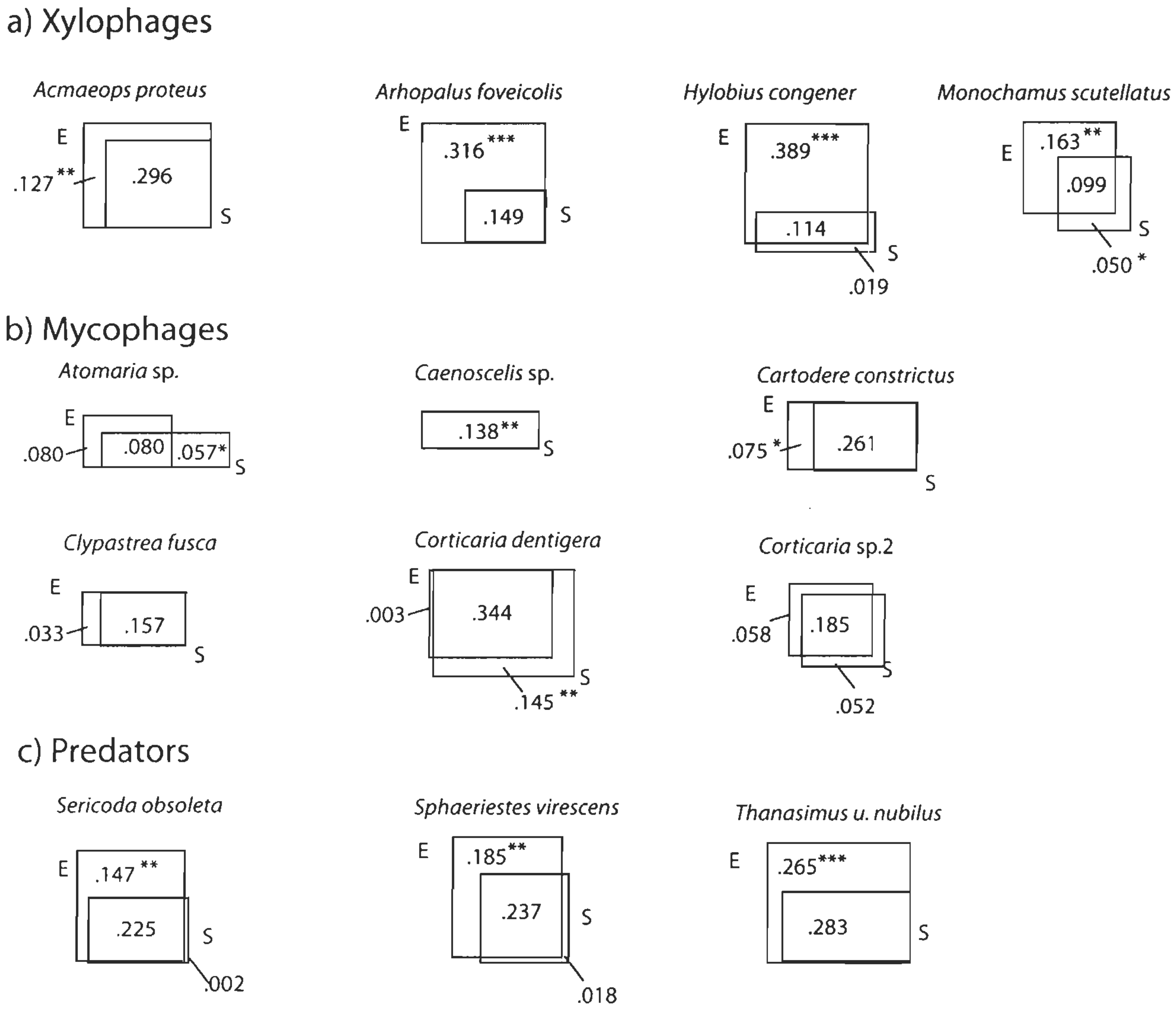

Figure 2.4. Partition of the variation ($R^2_{Y|Xadj}$) of species distribution between the two groups of environmental (E) and spatial (S) variables. Results are shown for each saproxylic functional groups. *: $P<0.05$; **: $P<0.01$; ***: $P=0.001$ after 999 Monte Carlo permutations on testable partitions.

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CHAPITRE 3

DISSIMILAR PATTERNS IN HABITAT SELECTION BY ADULT XYLOPHAGOUS BEETLES VS LARVAL COLONIZATION OF RECENT SNAGS AFTER FIRE IN BOREAL FOREST.

3.1 Résumé

Nous avons identifié les facteurs qui affectent la colonisation initiale des épinettes noires tuées par le feu pour cinq taxons xylophages (*Acmaeops proteus proteus* Kirby, *Acmaeops pratensis* Laicharting, *Monochamus scutellatus scutellatus* [Say], Scolytinae spp. and *Melanophila fulvoguttata* [Harris]) dans le nord de la taiga canadienne. De plus, nous avons évalué si l'abondance des adultes l'année même du feu était reliée à la colonisation larvaire subséquente. Les arbres peu brûlés et possédant une écorce épaisse étaient plus susceptibles d'être colonisés par la plupart des taxons. Ces caractéristiques sont reconnues pour affecter positivement la qualité nutritionnelle des tissus subcorticaux. La sévérité du feu à l'échelle du peuplement était aussi un important prédicteur de l'émergence des néonates alors que la distance aux habitats-sources, même pour ceux étant très éloignés, n'a pas eu d'impact négatif. À l'exception de *A. pratensis* et *M. fulvoguttata*, la colonisation effectuée par les adultes après feu n'était pas optimale puisque des différences marquées ont été remarquées entre les caractéristiques d'habitat sélectionnées par les adultes et celles résultant en une plus forte production de néonates. La plupart des adultes étaient plus abondants dans les peuplements ou les paysages sévèrement brûlés à l'opposé des néonates. La plus grande concentration de volatiles dans les milieux sévèrement brûlés pourrait avoir attiré davantage d'adultes en phase de dispersion malgré le fait que ces conditions ne soient pas optimales pour le développement larvaire. Ce résultat contre-intuitif pourrait résulter d'une pression évolutive ayant majoritairement poussé les espèces à détecter un substrat rare et ce, dans une matrice forestière non-brûlée. Nonobstant ce comportement non-optimal, les brulis, incluant les peuplements fortement brûlés, représentent une opportunité reproductive pour les espèces xylophages considérant la très grande quantité de substrat qu'ils contiennent comparativement à la matrice non-brûlée.

3.2 Abstract

We identified the factors that affect the early colonization of fire-killed black spruce tree by five xylophagous beetle taxa (*Acmaeops proteus proteus* Kirby, *Acmaeops pratensis* Laicharting, *Monochamus scutellatus scutellatus* [Say], Scolytinae spp. and *Melanophila fulvoguttata* [Harris]) in the northern Canadian lichen boreal forest. Furthermore, we evaluated if adult abundance the same year as the fire was related to the subsequent larval colonization of snags. At the tree-level, thick-barked and lightly burned trees positively influenced the occurrence of most taxa. These attributes were likely to affect the nutritional quality of the subcortical tissues. Fire severity at the stand level was also an important predictor of neonate emergence whereas distance to source habitats, even if remote, had no negative impact. With the exception of *A. pratensis* and *M. fulvoguttata*, the post-fire colonization by adults was not optimal as striking differences were noticed between habitat attributes that best predict effective larval colonization of snags and adult occurrence the same year as the fire. Adults of most species were more common in severely burned patches as opposed to emerging neonates. Higher volatile concentration in severely burned patches could have attracted more dispersing adults even if these conditions were not optimal for larval development. This counterintuitive result may be caused by an evolutionary pressure that pushed species to detect scarce substrates in a mostly unburned matrix. In this respect, burnt patches, including severely burned ones, still represent a reproductive opportunity for xylophagous beetles considering the high amount of suitable substrates they encompass compared to the unburned matrix.

3.3 Introduction

Wildfires constitute the most important natural disturbance in northern boreal forests of Canada (Rowe and Scotter 1973). One obvious consequence of stand-replacing fires in the boreal landscape is the production of huge amounts of woody detritus all at once (Boulanger and Sirois 2006). This dead wood is an habitat for a tremendous diversity of "saproxylic" insects (Saint-Germain et al. 2004a, Boulanger and Sirois 2007), i.e. species that 'depend for at least part of their life cycle upon dead or dying wood of moribund or dead trees, or upon wood-inhabiting fungi, or upon the presence of other saproxylic species' (Speight 1989). Among saproxylic species, several are truly xylophagous as they feed directly onto the subcortical and/or xylem tissues of dead trees (Haack and Slansky 1987). In northern boreal forests, most of these taxa belong to the Cerambycidae, Buprestidae and Curculionidae (mostly Scolytinae) families (Boulanger and Sirois 2007, Boulanger et al. submitted). Members of these families use the recently generated woody debris as feeding substrates during their larval development.

Colonization by insects occurs shortly after tree death with most species arriving during the year of the fire (Boulanger and Sirois 2007, Boulanger et al. submitted). The use of snags by saproxylic beetles is known to be affected by various tree-level characteristics. Thicker bark and phloem are known to increase larval survival (Peddle et al. 2002). Large diameter trees are proportionally more susceptible to be colonized than smaller trees (Saint-Germain et al. 2004b,c) whereas moisture content (Savely 1939, Saint-Germain et al. 2007a, Kelsey and Joseph 1999), age and tree vigor before death (Saint-Germain et al. 2004b,) may also influence larval colonization. In fire-killed trees, most species have been shown to be more abundant in lightly or moderately burned trees than in severely ones (Richmond and Lejeune 1945, Cerezke 1977, Saint-Germain et al. 2004b,c). Fire severity usually reduces the tree nutritional quality which in turn has a great impact on larval survival (Haack and Slansky 1987). Substrate requirements for xylophagous species colonizing windthrow or recently dead trees in unburned forests have been more thoroughly studied (see Siitonen 2001, Bouget 2004) than in a post-fire context. Host selection and suitability in a post-fire context are largely unknown for most xylophagous species (Saint-Germain et al. 2004b). As environmental conditions shortly after fire are markedly different from those occurring in unburned forests (Parmeter 1977), one may expect that fire-related attributes should greatly affect the colonization.

According to the optimal oviposition theory (= preference-performance hypothesis, Jaenike 1978), a species should select hosts that will enhance its lifetime fitness (Parker and Maynard Smith 1990) by maximizing larval performance (Thompson 1988,Scheirs and DeBruyn 2002). Even though local fire severity is known to largely affect the abundance of dispersing xylophagous adults the same year as the fire, other landscape-scale characteristics may also have an important role (Boulanger et al. submitted). Moreover, although xylophagous species are known as good disperser, very remote burned habitats may be less colonized than areas located near source habitats (unburned forests or other recent burns). Such relationships between variables affecting host selection by adults and those affecting neonate abundance in fire-killed trees have never been explored before.

During the summer of 2005, several lightning-ignited fires burned 232 914 ha of mostly mature black spruce (*Picea mariana* [Mill] B.S.P.) forests in the James Bay area. This offered a unique opportunity to study the post-fire colonization of burnt trees at multiple spatial scales by considering both adult abundance and/or activity during the year of fire and the subsequent larval colonization. The objectives of this study were two-folds. First, we aimed to identify the environmental factors that affect the colonization of fire-killed black spruce by xylophagous larvae. Effects were assessed at the tree-level but also at larger spatial scales by including habitat characteristics related to burned- and source habitat qualities that are known to affect adults (Savely 1939, Peddle et al. 2002, Saint-Germain et al. 2004a,b,c). Second, in order to test the optimality theory for xylophagous beetles after fire, we evaluated if larval colonization was effectively related to adult abundance and/or activity the same year as the fire. To do so, multi-scale habitat characteristics selected by dispersing adults the same year as the fire were compared to those affecting beetles in snags.

3.4 Material and methods

3.4.1 Study Area.

The study area is located in the northern boreal forest of Québec, Canada, in the lichen woodland ecosystem (Rowe and Scotter 1973) of the James Bay area (Chapter 1, figure 1.1). The climate is low-subarctic with a mean annual air temperature of –3.6 °C while January and July temperatures average –25 and 13°C respectively. Annual precipitation averages 637 mm, 40 % of which falls as snow (Environment Canada 1993). Even-aged black spruce (*Picea mariana* B.S.P. [Mill.]) and jack pine (*Pinus banksiana* Lamb.) forests occupy every non-edaphically limiting site. Uneven-aged stands dominated by black spruce are found on paludified sites on the lowlands, intermingled with extensive bogs and fens. Wildfire is the most important natural disturbance in this area and its average recurrence cycle is approximately of 100 years (Parisien and Sirois 2003). There is no fire control in this region except in the immediate vicinity of municipalities and hydroelectric facilities.

3.4.2 Sampling dispersing adults.

Sixty-six plots were selected within a 76 483 ha (52°00 N, 78°00 W) area that burned between May 29th and June 9th 2005 (Chapter 1, figure 1.1). Plots were systematically located by pairs every 500 m along the two major roads crossing the burned patch. Within seven days after the onset of the fire, one trunk-window trap (TWT) (Kaila 1993) was installed in each plot to sample adult xylophagous beetles. The trap was attached at breast height, perpendicularly along the trunk of a burned black spruce located at the center of each study-plot. A funnel was placed under the plate to collect the falling beetles in a jar filled with ethylene glycol as a killing and preserving agent.

Traps were operated from June 5th to August 3rd 2005. Plots were georeferenced using the Global Positioning System and were included in a geographical information system (GIS).

3.4.3 Collecting emerging beetles.

In order to characterize the effective colonization of burned trees by xylophagous larvae, one bole section was collected, in early June 2006, from each of three burned black spruces in 60 of the 66 study-plots (6 plots were dropped because of logistic constraints) established in 2005. Each bole section was 50 cm long and was collected 1-m above the ground on a burned black spruce of at least 10 cm of diameter at stump height (DSH). Bole sections were then placed in cloth bags and carried to the lab, where they were placed in rearing conditions in a field insectarium. Ends of each bole section were waxed to prevent excessive drying. Boles were then screwed vertically under a rack shelf and surrounded by a fine-mesh tissue. A funnel and a jar filled with a 40% ethanol solution with traces of household vinegar (5% acetic acid) was placed under each bole section to collect and preserve emerging adults or falling larvae. Bole sections were kept in rearing conditions from June 2006 to November 2007. Throughout this period, emerging xylophagous beetles were sorted periodically. Identification was completed to the species level except for difficult taxa (*Chrysobothris*, *Pityophtorus* spp.).

3.4.4 Environmental characterization.

Environmental attributes were recorded at the tree, plot and landscape scales. At the tree scale, fire severity was estimated as the proportion of charred bark on the main stem (Appendix C1). Bark thickness was measured to the nearest 1/100th mm on four equidistant points on each side of the bole section. One cross section of approximately 3 cm thick was collected at 1-m above the ground on every sampled tree. Cross sections were put in hermetically sealed bags in the field to prevent moisture loss and later placed in a freezer to stop further fungal or bacterial degradation prior to laboratory analyses. Remaining bark on cross sections was removed before sections were weighed to determine their green mass. Then, they were oven-dried at 70 °C in the laboratory until a constant mass was reached. Dry mass was determined from the last weighting. The moisture content ($g.g^{-1}$) was estimated from the mass loss after drying and was expressed as a proportion of dry mass. Cross sections were considered cylindrical and volume was estimated by approximating the mean diameter and thickness to the nearest 1 mm. Wood density ($g.cm^{-3}$) was expressed as dry mass over dry volume.

At the plot scale, environmental attributes related to fire severity, as well as burned tree DSH and abundance, were measured in each plot (Appendix C1, see also Boulanger et al. submitted for more details). Fire severity was also estimated at the landscape scale from Landsat 5 TM satellite images taken after fire, in July 2005. According to the Normalized Burn Ratio (Epting et al 2005), each pixel of coniferous stands (burned or unburned) was classified as either unburned, lightly, moderately, or severely burned. Areas of unburned, lightly, moderately and severely burned coniferous forest were estimated within a 250 m radius. We did not use larger radii in order to avoid buffer overlapping between plots and thus respect their spatial independence (Holland et al. 2004). Large (>10ha) unburned coniferous stands as well as the fire edges were delineated using these data. Distances to these habitats were measured as well as distance to two recent fire that occurred in 2002.

3.4.5 Data analyses

Statistical analyses were restricted to xylophagous taxa that occurred in at least ten bole sections. Following this criterion, five taxa were considered in the analyses including three cerambycids (*Acmaeops proteus proteus* [Kirby], *Acmaeops pratensis* [Laicharting] and *Monochamus scutellatus scutellatus* [Say]), one buprestid (*Melanophila fulvoguttata* [Harris]) and Scolytinae. This latter taxa was treated as a whole since single species were too uncommon or occurred in too few bole sections to be analyzed separately. *A. proteus proteus* and *A. pratensis* were collected as last-instar larvae whereas all other species were collected as emerging adults.

3.4.5.1 Effect of tree scale variables on neonates.

At the tree scale, we tested 18 biologically plausible models that included the characteristics of the burned trees (Appendix C2). We mostly focused on characteristics that may be attributed to the fire itself (fire severity, moisture content) but also to the tree (diameter, bark thickness, wood density). As the larval colonization may respond to intermediate fire severity and thus be nonlinear, some models included fire severity as a quadratic term. In order to consider that the quality of subcortical tissues might be less affected by fire severity in thick that in thin barked trees, we tested for an interaction between fire severity and bark thickness in several models. These models were tested on presence/absence data using binary logistic regressions for all taxa except for *A. proteus proteus* because this species was fairly abundant (n=384) and occurred in nearly 67% of the bole sections. Abundance data of this species was modelled using negative binomial regressions in order to consider overdispersion. The most parsimonious models for each species were selected according to the Akaike's Information Criterion corrected for small sample sizes (AIC_c). Multimodel inferences were used when the AIC_c weight of the top-ranking model was lower than 0.90 (Burnham and Anderson 2004). The effect of bark thickness was estimated by multimodel inference using models including this predictor but excluding its interaction with fire severity. Likewise, the linear effect of fire severity was tested by multimodel inference using models including this predictor but excluding its quadratic term and/or its interaction with bark thickness.

3.4.5.2 Comparison between plot and landscape variables affecting neonates and adults

Trunk-window traps are useful tools to study the effects of environmental variables on saproxylic coleopteran abundance/activity (Boulanger and Sirois 2007, Boulanger et al. submitted) but they cannot be used to assess the effect of tree-scale variables on the colonization of burned trees (Wikars et al. 2005, Saint-Germain et al. 2006). In order to compare neonate colonization with adult abundance/activity, we had to rely on the comparison of the effects of environmental variables measured at the same spatial scale, i.e. coarser than tree-level. Indeed, we tested 22 different models to evaluate the effects of environmental attributes at the plot and landscape scales (Appendix C2) for both neonates and adults. Obviously, neonate colonization patterns may rely on adult behaviour the same year as the fire and so models were built in order to account for such behaviour. Indeed, candidate models included attributes related to burned habitat quality variables and/or source habitat variables and were developed in order to include variables associated with one or several spatial scales. Burned habitat quality was assessed according to the size and abundance of burned trees at the plot scale and to fire severity at the plot and nearby (250 m) scales. Source habitats were considered to be habitats from which colonizing adults may immigrate during the summer in which the forest has burned (Saint-Germain et al. 2008, Boulanger et al. submitted). Predictors associated with these habitats were related to either unburned forest or the recently burned forests and thus encompassed many spatial scales (Appendix C1) as dispersal abilities of post-fire xylophagous adults are thought to be important (Schütz 1999, Boulanger et al. submitted).

To avoid pseudoreplication (Hurlbert 1984), data from rearing were pooled at the plot level. Binary logistic regressions were used to test the 22 different models on presence/absence of neonates per plot for all species except *A. proteus proteus* since this species occurred in 92 % of all plots (see also above). Bias-reduction method (Kosmidis 2007) was used to fit presence/absence data of *M. fulvoguttata* since quasi-separation situations occurred at least once when testing models. For *A. proteus proteus*, models were tested using linear regressions on mean number of fallen larvae per bole section at the plot level. Mean larval abundance of *A. proteus proteus* were log(x+1) transformed before analyses to reduce overdispersion. Best models were selected using the AIC_c criterion while multimodel inference was used when several models were competing for the first place (weight < .90). As in tree-scale models, the linear effect of fire severity at the plot scale ($Fire_{stn}$) was tested by multimodel inference using only the models including this predictor but excluding its quadratic term.

For adult data, negative binomial regressions were used for *A. proteus proteus* and *M. scutellatus scutellatus* whereas occurrence of the remaining and less common taxa was modelled using logistic regressions. Bias-reduction method was used to model the occurrence of *A. pratensis* adults as quasi-separation situations occurred for some models. Best model identification and multimodel inference were assessed as for rearing data.

3.4.5.3 Relation between adult and larval occurrence

In order to estimate if abundance or occurrence of adults during the summer in which the forest has burned is a good predictor of effective tree colonization, we modelled both of these predictors at the plot-level. For *A. proteus proteus*, abundance of adults in TWT in 2005 and mean abundance of larvae per bole section placed in rearing conditions were first standardized to the same mean and variance and then modelled by simple linear regression. For all other taxa, one-tailed Fisher's exact method was used to assess if the presence/absence of adults in 2005 was related to presence/absence of emerging neonates in rearing.

For all taxa except *A. proteus proteus*, plots where adults were collected in 2005 but where larvae were not recorded in rearing were classified as "false positive". Obviously, these events do not mean that there was no effective colonization of trees in a given plot since only a small fraction of the total volume of burned trees was sampled and that TWT do not collected every dispersing adult that may have reached the plot. Nevertheless, it provides a useful assessment of discrepancy in sampled plots, where adults were present without effective larval colonization. False positive events were then modelled by logistic regressions using the previous 22 models at the plot and landscape scales to estimate if they were linked with any environmental attributes. For *A. proteus proteus*, differences between standardized abundance of adults and mean larval abundance per bole were modelled by linear regressions. Multimodel inference was used as above to assess effects of these environmental attributes.

Analyses were performed using R 2.8.1 (R Development Core Team 2008). Negative binomial regressions were computed using the package *MASS* v7.2-45 (Venables and Ripley 2002) whereas the package *brglm* v0.5-4 (Kosmidis 2007) was used for bias-reduced logistic regressions.

3.5 Results

3.5.1 Abundance and diversity

A total of 1140 xylophagous beetles (adults and mature larvae) belonging to at least 15 taxa were recorded from bole sections. Among these, *A. proteus proteus* was the most abundant (n=384) and prevalent (present in 66.7 % of all bole sections and in 91.7% of the plots, Appendix C3). Scolytinae taxa were also abundant (Appendix C3), especially *O. caelatus* (n=364), *Ips* spp. (n=165) and *Crypturgus borealis* (n=137) but they were clumped in few bole sections (5.0%, 5.0% and 1.4% respectively).

3.5.2 Effect of tree scale variables on neonates

Fire severity and bark thickness appeared to be the most important variables to predict xylophagous beetle abundance or occurrence at the tree-level. These two predictors were included in all top-ranking models except for *A. pratensis* (Appendix C4). Along with these variables, tree diameter was also included in top-ranking models for *A. proteus proteus*, *M. fulvoguttata* and *M. scutellatus scutellatus*. Wood density and moisture content were also included in the best models of the last two species as well as for *A. pratensis*.

Occurrence or abundance was negatively related to tree-level fire severity for four out of the five taxa studied (Table 3.1). Bark beetles and *M. fulvoguttata* were completely absent from severely burned (Fire = 4) trees. Proportionally, burned trees that were still alive (fire severity = 1) at the time of sampling were more colonized by *A. proteus proteus* (75%), *M. fulvoguttata* (37.5%) and bark beetles (50%). Bark thickness had a strong positive effect on *A. proteus proteus*, *M. fulvoguttata* and Scolytinae spp. (Table

3.1). The effect of bark thickness differed depending of fire severity for *A. proteus proteus* ($P < 0.05$) and *M. scutellatus scutellatus* ($P < 0.01$). For both species, bark thickness had no effect on their occurrence or abundance at low fire severity (Fire ≤ 2) whereas it had a positive effect on severely burned trees (Fire >2) (Figure 3.1). Physical properties of xylem had a weak influence only on *M. scutellatus scutellatus* as its occurrence was positively ($P < 0.05$) related to moisture content (Table 3.1).

3.5.3 Comparison between plot and landscape variables affecting neonates and adults

3.5.3.1 Adult data.

Top-ranking models for dispersing adults of all taxa, except *M. fulvoguttata*, included predictors measured at the nearby and/or remote spatial scales in addition to local burned habitat quality variables even though the weights of these models were rather low (Appendix C6). Nevertheless, abundance of *A. proteus proteus* and *M. scutellatus scutellatus* adults were significantly related to variables measured at the remote and nearby spatial scale respectively. Dispersing adults of *A. proteus proteus* were more common as we get further from the 2002 burnt, i.e. in the more severely burned northern area (Table 3.2, figure 3.3a). Likewise, *M. scutellatus scutellatus* adults were significantly ($P<0.05$) more abundant as the amount of unburned forests in a 250m radius increased (Table 3.2). Adults of this species were also more common ($P<0.01$) as the basal area in burned stands increased. Fire severity at the local scale had a significant effect on adults of both *M. fulvoguttata* and *A. pratensis*. The latter species was more common in severely burned plots while *M. fulvoguttata* favoured lightly burned plots.

3.5.3.2 Rearing data.

For most taxa, burned habitat quality variables were more likely to affect the colonization of burned trees than source habitat attributes. Most top-ranking models included burned habitat quality variables at the plot scale, especially fire severity, (Appendix C5). Top-ranking models included only burned habitat quality variables measured in the plot for three taxa (*A. proteus proteus*, *M. scutellatus scutellatus* and *A. pratensis*). Most species in this study did not colonize severely burned plots or were more common in lightly burned plots (Table 3.2). Occurrence of *M. scutellatus scutellatus* was positively related to moderately burned plots. *A. pratensis* was the only species to occur more often as the amount of severely burned forest in a 250m radius increased (Table 3.2). Source habitat variables were very seldom included in top ranking models and none had a significant negative effect on larvae occurrence or abundance (Table 3.2).

Indeed, dispersing adults showed striking different patterns for three taxa when compared to the effective larval colonization of burnt trees. Adult occurrence during the summer in which the forest has burned was positively and significantly related to larval colonization for only two species (*A. pratensis* and *M. fulvoguttata*) (figure 3.2). Both species show non-significant discrepancy between neonates and adults regarding preferences for fire severity. For all other species, neither adult abundance nor occurrence was related to the effective colonization of burnt trees. Furthermore, for all these latter species, the effect of fire severity on adult occurrence was completely different from the effective larval colonization of burnt trees (Table 3.2). Adults of *A. proteus proteus* were more common in the more severely burned northern area (figure 3.3a) even though neonate abundance was highest in lightly burned trees. Furthermore, false positive events were recorded more often in severely burned stands for Scolytinae (Table 3.2, figure 3.3b). Likewise, *M. scutellatus* adults avoided large amounts of unburned forests in a 250m radius whereas larval occurrence was highest in moderately burned plots (Table 3.2).

3.6 Discussion

3.6.1 Effect of substrate quality on neonate abundance

Fire severity and bark thickness were the most important variables to predict abundance/occurrence in fire-killed trees. With the exception of *A. pratensis*, xylophagous taxa were more common in lightly or moderately burned trees whereas bark thickness had a positive impact on larval colonization for several species, especially in severely burned trees. Several studies (e.g. Richmond and Lejeune 1945, Cerezke 1977, Saint-Germain et al. 2004a,b) have already pointed out that severely burned trees, especially for species exhibiting thin bark, were less colonized by xylophagous beetle larvae. Both characteristics may be linked to the suitability of subcortical (phloem and cambium) tissues, especially its moisture content, as nearly all species reported in this study spend at least part of their life cycle as larvae in the xylem-bark interface (Downie and Arnett 1996). Rapid moisture losses in the subcortical area can be deterrent for larvae survival (Savely 1939, Furniss 1965, Saint-Germain 2004a,b). Nevertheless, moisture content was identified to have a positive effect on larvae occurrence for *M. scutellatus scutellatus* but not for other species. Such a significant effect for this deep borer species only was probably related to the fact that moisture was estimated without distinction between subcortical tissues and xylem. All other species feed primarily on phloem and as such, they should respond to moisture content measured in the subcortical area only. One may argue that severely burned trees should experience faster moisture losses in the subcortical tissues as they are located near the wood-atmosphere interface and hence support fewer larvae. Effect of bark thickness may also be related to subcortical moisture content as insulating properties of bark should increase along with bark thickness. Effect may be especially important in severely burned trees where thick bark may partly compensate for higher moisture losses caused by severe charring. Furthermore, trees with thick bark should have thicker phloem which may provide higher nutritional content for larvae and increase survival (Amman 1972, Haack and Slansky 1987, Reid and Glubish 2001, Peddle et al. 2002).

3.6.2 Relation between effective colonization and dispersing adult

The characteristics of the burned habitat were important predictors for both neonates and adults. Fire severity measured at the plot and/or landscape scale had the most important impact, a finding that was previously noticed for these taxa (Boulanger et al. submitted). Furthermore, distance to source habitat did not have any negative effect on neonates and adults. Limited dispersal from source habitats can result in lower adult colonization in remote colonisable stand (Turchin and Thoeny 1993, Franklin et al. 2000). Nevertheless, most remote patches were probably within the dispersal range of species (Boulanger et al. 2010 submitted) as most are thought to have strong dispersal capacities.

According to the optimality theory, species should select attributes that maximize species fitness (Parker and Maynard Smith 1990). Dispersing adults should thus select habitats and hosts that will allow higher survival, greater larval growth and faster development (Jaenike 1978) or higher adult realized fecundity (Scheirs and DeBruyn 2002). In that sense, a general agreement is expected between post-fire characteristics that best predict the abundance of xylophagous larvae and colonizing adults as shown by adults and neonate colonization patterns of *A. pratensis* and *M. fulvoguttata*. In both cases, dispersing adults and neonate occurrence was highly dependent on fire severity (either measured on the trunk or at larger spatial scales). Nevertheless, high discrepancy was noted between attributes leading to higher neonate abundance and those affecting dispersing adults for all other taxa. Such discrepancy was mainly due to different effect of fire severity on both life stages. Adults of these species were attracted to severely burned forests or avoided areas with high amount of unburned forests whereas larvae were more common in lightly or moderately burned trees/plots. Such discrepancy between adult post-fire preferences and larvae abundance/occurrence of xylophagous species was not yet reported in other studies.

This discrepancy is a counterintuitive result. Difference between larval colonization and habitat attributes that are selected by adults may have consequences on species fitness (Allison et al. 2004). Non-optimal habitat selection by adults was already reported for other insects (Rauscher 1979), including saproxylic taxa (Saint-Germain et al. 2010). Such behaviour of xylophagous adults in a post-fire context may be the result of a selection pressure that mostly pushed these species towards the detection of suitable hosts, e,g, recently dead trees, in "green" forests rather than in burned forests. Although commonly associated with fire-killed trees, all species collected in sampling can also breed in recently dead trees that were not killed by fire (Hanks 1999, Saint-Germain et al. 2007b). Furthermore, several of these species were already reported from other ecosystems (Saint-Germain et al. 2004a,b,c, Janssen et al. 2009) where expected fire interval is very long (Rowe and Scotter 1973). In a heterogeneous landscape, natural selection may not consistently favour the use of a transient resource over another one, more consistently available through time (Thompson 1988). Dead trees found in unburned forests may represent a more stable input of suitable substrate than fire-killed trees. In the geographical range of every species studied here, fire occurrence is very heterogeneous through space and time, with some years and regions where burns are very sparse (Stocks et al. 2002, Saint-Germain et al. 2008). Indeed, although the long-term abundance of xylophagous species may be enhanced in ecosystems with frequent stand-replacing fires (Wikars 1992, McCullough et al. 1998), long-term survival in these ecosystems mostly relies on woody debris produced in unburned forests (Saint-Germain et al. 2008).

Higher attraction to severely burned stands by xylophagous species may be related to the amount of attractive volatiles emitted by such habitats. Xylophagous species evolved capacities to detect the substrate at long range by using an array of volatiles that mostly discriminate the state (e.g. living vs dead, fresh vs advanced decay) and species of the tree (Allison et al. 2004, Pureswaran et al. 2004). Some species developed abilities to locate the burned patches by using cues that are only fire-driven, such as smoke or infrared (Frost 1984, Schütz 1999, Allison et al. 2004). These volatiles may only play a role at the very beginning of the dispersal phase, i.e. during the burning itself. Most xylophagous species collected as adults during sampling were abundant 32 to 67 days after the fire was down (Boulanger et al. submitted). In absence of smoke plumes or infrared emission by fire, these species should have mainly use the same cues to detect fire-killed trees as those in unburned forests. In this context, it is doubtful that these species evolved abilities to discriminate between lightly and severely burned trees at great distance since both are thought to emit the same volatiles but in different concentrations (Kelsey and Joseph 2003). However, one would expect that increasing concentration of post-fire volatiles should be more attractive for dispersing xylophagous species using these cues to locate potential hosts (Kelsey and Joseph 1999, Pureswaran et al. 2004). Substantial amounts of attractants, including ethanol, may be emitted by burned trees, especially by severely scorched ones (Kelsey and Joseph 2003) or those under high temperature or solar radiation (Kelsey and Joseph 1999). Higher amount of these volatiles may have caused the greater attraction of several colonizing species to severely burned stands.

Even though more adults were attracted to severely burned forests emitting abundant volatiles, lower effective colonization in such conditions may have resulted from the egg-laying behaviour of the females rather than from high larvae mortality. Females may assess tree characteristics once landed on the substrate which obviously may affect the effective colonization of the tree. For example, female *M. scutellatus* are known to assess phloem thickness during scar excavation before ovipositing (Peddle et al. 2002) and lay their eggs only in boles with sufficient moisture content (Dyers and Seabrook 1978). Furthermore, females of the cerambycid *Arhopalus tristis* favoured burnt over unburned boles to lay their eggs (Suckling et al. 2001). Saint-Germain et al. (2006) have noticed that xylophagous beetles use primary attraction at a coarser scale to locate potential hosts whereas the final assessment of the optimal substrate is only made *a posteriori* via random landing. As such, the initial dispersal of xylophagous beetles towards the burned substrate may be considered as a non-optimal strategy whereas females may actually have an "optimal" egg-laying behaviour. However, such hypothesis remains to be explored.

Buprestidae poorly respond to host volatiles (Chénier and Philogène 1989, Campbell and Borden 2009) but rather rely on visual cues to locate potential host (Campbell and Borden 2009). Even though such assessment were not yet studied, one may hypothesize that these taxa are able to discern between severely and lightly scorched trees, at least when they are at close range of the substrate, as tree's reflectance should greatly differ with charring. This may explain why *M. fulvoguttata* adults were not attracted to areas with high volatile concentration but were rather occurring more often in lightly burned stands which contained more suitable substrates. Likewise, as the assessment of visual cues may only be made at a very small scale ($\leq$ 2m, Campbell and Borden 2006), this may explain why adults of *M. fulvoguttata* primarily responded to stand-level attributes. This differs from cerambycids which respond to landscape-scale attributes in addition to stand-level variables, as tree volatiles can be effective at very large scales.

One may view this non-optimal behaviour, i.e. the use of severely burned stands, as a costly strategy that should lead to lower species fitness than the use of unburned trees. Non-optimal strategy may be used if the rate of food discovery is higher in habitat of lower suitability (Rauscher 1979). In this area, substrate volume is much higher (38.3 $m^3.ha^{-1}$) in burned patches than in unburned stands (0.6 $m^3.ha^{-1}$) (Boulanger et al. unpubl. data). Indeed, despite lower larval occurrence in severely burned trees, such behaviour may lead to higher general survival than in unburned forests considering the relatively high volume of substrate in burned stands. As a result, attraction to severely burned patches may still be viewed as an opportunity, yet not a panacea, for xylophagous species.

Table 3.1. Effects of environmental variables on either the abundance (A. proteus) or occurrence (remaining taxa) of seven xylophagous taxa in bole sections of burned trees. Multimodel inference was used when the weight (ω i) of the top-ranking model was below 0.90.

Taxa	***Fire***[a]	***Fire***^{2}	***Diam***	***Bark***[b]	***Bark*Fire***	***Moisture***	***Density***
Acmaeops proteus Kirby	--[c]		+	+++	+		
Acmaeops pratensis Laicharting							
Melanophila fulvoguttata (Harris)	-			+++			
Monochamus scutellatus (Say)[d]		--		-	++	+	
Scolytinae spp.	--			+			

a. Effect of *Fire* was determined from models including this predictor but excluding *Fire*^{2} and *Bark*Fire*.

b. Effect of *Bark* was determined from models including this predictor but excluding *Bark*Fire*.

c. +, - : $P<0.05$; ++, -- : $P<0.01$; +++, --- : $P<0.001$.

d. Effects inferred from the best model only (Sb18, ω = .947)

Table 3.2. Effects of environmental variables used to predict either the abundance or occurrence of xylophagous taxa in bole sections and in trunk-window traps as well as "false positive events" (see text) at the stand and landscape scales. Environmental variables were related to either burned or source habitats and were classified according to the spatial scale (local, nearby, remote) they encompassed. Multimodel inference was used when the weight (ω_i) of the top-ranking model was below 0.90.

		Burned habitat attributes						**Source habitats**					
		Local			**Nearby**			**Local**		**Nearby**	**Remote**		
Species	**Model**	***Firestn*[a]**	**$Firestn^2$**	***BasArea***	***BurnResSev***	***BurnResMo***	***BurnResLi***	***Snag12***	***Log12***	***Unb250***	***Dist10ha***	***DistEdge***	***Dist2002***
Acmaeops proteus Kirby	Larvae												
	Adults[a]		--										+++
	Difference 2005-2006												+
Acmaeops pratensis (Laicharting)	Larvae			-	+					-			
	Adults	+											
	False positive						+						

		Burned habitat attributes						**Source habitats**					
		Local			**Nearby**			**Local**		**Nearby**	**Remote**		
Species	**Model**	***Firestn***^{a}	***Firestn***^{2}	***BasArea***	***BurnResSev***	***BurnResMo***	***BurnResLi***	***Snag12***	***Log12***	***Unb250***	***Dist10ha***	***DistEdge***	***Dist2002***
Melanophila fulvoguttata (Harris)	Larvae	-											
	Adults	-											
	False positive												
Monochamus scutellatus (Say)	Larvae		-										
	Traps 2005^a			++				+		-			
	False positive												
Scolytinae spp.	Larvae	--											
	Adults												
	False positive	+			-								+

a. Results from negative binomial regressions.

b. No model testing since complete separation occurred in when testing some models

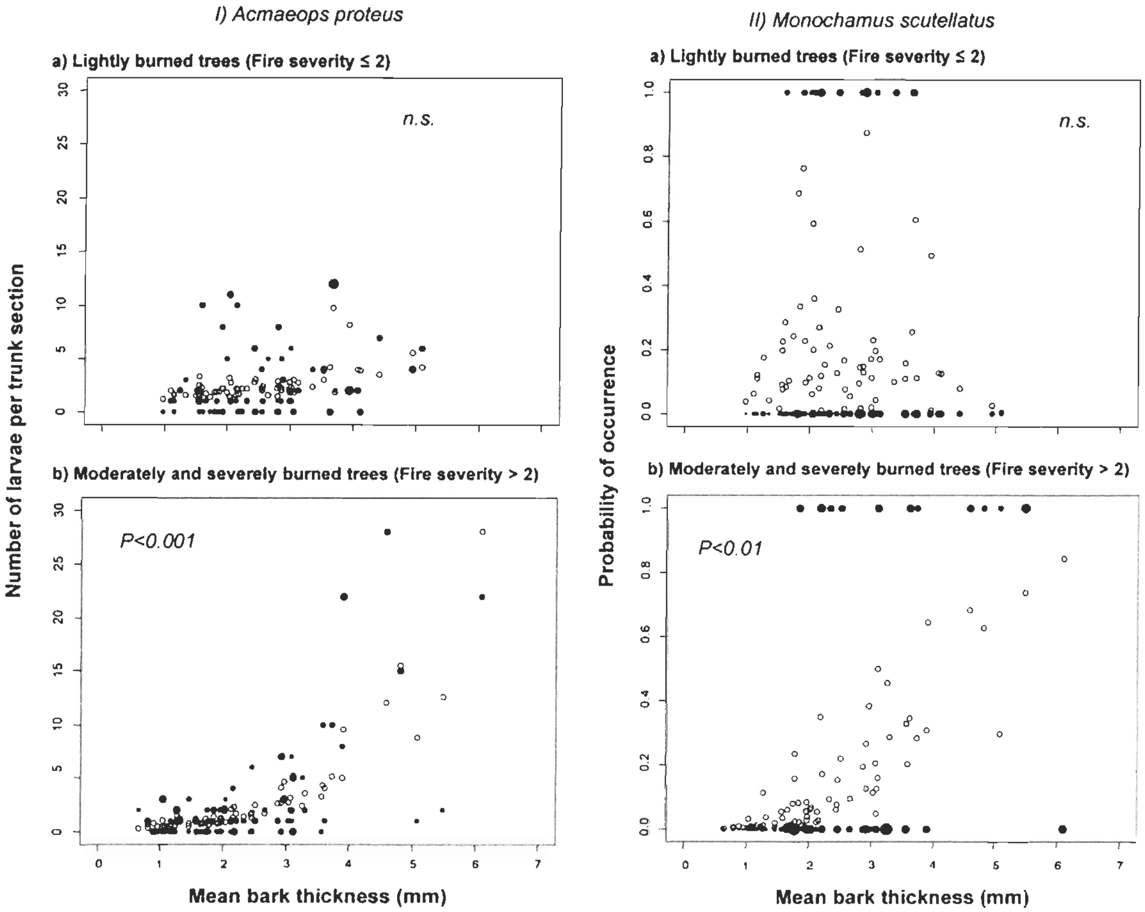


Figure 3.1. Effect of bark thickness on last-instar larvae abundance of I) Acmaeops proteus and occurrence of II) Monochamus scutellatus neonates in a) lightly and b) moderately/severely burned trees. Black circles: raw values. White circles: predicted values calculated when modelling either abundance or occurrence of neonate with the predictors included in the best model according to AICc but excluding fire severity and interaction with bark thickness for the illustration purpose. Size of black circles is proportional to tree diameter and moisture content for A. proteus and M. scutellatus respectively since those predictors were significant after multimodel inference (see table 3.1).

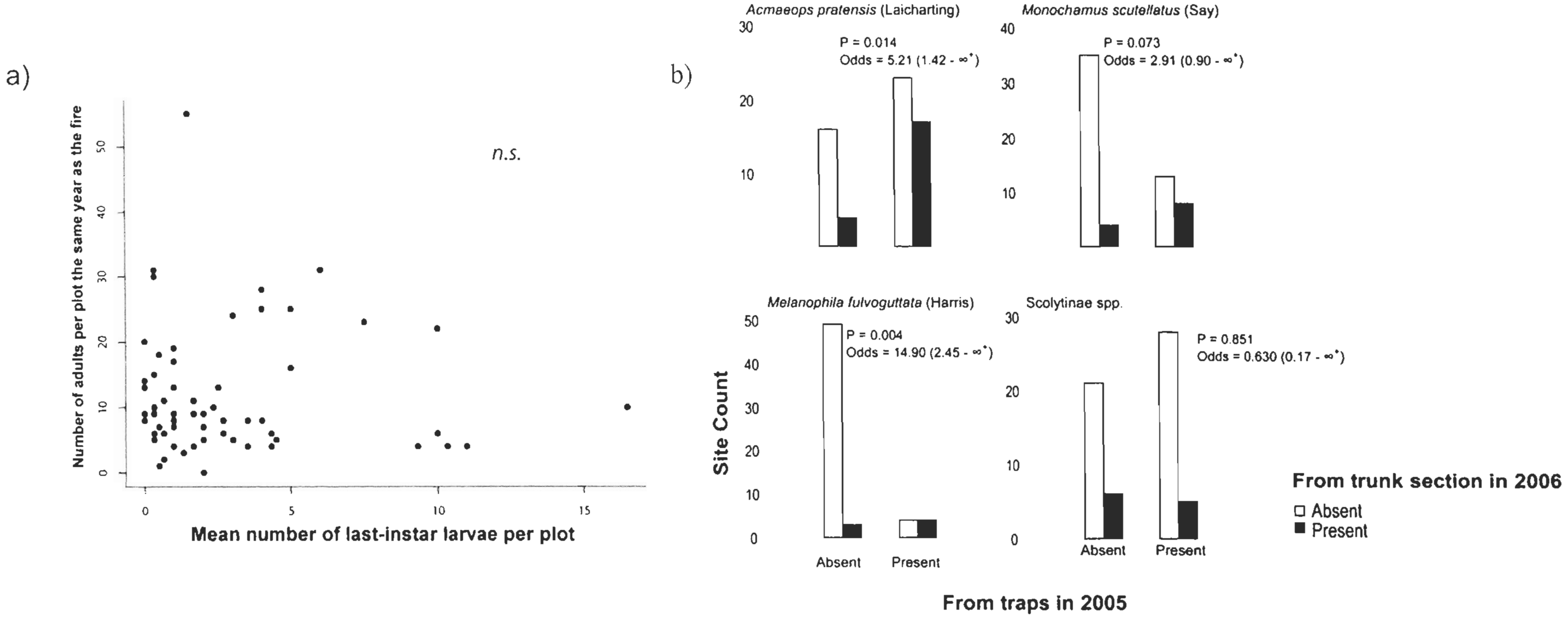
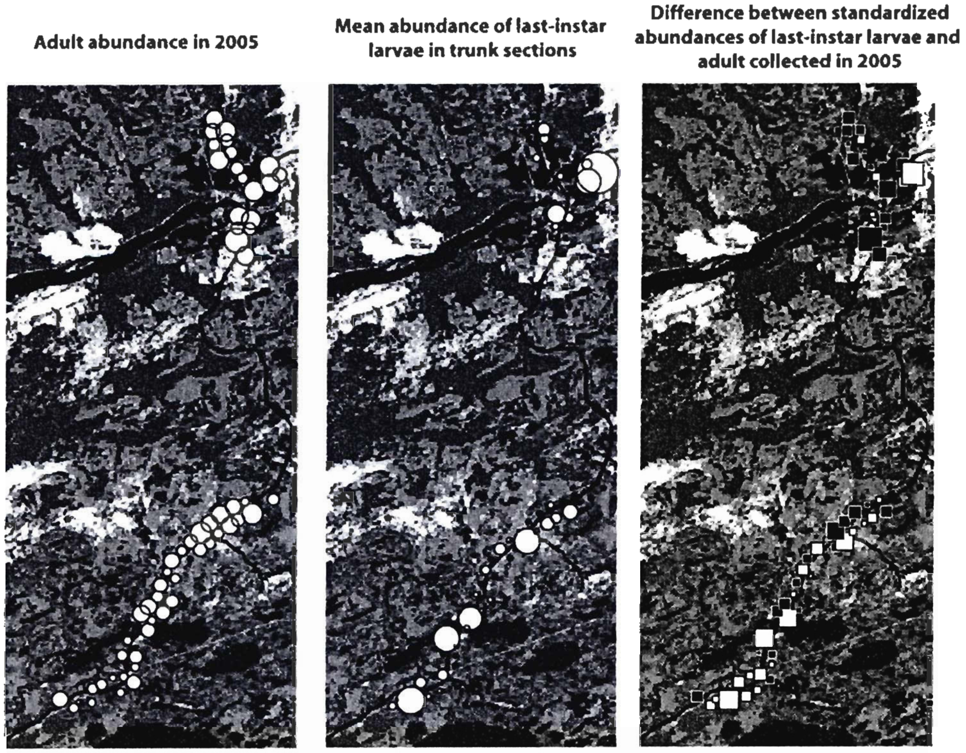


Figure 3.2. a) Relation between abundance of adults the same year as the fire and last-instar larvae in bole sections for A. proteus (P>0.05). b) Number of sites where emerging neonates occurred (black bars) or not (white bars) in bole sections when dispersing adults were either present or absent the same year as the fire. Relation between both binary variables was assessed with one-tailed Fisher's exact test. Odds > 1 indicate significant positive relation between previous occurrences of adults in 2005 on subsequent occurrences of neonates in bole sections.

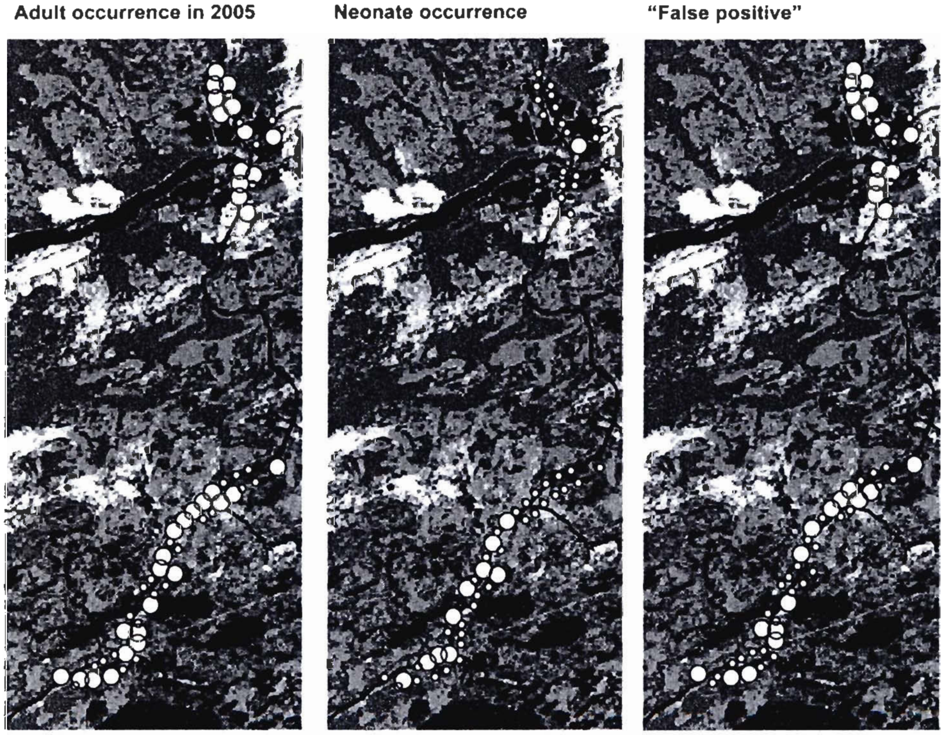
a) *Acmaeops proteus proteus*


Adult abundance in 2005

Mean abundance of last-instar larvae in trunk sections

Difference between standardized abundances of last-instar larvae and adult collected in 2005

b) Scolytinae


Adult occurrence in 2005

Neonate occurrence

"False positive"

Figure 3.3 (previous page) a) A. proteus proteus: Mapped abundance of adults the same year as the fire and mean abundance per plot of last-instar larvae collected from bole sections. Circle size is proportional to standardized abundance of either adults or larvae. Difference in standardized abundance of adults collected in 2005 and larvae collected in trunk sections is also shown. Black square represents plots where adults were proportionally more abundant than larvae whereas white squares represent the opposite. Size of square is proportional to observed difference. b) Scolytinae. Mapped occurrence of adult the same year as the fire and neonates collected from bole sections. Occurrence of "false positive events", i.e. plots where adults were collected in 2005 but where no neonates emerged from bole sections is also shown. Big circles : presence ; small circles : absence.

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CHAPITRE 4

FIRE SEVERITY AS A DETERMINANT FACTOR OF THE DECOMPOSITION RATE OF FIRE-KILLED BLACK SPRUCE IN THE NORTHERN BOREAL FOREST

4.1 Résumé

Plusieurs variables peuvent influencer le processus de décomposition des arbres tués par le feu. Dans cette étude, nous avons testé l'effet de plusieurs variables, à l'échelle de l'arbre et du peuplement, sur la décomposition des débris ligneux d'épinette noire (*Picea mariana* [Mill.] B.S.P.) après feu. Les données proviennent de 474 individus qui ont brûlé 17 ans avant l'échantillonnage. Le taux de décomposition moyen était relativement bas (k = .013) et était minimal chez les chicots très sévèrement brûlés (k = .001) et maximal chez les débris au sol légèrement brûlés (k = .027 - .036). La position de l'arbre et la sévérité du feu représentaient les plus importantes variables influençant les taux de décomposition alors que les variables mesurées à l'échelle du peuplement n'étaient que marginalement significatives. Ces deux variables ont fortement influencé le taux d'humidité des débris ligneux postfeu, ceux présentant un grand contact avec le sol ainsi que ceux étant légèrement brûlés possédant un taux d'humidité plus élevé et un taux de décomposition plus rapide. Les faibles taux d'humidité relevés sur les arbres très sévèrement brûlés seraient causés par une chute plus rapide de l'écorce. Une forte sévérité du feu pourrait aussi retarder le processus de décomposition en ralentissant la chute des chicots. Les taux de décomposition plus rapides chez les arbres légèrement brûlés pourraient résulter d'une plus forte colonisation initiale par les insectes xylophages. En raison de son impact considérable sur la décomposition des débris ligneux, la sévérité du feu pourrait fortement influencer plusieurs processus biologiques postfeu associés à la nécromasse ligneuse ainsi que les émanations de carbone provenant des peuplements brûlés.

4.2 Abstract

Several attributes might influence the decomposition process of fire-killed trees. Here, we tested various tree- and plot-level variables on the decomposition rate of fire-killed black spruce (*Picea mariana* [Mill.] B.S.P.) in the northern boreal forest. Data were collected from 474 individuals burned 17 years prior to sampling. Mean decomposition rate was relatively slow (k = .013) and was lowest for severely burned snags (k=.001) and highest for lightly burned logs (k=.027 - .036). Vertical position and fire severity were the most important variables influencing the decomposition rates while plot-level variables were marginally significant. Both predictors strongly influenced the moisture content of fire-killed trees. Logs with greater contact with the ground and lightly burned trees had higher moisture content and faster decomposition rates. Very severely burned trees had lower moisture content because of faster bark shedding. This hampered the decomposition process by slowing the snag falling rate. Higher decomposition rates in lightly burned trees may result from greater colonization by early xylophagous species. By having a considerable impact on the decomposition of woody debris, fire severity may strongly influence many post-fire biological processes related to the woody necromass as well as carbon emission from burned stands.

4.3 Introduction

Coarse woody debris (CWD) is a conspicuous feature of forest ecosystems. Structural and functional roles of CWD in forest ecosystems have been recognized at both local and global scales (Kasischke and Stocks 2000). In the boreal forest, fire is known to produce very large amounts of woody detritus (Bond-Lamberty et al. 2002; Boulanger and Sirois 2006; Angers 2010). Fire-killed trees represent a habitat for a tremendous diversity of saproxylic species, including several insect taxa (Saint-Germain et al. 2004; Boulanger and Sirois 2007). Dead woody material decomposes rather slowly (Harmon et al. 1986) and may form important carbon and nutrient pools that may have long-term significance for cycling of carbon and nutrients in woodland ecosystems (Laiho and Prescott 2004). Consequently, such large and sudden inputs of CWD after fire are known to affect the local carbon budget of these ecosystems (Wang et al. 2002, 2003).

The decomposition of CWD includes the fragmentation and the mineralization of the woody biomass. During the decomposition process, wood loses mass with time as the complex organic compounds (lignin, cellulose, hemicellulose) are degraded by fungal activity or lost through leaching (Harmon et al. 1986). This process depends on various factors measured at many spatial scales. Several of these factors have a direct influence on temperature and moisture content of CWD, both of which affect the metabolism of heterotrophic organisms, mainly basidiomycetes, involved in the decomposition process of dead wood (Rayner and Boddy 1988). Indeed, mean annual temperature (Yatskov et al. 2003; Gough et al. 2007) and precipitation (Progar et al. 2000) strongly influence the decomposition of CWD at the regional scale. Temperature and moisture conditions prevailing in dead wood are influenced by several factors at the plot and tree levels which may in turn influence the decomposition rates of CWD. Such factors may include slope aspect and angle, canopy openness, soil humidity, CWD diameter and vertical position and the colonization by insects (Harmon et al. 1986; Schowalter 1992; Naesset 1999). The great majority of studies reporting the effects of environmental conditions on CWD decomposition were done in unburned forests (cf. Laiho and Prescott [2004] for a review). As post-fire micro-climatic conditions are likely to be much more different than in unburned forests (Parmeter 1977), the decomposition of fire-killed trees should follow a contrasting pathway compared to CWD produced in closed-canopy forested.

Charring may induce physicochemical changes in dead wood, including pH, albedo and temperature (Shorohova et al. 2008), though the direct effects of these changes on the decomposition rate of post-fire CWD have not been fully investigated. Nevertheless, some authors (Boulanger and Sirois 2006; Angers 2010) have recorded very slow decomposition rates in fire-killed spruce species while others did not find any effect of charring (Shorohova et al. 2008). Fire may slow down the decay process by removing the canopy and making post-fire CWD more subject to high solar radiations and winds which may accelerate moisture loss compared to woody debris produced in closed-canopy forests. Moreover, fire-killed trees tend to stand upright longer and loose bark faster than dead trees in unburned forests, which may slow the decay rate (Boulanger and Sirois 2006; Angers 2010). Considering their slow decomposition rates, fire-killed trees are thought to contribute to the formation of an important carbon reservoir in the boreal ecosystem (Kasischke 2000). One should expect that environmental conditions (e.g. canopy openness, charring, temperature, humidity) in burned stands should strongly vary with fire severity and that such variation could be directly translated to the decomposition rate of post-fire CWD.

In 1989, 20 870 km^2 of forest burned in the James Bay area, Québec (Couturier and Saint-Martin 1990). This offered a unique opportunity to study the effects of various environmental factors that are thought to influence the decomposition rates of fire-killed trees. A recent study carried out along a 29-years burned site chronosequence in burned sites, held in the same area (Boulanger and Sirois 2006), found large variations in wood density losses in post-fire black spruce CWD, especially in ≥13 years old burns. Although the decomposition rates in the latter study were assessed according to CWD position (snag vs log), it was not meant to report the effect of other factors, including fire severity, which could explain such variation in this process. Indeed, the main objective of the present study was to assess the decomposition rates of fire-killed black spruce in the northern boreal forest. More specifically, we wanted to i) assess the impact of biotic and abiotic variables, most notably fire severity, measured at the tree- and plot-levels, on the cumulated wood density losses and the moisture content of CWD 17-years after fire and ii) estimate the influence of tree-level factors on snag falling rate.

4.4 Material and methods

4.4.1 Study area

The study area is located in the northern boreal forest of Québec, Canada, in the vicinity of the James Bay area (Figure 4.1) in the lichen woodland ecosystem (Rowe and Scotter 1973). The climate is low-subarctic with a mean annual air temperature of –3.6 °C while January and July temperatures average –25 and 13°C respectively. Annual precipitation averages 637 mm, 40 % of which falls as snow (Environment Canada 1993). Even-aged black spruce (*Picea mariana* B.S.P. [Mill.]) and jack pine (*Pinus banksiana* Lamb.) forests occupy every non-edaphically limiting site. Uneven-aged stands dominated by black spruce are found on paludified sites on the lowlands, intermingled with extensive bogs and fens. Wildfire is the most important natural disturbance and its average recurrence cycle is approximately 100 years in this area (Parisien and Sirois 2003). There is no fire control in this region except in the immediate vicinity of municipalities and hydroelectric facilities.

Eighty-nine plots were located in two contiguous patches (50371 and 377 750 ha respectively) that burned between June 24 and September 10, 1989 (Figure 4.1). Since access to potential sampling sites is very limited in these remote areas, plots were systematically distributed by pairs at each km along the two major roads crossing the burned patches. Plots of a given pair were located on each side of the road respectively and were separated by 1 km. Circular plots of 100 m^2 (radius = 5.68 m) were established only in plots including at least three fire-killed black spruces of $\geq$10 cm of diameter at stump height (DSH). Sampling was conducted in June and July 2006, i.e. seventeen years after fire.

4.4.2 Plot characterization

In each plot, the diameter of each living tree $\geq$ 2 cm of DSH was measured to estimate basal area ($m^2.ha^{-1}$). Living trees included trees that survived the 1989 fire as well as post-fire regenerating stems. Shrub cover (between 1 and 3 m of height) was assessed according to five covering classes (Table 4.1). Dominant drainage class (Doucet and Côté 2009), from 1 (i.e. rocky, xeric sites) to 6 (i.e. treed bogs or fens), was determined in the plot (Table 4.1). Slope angle and aspect were also noticed (Table 4.1).

4.4.3 CWD characterization

Sampling was limited to CWD resulting from fire-killed black spruce with DSH >10cm. Woody debris or dead trees present before fire was distinguished from debris produced at the time of fire as the latter lacked charcoal on the main trunk, whereas the former showed large areas of scorched wood. Position of debris (snags, logs or stump) was recorded. Standing woody debris $\leq$ 1.5 m of height were considered as stumps whereas those $\geq$ 1.5 m were considered as snags. Only woody debris having its stump inside the circular plot was measured and considered in the analyses even if part of the debris was were outside the plot boundaries. All CWD with DSH $\geq$ 10 cm were sampled in each plot. Proportion of contact with the ground or the lower herbaceous layer (< 5 cm high) was evaluated for logs (Table 4.1). Char height is known to be a good proxy of fire intensity (Hély et al. 2003). Accordingly, on each fire-killed stem, the maximum height on the stem where scorched twigs with diameter ≥ 5 mm were found was noted as an index of fire severity (Table 4.1). Dead individuals were identified to the species level either in the field, based on general appearance and remaining cones, bark, and twigs, or in the laboratory using wood-anatomy criteria (Hoadley 1990) when necessary. Remaining proportion of bark cover (Table 1) on the stem was visually estimated and classified as very low (< 10%), low (10-40%), moderate (40-70%), high (70-90%) and very high (≥ 90%). A thorough examination of the dead stems in the plot was completed in order to avoid any "double-sampling" of a given fire-killed individual. Two cross sections approximately 5 cm thick were sampled on every post-fire CWD. Hence, broken tops of snags on the ground were not considered separately as "logs". For either snags or logs, cross sections were collected at 100 and 200 cm from the stump collar. One cross section taken at 100 cm above the ground was sampled from stumps.

Samples were put in hermetically sealed bags in the field to prevent moisture loss and then placed in a freezer within 12 hours to stop further fungal or bacterial degradation prior to laboratory analyses. Remaining bark on samples was removed. The cross sections were weighed for green mass and then ovendried at 70 °C until a constant mass was reached. Dry mass was determined from the last weighing. The moisture content was estimated from the mass loss after drying and was expressed as a proportion of dry mass. The volume of cross sections was measured on dry samples. Cross sections were considered cylindrical and volume was estimated by approximating the mean diameter and thickness of the cross sections to the nearest 1 mm. Wood density ($g \cdot cm^{-3}$) was expressed as dry mass over dry volume. Samples with large amounts of lignin (n=5, 0.55% of overall samples) corresponding to compression wood or branch knots were discarded (Erickson et al. 1985).

4.4.4 Statistical analyses

4.4.4.1 Decomposition rates

We assessed the decomposition rate of fire-killed trees as the proportion of wood density lost since death as CWD fragmentation was considered to be negligible. Trees were assumed to be killed by the fire in 1989, although some trees may have survived for few years after fire in lightly and moderately burned stands (Angers 2010). Decomposition rate of CWD is generally reported as a constant (k_m) expressing the proportion of wood density lost each year. In order to make valuable comparisons with other studies, we estimated the decomposition rate of each fire-killed tree by assuming that mass loss follows a negative exponential model as a function of time after tree death (Olson 1963):

(1) $Y_t = Y_0.e^{-km.t}$

where Y_0 is the initial wood density and Y_t the wood density at time (t = 17 years) of sampling. Initial wood density may be set from reported values (Jessome 1977) or from the average density in living trees located in the vicinity of the sampling area (Boulanger and Sirois 2006). However, setting these values as the initial wood density may introduce large bias in wood density loss (Naesset 1999; Mäkinen et al. 2006). Indeed, wood density prior to death may strongly vary according to various tree and site attributes (e.g. Harmon et al. 1986; Zobel and van Buijtenen 1989). Using data collected from living trees in the vicinity of the study area, ten regression models were built in order to predict wood density according to tree diameter, plot drainage class and growth rate of trees (see supplementary material S4 for details). According to AIC_c, the most parsimonious model to predict wood density did only include growth rate (Appendix D4). This model explained 29 % of total variation of wood density data in living trees. Even though the latter model still included a certain level of uncertainty, the addition of other variables did not improve the model significantly. Hence, this model was used in order to estimate the initial wood density of fire-killed trees. Similar models were already used for such purpose (Naesset 1999, Mäkinen et al. 2006).

Decomposition rate was estimated with respect to the position of the debris and as a function of fire severity. Decomposition rate of logs was assessed in two ways. First, cumulative decomposition rate was assessed using the wood density loss since tree death. This decomposition rate is likely biased as it does not make any distinction between the time period elapsed as snag before breakage or uprooting. Mean time since falling is very difficult to determine exactly for logs. Indeed, woody debris may have fallen anytime during the 17 years post-fire period. Furthermore, snags of several tree species were shown to fall at an irregular rate through time (Garber et al. 2005). However, recent studies demonstrated that fire-killed black spruces fall at a regular rate after tree death (Boulanger and Sirois 2007; Angers et al. 2010). Therefore, we considered the half time after fire (0.5*17 post-fire years = 8.5 years) as the average time since snag fall. Afterwards, we estimated wood density of each log at the average time of snag fall using snag decomposition rate modulated by fire severity. Decomposition of logs was then estimated according to the previous exponential model (1) but using the estimated wood density at time of falling ($Y_{t=8.5}$) as the initial wood density along with the measured wood density (Y_t).

4.4.4.2 Effect of tree level attributes

At the tree level, we developed and tested 8 biologically plausible regression models to predict either the moisture content or the decomposition rate of fire-killed spruce (Appendix D1). Tree-level models were tested by means of mixed linear regressions. Some models tested for an interaction between fire severity (Fire) and the vertical position (Contact0: snags vs logs) of the CWD. Since stumps were uncommon compared to either snags or logs, data were pooled with snags in this analysis. Best models testing for both moisture content and percentage of wood density loss were selected according to the corrected Akaike's Information Criterion (AIC_c). Significance of parameters in the best model was determined by ANOVA using the difference between deviance of the reduced and the full models.

As a complement, we estimated if bark cover remaining on the logs and snags was dependant of fire severity by using separate chi-square tests.

4.4.4.3 Effect of plot-level attributes

Eight additional models were developed to test plot-level attributes on moisture content and wood density loss (Appendix D1). Effects of plot-level variables were evaluated after removing the effect of tree-level variables. First, we computed the best models to predict wood density loss and moisture content at the tree-level identified earlier but in which we removed plot as a random effect. Then, residuals were computed and averaged by plot and then used as a dependant variable to assess the effects of plot-level variables. Effects of plot-level variables were likely to vary according to the position of the debris (either standing or fallen). Indeed models were tested separately on snags, logs and specifically on logs with close contact with the ground (>40% of their total length; n=80). Best regression models were selected according to the AICc. Multimodel inferences were used when the AIC_c weight of the top-ranking model was lower than 0.90 (Burnham and Anderson 2004).

4.4.4.4 Snag falling rate

In this study, falling of snags included either uprooting or breakage of the stem from the ground to a maximum of 1.5 m. Consequently, stumps were considered as fragmented snags in these analyses. Falling rate of snags was assumed to be regular over time and was assessed according to a negative exponential. Falling rate (k_f) was estimated by using the percentage of CWD still standing (Y_t) after 17 years (t) for each fire severity class (lightly to very severely burned trees, see Table 4.1). We considered that every tree died standing ($Y_0 = 100$). Four regression models were developed to test the effect of tree-level variables on the probability of snag fall. Effects of these variables were assessed with mixed logistic regression models with plot as the random effect.

All analyses were performed using R 2.8.1 (R Development Core Team 2008). Mixed regression models were computed using the lmer function in the *lme4* package v. 0.999375-31 (Bates and Maechler 2009). R^2_{LR} for mixed linear regression models were computed as proposed by Magee (1990).

4.5 Results

4.5.1 Decomposition rate

Overall, the decomposition rates (k_m) of the 474 fire-killed trees averaged .013. Mean cumulative decomposition rate of post-fire CWD was lower in snags (k_m = .009) than in logs (cumulative k_m=.017) (Table 4.2). Decomposition rate of both snags and logs was inversely related to fire severity. Mean snag decomposition rate was lowest in very severely burned trees (k_m=.001) and highest in lightly burned trees (k_m=.018). The same pattern was recorded in logs as cumulative decomposition rate varied from .007 to .027 in very severely and lightly burned trees, respectively. For logs, decomposition rates were higher when considering the estimated time since snag fall rather than time since tree death. Decomposition rate since snag fall averaged .023 and was lowest in severely burned trees (k_m=.015) and highest in lightly burned trees (k_m=.036) (Table 4.2).

4.5.2 Effects of tree- and plot level attributes

4.5.2.1 Wood density loss

The full model tested for wood density loss at the tree level was by far the most parsimonious (ω = .999, Table 4.3a). Fire severity (Δdeviance = 34.96) and the position (Δdeviance = 20.13) of fire-killed trees had important effects on wood density loss. Both maximum diameter and wood density prior to tree death had a positive impact on wood density loss although their independent contribution in the final model was lower (Δdeviance = 13.67 and 13.53, respectively).

At the plot level, top-ranking models for either snags, logs or logs with close contact with the ground showed rather low AIC_c weights (ω_i < .5, Appendix D2), indicating that other models also received a certain level of support. Indeed, goodness-of-fit of top-ranking models as assessed from R^2_a values was particularly low (< .053). Wood density loss in snags was higher in north aspect plots whereas logs decayed more rapidly with increasing basal area of living trees. No other plot-level variable was significant (Appendix D3).

4.5.2.2 Moisture content

Effects of tree-level variables on moisture content were similar to those noticed for wood density loss. The full model showed the highest level of support ($\omega \sim 1.000$, Table 4.3b). Logs, especially those with close contact with the ground, had higher moisture content than snags. Significant interaction occurred between fire severity and the vertical position of CWD. Fire severity had a detrimental impact on moisture content but differences were mostly noticed in logs. Moisture content in snags was similar between fire severity classes and never exceeded 30 % on average. Maximum diameter of the fire-killed tree had a positive effect on moisture content (Δdeviance = 15.29).

No plot-level model received high ($\omega_i \leq .442$) level of support for all types of CWD considered (Appendix D2). Except for top-ranking models of logs with close contact with the ground, most models have rather low R^2_a values especially for models tested on all logs. Indeed, drainage was the only significant variable that was positively related to moisture content of snags whereas no plot-level variable was significant for logs (Appendix D3).

4.5.3 Bark cover

Fire severity had an important effect on CWD remaining bark cover for both snags ($\chi^2_{(0.05,\ 12)} = 179.6$, $P<.001$) and logs ($\chi^2_{(0.05,\ 12)} = 170.9$, $P<.001$) (Figure 4.2). Very low bark cover was recorded for most severely (46.3%) or very severely (78.4%) burned trees whereas the great majority (66.9%) of lightly burned trees still retained a very high bark cover.

4.5.4 Snag falling rate

Post-fire snag falling was strongly affected by fire severity. The model including only fire severity received the highest level of support among the four tested models but its weight was rather low ($\omega = .363$, Table 4.4). Yet, including other variables in models did not change much AIC_c and deviance values (Table 4.4). Snag falling rate was inversely related to fire severity. Thirty-three percent of the lightly burned trees were still standing compare to 55 % for very severely burned trees (Table 4.5). Assuming a negative exponential model, snag falling rate varied from 0.035 ($T_{50} = 20.0$ years) for very severely burned trees to 0.065 ($T_{50} = 10.7$ years) for lightly burned trees (Table 4.5).

4.6 Discussion

This study is among the very few (e.g. Bond-Lamberty et al. 2002; Manies et al. 2005; Boulanger and Sirois 2006; Shorohova et al. 2008; Angers 2010) that have studied the decomposition of CWD in a post-fire context. Indeed, our results show that among the numerous factors that are likely to influence the decomposition rate of post-fire killed trees, fire severity was the most important one.

4.6.1 Decomposition rate (k_m)

Estimated decomposition rate (k_m=.013) of fire-killed black spruce was relatively low compared to other *Picea* species in northern Europe and boreal North America, although it lies within the range previously noticed for these taxa (cf. Harmon et al. 1986; Laiho and Prescott 2004). Average decomposition rates for spruce species varied between 0.02 and 0.035 (e.g. Harmon et al. 1986; Rock et al. 2008; Angers et al. 2010) although slower rates have been noticed elsewhere (Boulanger and Sirois 2006; Angers 2010). Although such low decay rates may be a consequence of the relatively cold climatic conditions and low associated microbes and fungal respiration (Wang et al. 2002; Trofymow et al. 2002) prevailing in the study area, the post-fire context is thought to have strongly slowed the CWD decomposition process.

4.6.2 Effects of tree- and plot-level variables on k_m

Tree-level variables were much more important than plot-level ones for predicting post-fire wood density losses. Plot-level impact of fire severity as measured from the basal area of living trees was probably embedded in effects of fire severity measured at the tree-level as both predictors are likely to be highly collinear. Among tree-level factors, vertical position and fire severity were the most important predictors of wood density loss of fire-killed black spruce; to a lesser extent, CWD diameter and initial wood density had also a positive effect on wood density loss. Wood density loss clearly increased when CWD had a higher contact with the ground and as fire severity decreased. Logs were two to three times more decayed (cumulative k_m=.017 ; k_m since fall = .023) than snags (k_m=0.009), a finding consistent with earlier studies (Harmon et al. 1986; Boulanger and Sirois 2006). Increasing fire severity strongly depleted the decomposition rate of fire-killed black spruce. Very severely burned trees, especially those that were still standing, were virtually undecayed (k_m=.001) and showed decomposition rates among the slowest ever recorded for spruce species. Boulanger and Sirois (2006) found similar decomposition rates ($k_m = 0.00 - 0.021$) in the study area for severely burned fire-killed black spruce. At the other end, decomposition rates for lightly burned trees (snags: $k_m = 0.018$; logs: $k_m = 0.036$) were similar to those noticed for *Picea* CWD produced in comparable unburned northern boreal ecosystems (e.g. Krankina and Harmon 1995; Naesset 1999; Laiho and Prescott 2004; Angers et al. 2010).

Except for initial wood density, all tree-level variables had a direct impact on moisture content, which may strongly affect post-fire CWD decomposition rates. Laiho and Prescott (2004) already mentioned that environmental factors likely to affect the decay rate of CWD are mostly the derivatives of temperature, moisture and aeration of the substrate. Moisture content is viewed as one of the main factor limiting CWD decomposition (Harmon et al. 1986; Boulanger and Sirois 2006). Wang et al. (2002) found that CWD decay rate was strongly dependant on moisture content below 43.1%. It is generally assumed that fungal wood decomposers, especially basidiomycetes, virtually cease respiration activities below 30% of the fibre saturation point (Erickson et al. 1985; Rayner and Boddy 1988). Logs, especially those with close contact to the ground had much more moisture than snags. Causes of higher moisture content in logs are obvious as this type of CWD is less subject to wind dessication compared to snags. Moreover, higher humidity can be provided by passive uptake from the soil for logs with close contact to the ground. Likewise, smaller diameter CWD tends to dry more rapidly (Erickson et al. 1985) which should hamper wood density loss.

Fire severity strongly influenced moisture content as it never exceeded 40% in severely and very severely burned trees, except for logs in very close (>70 %) contact to the ground. Effect of fire severity on moisture content was only noticed for logs as moisture content in snags was similar among fire severity classes. High fire severity strongly depleted moisture content in post-fire CWD by means of faster bark shedding. In this study, bark shedding was much faster as fire severity increased. Debarked trees should experience faster moisture loss which in turn dampens decay of wood (Rayner and Boddy 1988). Fast bark shedding was already noticed in severely burned trees (Wikars 2002; Boulanger and Sirois 2006, Angers 2010) and was identified as a major factor influencing moisture loss of post-fire CWD (Boulanger and Sirois 2006). In lightly burned logs, high bark cover may help to retain moisture from both precipitations and soil as opposed to snags. One may therefore hypothesize that high bark cover was probably not sufficient to lessen moisture loss from wind desiccation in snags. Nevertheless, snags with high bark cover were more decayed than debarked ones. Consequently, potential effect of bark cover on moisture content in snags should not be ruled out. Studies have shown that moisture content in snags clearly decreases from time since tree death (Boulanger and Sirois 2006). Slower bark shedding rate in lightly burned snags may have reduce the rate of moisture loss and maintain the fungal decomposition activities for a longer time period after fire than in severely burned trees that experienced faster bark shedding. As snags in this study were still standing after a long time period (17 years), most individuals have probably already attained stable low moisture content and differing rates of moisture losses related to fire severity (and by extension to bark cover) may have been overlooked.

4.6.3. Snag falling rates and fire severity

Fire severity also affected the overall decomposition rate of post-fire CWD by strongly influencing the snag falling rate. These rates were relatively low compared to values obtained for *Picea* spp. snags in unburned forests (Krankina and Harmon 1995; Angers et al. 2010), although some authors found lower rates elsewhere

(Storaunet and Rolstad 2004; Aakala et al. 2008). Similar falling rates were already recorded in a post-fire context (Boulanger and Sirois 2006; Bond-Lamberty and Gower 2008; Hageman et al. 2009) though others (Passavoy and Fulé 2006; Angers 2010) reported much faster rates. Snag falling rate was almost two-times slower (k_f = .035) for very severely burned trees compared to lightly burned trees (k_f = .065). This result is quite surprising as one may hypothesize that severe fire may expose the root system and make snags more vulnerable to blowdown. However, the only other study that has assessed the effect of fire severity on snag falling rate (Angers 2010) found a similar result. As lightly burned snags decompose much faster than severely burned ones, they probably become more rapidly susceptible to stem breakage with time since tree death (Everett et al. 1999; Angers 2010). As more decayed fire-killed trees may have fallen earlier, reported decomposition rates for snags are probably underestimated. As such, log decomposition rates are rather overestimated as wood density at time of falling may have been lower than currently estimated.

Although such effect was not investigated in the present study, one should not rule out the potential impact of early xylophagous colonizers on the decomposition rate of burned trees. Several of these taxa may affect the subsequent decomposition of CWD (Edmonds and Eglitis 1989; Schowalter 1992) by vectorizing fungi in dead wood (Kirisits 2004) As most of these species colonize more intensively lightly than severely burned trees (Saint-Germain et al. 2004), this may also explain the faster decomposition rates in such post-fire conditions. Moreover, greater tunnelling by xylophagous larvae in snags, especially at lower portions of the trunk (Saint-Germain et al. 2004), may have weakened lightly burned snags and hasten its fall to the ground.

One must note that, as opposed to the use of chronosequence or other types of time series, our use of wood density loss data coming from a single fire year (1989) may have overlooked potential changes in this process since tree's death. Indeed, this method rather measured the cumulative effects of various factors on the resulting wood density 17 years after fire. Therefore, the present study does not take into account potential changes in decomposition rates over time. Even though the negative exponential model is the most widely used to model the decomposition of wood since tree death (Harmon et al. 1986), Yatskov et al. (2003) found that it was not always appropriate as rates may vary with time after tree death. Moreover, results may have been different if older or younger burned patches would have been considered. Allowing for contrasting decay rates among trees and plots, variation in wood density loss would be likely to increase with time after tree death. Indeed, factors studied may have been more discriminating if older burns would have been sampled.

4.6.4 Concluding remarks

This study showed that fire severity was the most important variable to affect the decomposition of post-fire CWD. As a result, gross carbon release from dead wood should be spatially heterogeneous throughout the post-fire landscape, as it strongly depends on fire severity and dead wood volume. Although such hypothesis was not investigated in the present study, fire severity may affect the long term soil carbon storage. Indeed, very severely burned trees may participate to a larger extent to the carbon storage of the organic layers (Manies et al. 2005). As these debris decay more slowly, they have more chance to be buried by growing sphagnum than lightly burned trees. Along with net primary production estimates as well as other bio- and necromass respiration data collected after fire, such finer estimates of the decomposition rates of dead wood in a post-fire context may help to refine both local (Manies et al. 2005) and continental carbon cycling models (Bond-Lamberty et al. 2007).

Table 4.1. Tree- and stand-level variables used in the different regression models tested in the present study.

Variables	Description	Mean (Min-Max)
Tree level		
Contact0	Snag	Dummy
Contact1	Log, <10% contact with ground	Dummy
Contact2	Log, 10-40% contact with ground	Dummy
Contact3	Log, 41-70% contact with ground	Dummy
Contact4	Log, >70% contact with ground	Dummy
Fire	Fire severity on the trunk (1 : Highest burned twigs found in the 1st quarter of the total CWD length or height; 2: 2nd quarter; 3: 3rd quarter; 4: last quarter)	1* (1-4)
Dmax	Maximum diameter of CWD (cm)	13.2 (10.0-29.1)
InitDens	Estimated initial density of wood ($g.cm^{-3}$)	.504 (.383-.539)
Plot level		
Abiotic variables		
Drainage	Drainage classes (1 : bare rock to 6 : bog)	1-6
Slope_north	North (271-360° and 0-90°) aspect slope	Dummy
Slope_south	South (91-270°) aspect slope	Dummy
Slope_angle	Slope angle (%)	3.1 (0.0-24.0)
Biotic variables		
Shrub	Shrub cover (0: <10; 1: 10-30; 2: 31-50; 3: 51-70; 4: >70 %)	0* (0-4)
LivTree	Basal_area ($m^2.ha^{-1}$) of living trees	1.2 (0-15.0)

* Mode

Table 4.2. Mean decomposition rates (k_m) of snags and logs as a function of fire severity.

Fire severity	**Snag**		**Log**				
	Mean density (g.cm^{-3})	**k**	**Mean density (g.cm^{-3})**	**Cumulative k**	**Mean initial wood density (g.cm^{-3})**	**Mean wood density at snag fall (g.cm^{-3})***	**k since snag fall***
Light	.418 ± .096	.018 ± .020	.334 ± .110	.027 ± .021	.509 ± .027	.437 ± .023	0.036 ± .042
Moderate	.436 ± .110	.015 ± .021	.364 ± .115	.017 ± .021	.481 ± .038	.424 ± .034	0.019 ± .042
Severe	.470 ± .064	.005 ± .009	.438 ± .094	.009 ± .017	.498 ± .023	.477 ± .022	0.012 ± .034
Very severe	.508 ± .052	.001 ± .006	.449 ± 0.80	.007 ± .012	.504 ± .024	.500 ± .026	0.015 ± .025
Overall	**.465 ± .086**	**.009 ± .017**	**.385 ± .114**	**.017 ± .020**	**.501 ± .030**	**.458 ± .039**	**.023 ± .038**

*mean time since snag fall was estimated at $t_{17}/2$ (8.5 years) assuming a constant falling rate.

Table 4.3. Results from the best mixed regression model according to AIC_c used to predict a) the percentage of wood density loss (Sb8; k=9, AICc=4037.54, ω =0.999, Null deviance=145.55, R^2_{LR} = .306) and b) moisture content (Sb8; k=9, AICc=4735.94, ω =1.000, Null deviance=241.71, R^2_{LR} = .451) in CWD at the tree level.

	Wood density loss		**Moisture**	
Variables	**P[*]**	**Deviance[†]**	**P**	**Deviance**
Contact0	---[‡]	20.13[§]	---	132.27[‖]
Contact1	---		---	
Contact2	--		---	
Contact3	n.s.		-	
Fire	---	34.96	---	22.27
Dmax	+++	13.67	+++	15.29
InitDens	+++	13.53	n.s.	2.33
Contact0*Fire	n.s.	.26	+++	12.32

[*] Assessed from ANOVA between reduced and full models

[†] Deviance difference between the reduced and the full models

[‡] n.s.: not significant; +,-: P<0.05; ++,--: P<0.01; +++,---: P<0.001.

[§] Cumulate Δdeviance for all dummy variables

Table 4.4. Parameter estimates for the four regression models as well as the null model used to predict snag falling rate after fire.

Models	k	AIC$_c$	ω	Deviance
Null model*	2	-	-	645.1
Plot Fire	3	625.57	.363	623.3
Plot Fire InitDens	4	626.15	.271	622.7
Plot Fire Dmax	4	626.65	.211	623.2
Plot Fire InitDens Dmax	5	627.28	.154	622.6

*Including the intercept; "Plot" as random effect

Table 4.5. Snag falling rate (k_f) according to fire severity measured on the trunk assuming a negative exponential model.

Fire severity	% standing	k_f	T_{50}	T_{95}
Low (1)	33.3	.065	10.7	46.4
Moderate (2)	41.8	.051	13.5	58.3
Severe (3)	50.0	.041	17	73.5
Very severe (4)	55.5	.035	20.0	86.4

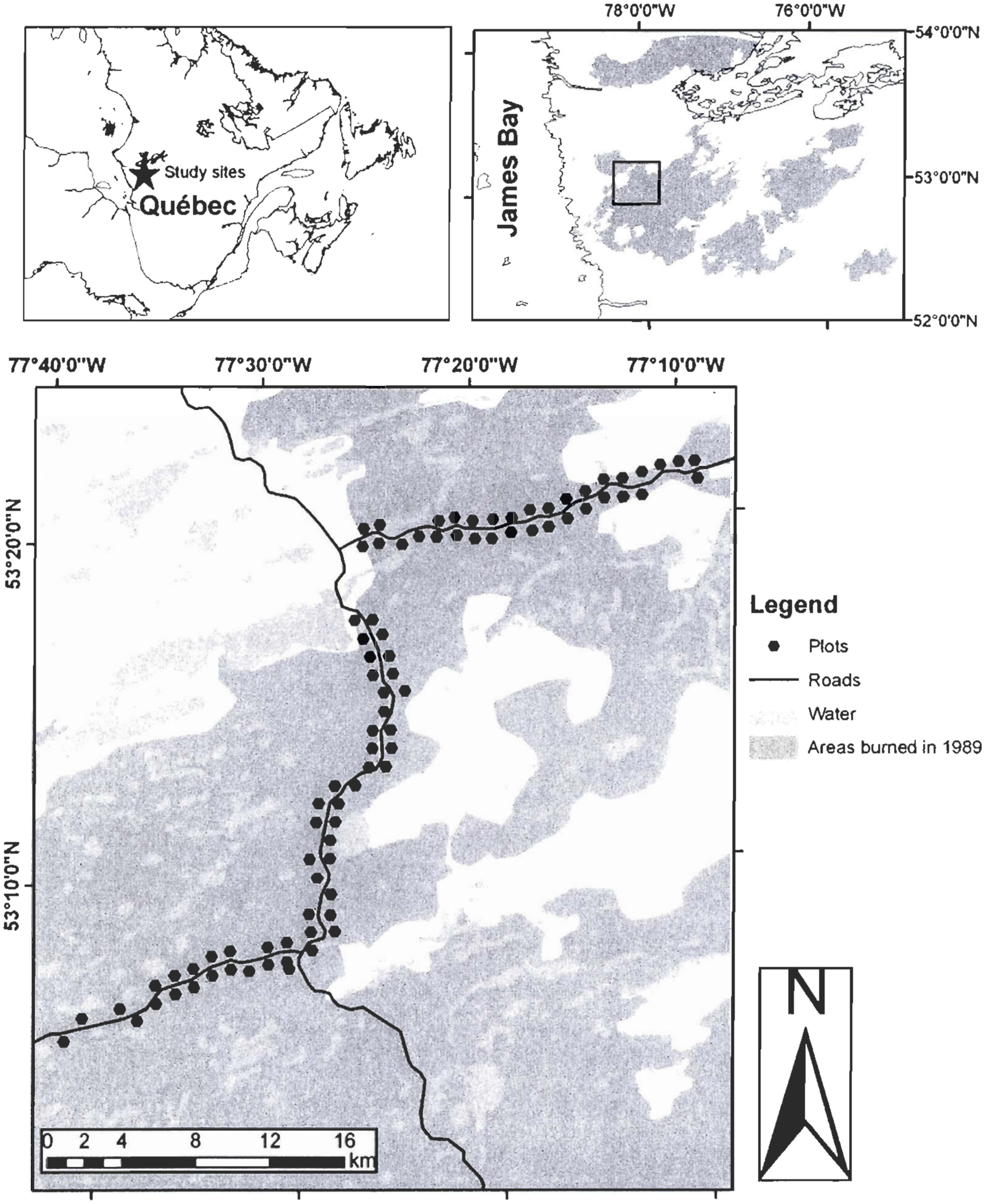

Figure 4.1. Map of the study area and plot location in the 1989 fire.

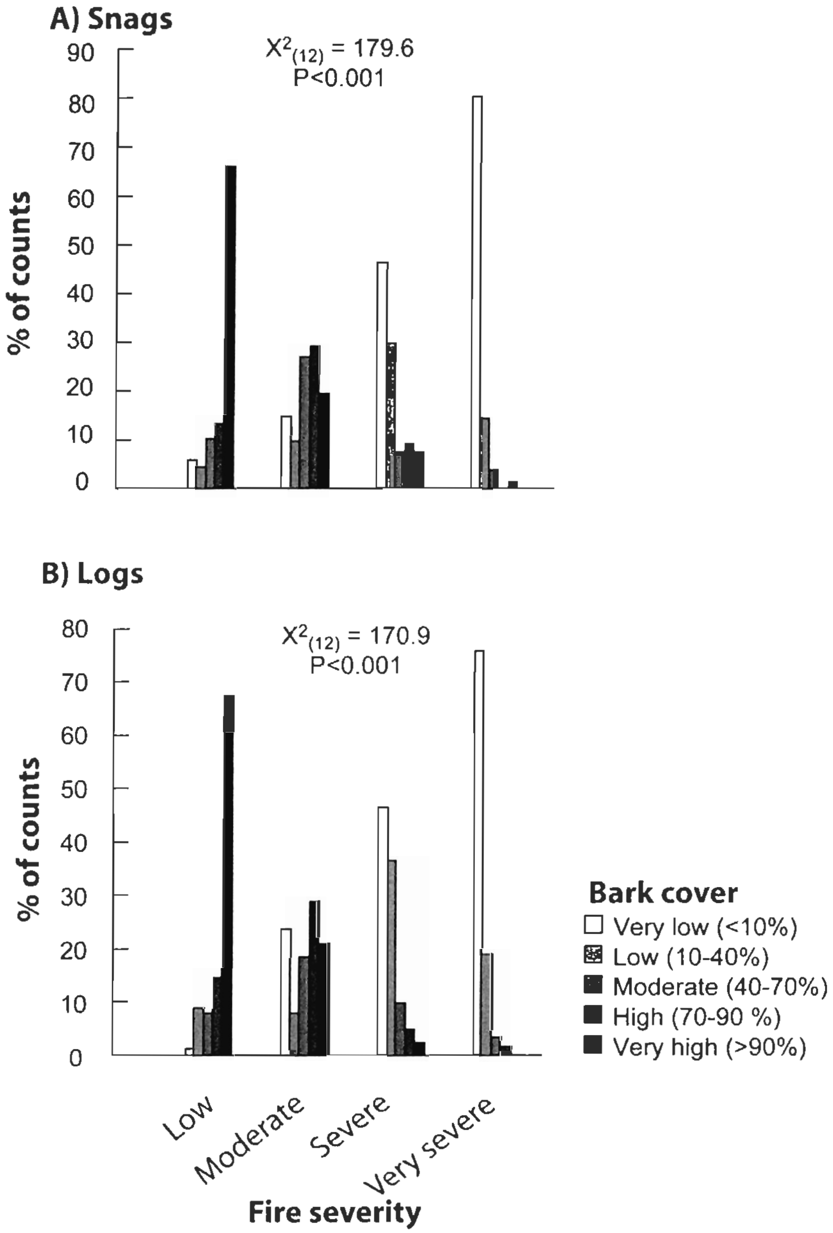

Figure 4.2. Proportions of a) snags and b) logs with very high (>90%), high (70%–90%), moderate (40%–70%), low (10%–40%), and very low (<10%) fractions of bark cover remaining on the trunk.

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DISCUSSION GÉNÉRALE

La sévérité du feu influence fortement le patron de colonisation saproxylique

Pour la très grande majorité des espèces, les caractéristiques de l'habitat brûlé influencent de façon beaucoup plus importante le patron de colonisation. Les attributs de l'habitat brûlé, plus particulièrement, la sévérité du feu, influence le patron de colonisation à de multiples échelles spatiales et ce, à la fois pour les adultes colonisateurs (chapitres 1 et 2) que pour les néonates (chapitre 3). De façon générale, les prédateurs et les xylophages adultes étaient plus abondants dans les paysages et les peuplements sévèrement brûlés alors que la sévérité du feu avait l'impact opposé sur les mycophages.

L'importance de la sévérité du feu sur la colonisation initiale devrait être une conséquence directe de l'impact de cette variable sur les propriétés nutritionnelles du substrat ligneux. Tel que mentionné précédemment, plusieurs espèces mycophages tendent à être plus abondantes dans les peuplements faiblement brûlés. Les substrats ligneux faiblement brûlés seraient moins susceptibles aux températures extrêmes ainsi qu'aux pertes importantes d'humidité (Parmeter 1977, Shorohova et al. 2008), particulièrement dans la région subcorticale. Ces conditions pourraient favoriser la croissance fongique (Harmon et al. 1986), notamment des ascomycètes, lesquels constituent la principale source alimentaire des espèces mycophages rencontrées dans la présente étude.

Pour les mêmes raisons, la sévérité du feu et, en contrecoup la qualité nutritionnelle des tissus subcorticaux, devraient avoir une incidence directe sur les espèces utilisant le substrat ligneux comme site de reproduction. À l'instar de constats effectués dans des études similaires (Richmond and Lejeune 1945; Cerezke 1977; Saint-Germain et al. 2004b, 2004c), l'occurrence et/ou l'abondance de plusieurs taxons xylophages à l'état larvaire était plus importante dans les arbres faiblement brûlés ou encore dans ceux possédant une écorce plus épaisse. Dans le cas des xylophages, l'humidité plus importante en région subcorticale dans ces circonstances pourrait favoriser la survie larvaire (Savely 1939, Furniss 1965, Saint-Germain 2004b,c).

Un comportement de colonisation multi-échelles

Le processus de dispersion et d'attraction vers les habitats où la quantité de volatiles est élevée est à même de fortement influencer le patron de distribution des espèces, processus où la prise en compte de caractéristiques environnementales à grande échelle spatiale est très importante. Ces caractéristiques devraient avoir un impact important pour les espèces possédant des capacités de dispersion importantes; celles-ci devraient percevoir leur environnement à une échelle plus grossière que les espèces à dispersion plus limitée (Wiens 1992; Suarez-Seone and Baudry 2002; Hirao et al 2008). Il a déjà été démontré que les espèces saproxyliques peuvent être influencées par des caractéristiques de l'habitat mesurées à une échelle spatiale plus grossière que le peuplement ou le substrat (Økland et al 1996; Holland et al 2004). De plus, l'orientation vers le substrat est reconnue pour être effective à une échelle relativement grande pour plusieurs espèces xylophages (Saint-Germain et al. 2007b). Notons néanmoins que les caractéristiques de l'habitat brûlé mesurées à des échelles plus fines demeurent tout de même importantes afin de décrire le patron de colonisation. Par conséquent, nous interprétons ce patron comme étant une conséquence directe d'une dynamique d'agrégation impliquant la sélection de caractéristiques de l'habitat brûlé à plusieurs échelles spatiales. En plus de la prise en compte de variables mesurées à des échelles spatiales relativement larges, le processus de dispersion peut subséquemment résulter en une sélection plus fine de l'habitat à mesure que les individus s'orientent vers le substrat à des fins reproductives ou alimentaires (Saint-Germain et al. 2006). Cette sélection multi-échelle serait donc elle-même une conséquence de l'émigration des individus depuis des habitats-sources éloignés.

Un comportement de colonisation non-optimal après feu chez les espèces xylophages

À la lumière des résultats présentés précédemment, cet effet de la sévérité du feu sur la colonisation larvaire des espèces xylophages est particulièrement contre-intuitif : comment les adultes peuvent-ils sélectionner des caractéristiques d'habitat, en l'occurrence les peuplements sévèrement brûlés, qui pourtant, mènent à une production inférieure de néonates? Selon la théorie de l'oviposition optimale, l'adulte devrait sélectionner les caractéristiques d'habitat qui procurent le meilleur fitness (Jaenike 1978; Thompson 1988; Scheirs et DeBruyn 2002). De tels comportements non-optimaux auraient été observés chez quelques espèces de lépidoptères (Rausher 1979) mais aussi chez des espèces de coléoptères saproxyliques (Saint-Germain et al. 2010). Rausher (1979) rapporte que ce type de comportement pourrait notamment s'observer lorsque la qualité de l'habitat varie de façon spatiotemporelle. Ces affirmations suggèrent que si une de ces ressources est beaucoup plus imprévisible dans le temps et dans l'espace que l'autre, les organismes devraient évoluer vers l'utilisation de capacités de détection et d'utilisation du substrat le plus stable spatiotemporellement (Thompson 1988). Ainsi, bien que les espèces xylophages capturées dans le cadre de cette étude aient été rapportées dans le bois brûlé ailleurs (ex. : Werner 2002; Saint-Germain 2004a,b,c; Boulanger et Sirois 2007), la totalité de celles-ci sont reconnues pour utiliser les débris ligneux non-brûlés à des fins reproductives (Hanks 1999; Saint-Germain et al. 2007a). Qui plus est, plusieurs de ces espèces ont été enregistrées à l'intérieur d'écosystèmes où le cycle de récurrence du feu est très long (Saint-Germain et al. 2004a,b,c; Janssen et al.

2009). Les arbres récemment morts retrouvés dans la matrice forestière non-brûlée devraient représenter un substrat pour lequel l'apport temporel et spatial est beaucoup plus stable que les débris ligneux produits par le feu (Siitonen 2001). En effet, l'occurrence des feux de forêts à l'intérieur de l'aire de distribution de ces espèces est très hétérogène à la fois dans l'espace et dans le temps, avec certaines années et certaines régions où les feux sont très rares (Stocks et al. 2002; Saint-Germain et al. 2008). En conséquence, bien que l'abondance des espèces xylophages puisse être accrue dans les écosystèmes où les feux de forêts sont fréquents (Wikars 1992; McCullough et al. 1998), leur survie à long terme dépend surtout des débris ligneux produits en forêt non-brûlée (Saint-Germain et al. 2008). Ainsi, le comportement non-optimal des espèces xylophages dans un contexte postfeu pourrait être le résultat d'une pression de sélection qui amena ces espèces à détecter et utiliser un substrat majoritairement produit en forêt verte plutôt qu'à l'intérieur de forêts brûlées.

Mais comment ce résultat évolutif se traduit dans un contexte postfeu ? Tel que mentionné précédemment, les espèces xylophages utilisent une variété, bien que limitée, d'indices afin de détecter le substrat adéquat. Ces indices permettent surtout de distinguer l'état de l'arbre (vivant, mort récemment ou depuis plus longtemps) ainsi que l'espèce ou le groupe d'espèces impliquées (Allison et al. 2004; Pureswaran et al. 2004). Il demeure probable que la capacité à détecter des indices propres au feu, i.e. la fumée et les infrarouges (Frost 1984; Schütz et al. 1999; Schmitz et al. 2002), puissent jouer un rôle dans la dispersion des adultes xylophages au moment même où le feu est toujours actif. Pourtant, dans le cas présent, l'abondance de plusieurs espèces était toujours, voire plus importante, plusieurs jours (32 à 67 jours) après que le feu se soit éteint (voir appendice A1). De plus, puisque le feu s'est éteint le 9 juin, il est fort probable qu'à cette date hâtive, la plupart des espèces n'aient tout simplement pas ou tout juste débuté leur période de vol (Yanega 1996, Y. Boulanger, obs. pers.). Par conséquent, la plupart des individus colonisateurs durent surtout utiliser des indices autres que la fumée et les infra-fouges afin de localiser le substrat. Ces indices ne devraient pas différer de ceux émis par les arbres morts en forêt non-brûlée (ex. : éthanol, α-pinene, Chénier et Philogène 1989; Allison et al. 2001). De plus, il serait surprenant que les espèces aient pu acquérir la capacité de distinguer à grande distance les arbres faiblement brûlés de ceux sévèrement brûlés puisque tous deux devraient émettre les mêmes volatiles quoiqu'en quantités différentes (Kelsey et Joseph 2003). Utilisant surtout des volatiles émis par des arbres récemment morts (qu'ils soient tués par le feu ou autrement), les individus se seraient donc majoritairement dirigés dans les paysages ou les peuplements contenant davantage de ces volatiles, en l'occurrence les peuplements sévèrement brûlés.

Les paysages où la concentration en volatiles est plus élevée devraient attirer davantage d'individus en dispersion utilisant ces composés afin de localiser des hôtes potentiels (Kelsey et Joseph 1999; Pureswaran et al. 2004). Il a été démontré des quantités importantes d'éthanol, un composé organique volatile constituant un attractant pour plusieurs espèces xylophages notamment (Allison et al. 2004), pouvaient être émis des arbres sévèrement brûlés (Kelsey et Joseph 2003) ainsi que de ceux soumis à des températures élevées et aux fortes radiations solaires (Kelsey et Joseph 1999). Ainsi, la plus grande abondance à très grande échelle de plusieurs espèces dans les paysages sévèrement brûlés pourrait justement être liée à la plus grande concentration de volatiles que ces paysages émettent et ainsi à leur plus grand pouvoir attractif sur des individus provenant majoritairement de sources éloignées. Qui plus est, ceci pourrait expliquer l'évitement des paysages faiblement brûlés ou comportant une forte proportion de peuplements non-brûlé à grande échelle.

Est-ce qu'un tel comportement non-optimal pourrait nécessairement affecter négativement le fitness des espèces colonisant les brulis ? En effet, d'aucuns pourraient voir cette stratégie comme étant très coûteuse dans un contexte postfeu comparativement à ce qui pourrait prévaloir en forêt non-brûlée. En plus de l'hypothèse soulevée précédemment, Rausher (1979) mentionne qu'une stratégie non-optimale peut être utilisée lorsque le « taux de découverte » du substrat est plus élevé dans un habitat pourtant de plus faible qualité. Ainsi, malgré une plus faible survie larvaire *per se* dans les arbres sévèrement brûlés, un tel comportement pourrait tout de même permettre de produire une grande quantité de néonates considérant la disparité entre la quantité de substrat disponible dans les brulis comparativement à celle observée dans la matrice non-brûlée. Conséquemment, malgré ce comportement non-optimal, les brulis peuvent tout de même représenter une opportunité pour les espèces xylophages.

Dispersion des adultes et patrons de colonisation

Les analyses laissent présager que l'éloignement des sources de colonisation potentielle aurait peu d'impacts sur la capacité des coléoptères saproxyliques adultes à atteindre l'habitat à coloniser. L'abondance des sources locales potentielles (e.g. débris ligneux présents avant feu), n'avait que très peu d'influence positive sur l'abondance des adultes colonisateurs. Qui plus est, à de rares exceptions, l'abondance ou l'occurrence de la très grande majorité des adultes colonisateurs était peu ou pas négativement influencée par la présence de peuplements non-brûlés à proximité, par l'éloignement de la matrice forestière ou d'autres peuplements brûlés récemment. En conséquence, l'éloignement des sources de colonisation n'eut qu'une influence limitée sur la structure d'autocorrélation spatiale des adultes l'année même du feu ainsi que sur la production subséquente de néonates xylophages.

D'aucuns pourraient ainsi en conclure que l'absence d'effets négatifs de l'éloignement des sources de colonisation potentielles, du moins à l'intérieur des limites géographiques imposées par le dispositif d'échantillonnage, serait conséquente aux très fortes capacités de dispersion présumées des espèces colonisatrices initiales. En effet, il est généralement admis que les espèces colonisant les débris ligneux nouvellement créés possèdent des capacités de détection et de dispersion importantes (Byers 2000; Bouget 2005) considérant la nature imprévisible et éphémère du substrat. En effet, plusieurs espèces rencontrées dans cette étude sont reconnues pour être activement attirées par la fumée (Frost 1984), les infrarouges (Schmitz et al. 2002) ou différents composés organiques volatiles émis par le substrat, leurs conspécifiques ou leurs proies (Allison et al. 2001; Allison et al. 2004). Certaines études expérimentales suggèrent d'ailleurs que plusieurs espèces saproxyliques initiales, des scolytes en l'occurrence, auraient les capacités nécessaires pour voler activement sur plusieurs dizaines de kilomètres (Atkins 1961, Jactel et Gaillard 1991). Par ailleurs, l'effet négatif de l'éloignement des feux récents sur des espèces majoritairement mycophages, pourrait résulter des plus faibles capacités de dispersion de ces organismes comparativement aux prédateurs et aux xylophages. Plusieurs espèces mycophages associées aux classes de décomposition avancées des débris ligneux, possèdent de très faibles capacités de dispersion, celles-ci allant d'une dizaine à quelques centaines de mètres (Ranius and Hedin 2001; Jonsson 2002). De façon évidente, ces débris ligneux constituent un habitat beaucoup plus stable et beaucoup moins imprévisible dans l'espace et dans le temps que l'habitat récemment brûlé (Siitonen 2001). Par conséquent, les capacités de dispersion des espèces mycophages retrouvées peu de temps après feu pourraient leur permettre d'accéder à des habitats potentiels situés à des distances beaucoup plus importantes.

L'interprétation de tels résultats se doit d'être prudente. En effet, plusieurs variables reliées à la dispersion depuis des habitats sources potentiels sont potentiellement colinéaires avec d'autres variables reliées à l'environnement brûlé. Ainsi, les peuplements faiblement brûlés devraient être plus abondants près des forêts non-brûlées alors que les habitats les plus sévèrement brûlés étaient aussi ceux les plus éloignés des feux de 2002. De plus, d'autres caractéristiques du paysage qui ne furent pas considérées dans cette étude (ex. : effet de bordure, complexité du paysage ou des patches) ont pu affecter la distribution spatiale des espèces saproxyliques (Holland et al. 2004, Wiens et Milne 1989). Bien que les sources locales ne semblent pas avoir eu un impact positif sur la colonisation postfeu, la dispersion d'individus survivants au feu et ce, depuis des habitats situés à proximité des points d'échantillonnage, ne peut être exclue complètement. Certaines études ont en effet démontré que les arthropodes épigés peuvent survivre à des feux de faible intensité (Ahlgren 1974, Paquin and Coderre 1997, Wikars and Schimell 2001). Dans une étude récente, Ulyshen et al. (2010) ont noté que certains coléoptères saproxyliques pouvaient survivre à des feux dirigés, de faible intensité. Néanmoins, la probabilité de survie des espèces saproxyliques, notamment des espèces subcorticales, après un feu naturel plus intense, est largement inconnue. Considérant ces incertitudes, l'importance relative des différents habitats sources dans le processus de colonisation postfeu demeure à démontrer.

Colonisation saproxylique et paradigme des métacommunautés

Il est de plus en plus admis que les les communautés locales peuvent être influencés par des phénomènes de dispersion liant ces mêmes communautés (Leibold et al. 2004). Par exemple, la théorie de la biogéographie insulaire (MacArthur et Wilson, 1967) ainsi que la théorie unifiée de la biodiversité et de la biogéographie (Hubbell, 2001) prédisent que les limitations imposées par la dispersion devraient grandement influencer la probabilité des individus à migrer vers l'habitat adéquat. Plusieurs modèles décrivant la dynamique spatiale de telles métacommunautés ont été décrits, lesquels se basent sur une influence plus ou moins grande des caractéristiques environnementales et de la dispersion. Le processus de colonisation postfeu implique nécessairement une forte dispersion des individus vers le nouvel environnement colonisable. Par conséquent, on devrait s'attendre à ce que ce processus se conforme à des modèles de métacommunauté impliquant de fortes influences des phénomènes de dispersion (ex. : *patch dynamic, mass effect*) (Leibold et al. 2004, Cottenie 2005). Ceci s'applique bien que les analyses démontrent un effet peu important de l'éloignement des sources de colonisation sur l'abondance locale. Conséquemment, l'échelle spatiale (et temporelle) de la présente étude n'était probablement pas suffisamment grande afin de pouvoir confirmer à quel modèle se conforment les métacommunautés postfeu.

La sévérité du feu affecte fortement la décomposition des débris ligneux

Le taux de décomposition moyen mesuré chez les épinettes noires brûlées ($k = 0,013$) dans le cadre de cette étude est relativement bas lorsque comparé à celui enregistré pour d'autres espèces d'épinettes (majoritairement entre 0,02 et 0,035) à l'intérieur d'écosystèmes boréaux (cf. Harmon et al. 1986; Laiho and Prescott 2004; Rock et al. 2008; Angers et al. 2010). Ce faible taux de décomposition serait directement relié au contexte postfeu. En effet, la sévérité du feu influence négativement les taux de décomposition notamment en accélérant la perte d'humidité et la chute de l'écorce, en ralentissant la fragmentation des chicots ainsi qu'en défavorisant la colonisation d'espèces saproxyliques.

La sévérité du feu influence fortement le contenu en eau des débris ligneux, celui-ci ne dépassant jamais 40 % chez les arbres très sévèrement et sévèrement brûlés, à l'exception des débris ligneux ayant une grande surface de contact avec le sol. Le taux d'humidité est généralement un des éléments limitant le plus la décomposition des débris ligneux (Harmon et al. 1986; Boulanger et Sirois 2006). En effet, les champignons impliqués dans la décomposition de la matière ligneuse, essentiellement des basidiomycètes, cessent virtuellement leurs activités détritiques lorsque le taux d'humidité est inférieur à 30 % du point de saturation des fibres (Erickson et al. 1985; Harmon et al. 1986; Rayner et Boddy 1988). Dans le cadre de cette étude, nous avons observé une chute de l'écorce plus rapide chez les arbres fortement brûlés. Le taux de perte du couvert cortical était d'ailleurs deux fois plus rapide chez ces individus que chez les arbres faiblement brûlés. Les arbres perdant plus rapidement leur couvert cortical serait plus assujettis aux pertes d'humidité ce qui affecterait directement le taux de décomposition (Rayner and Boddy 1988). Une perte plus lente du couvert cortical chez les arbres faiblement brûlés pourrait avoir réduit les pertes d'humidité dans les chicots et ainsi avoir maintenu l'activité détritique fongique sur une plus longue période.

La sévérité du feu influence fortement le taux de chute au sol des chicots. Ainsi, les taux de fragmentation des chicots étaient près de deux fois plus rapides chez les arbres faiblement brûlés (k = 0,065) comparativement à ceux notés pour les arbres sévèrement brûlés (k = 0,035). Le taux de chute pour l'épinette noire dans le présent contexte postfeu était relativement bas (voir aussi Boulanger et Sirois 2006; Bond-Lamberty et Gower 2008; Hageman et al. 2009) comparativement à celui observé en forêt non-brûlée (Krankina et Harmon 1995; Angers et al. 2010) bien qu'il n'y ait pas de tendance générale à tirer de la littérature (voir Storaunet et Rolstad 2004; Aakala et al. 2008 pour des résultats opposés). Les chicots faiblement brûlés se décomposant plus rapidement, ils deviendraient susceptibles de casser ou de renverser plus rapidement que ceux plus sévèrement brûlés (Everett et al. 1999; Angers et al. 2010). Du même coup, cette influence sur le taux de chute des chicots agirait directement sur le taux de décomposition de la matière ligneuse puisque les chicots, de manière générale, se décomposent beaucoup plus lentement que les débris ligneux au sol. En effet, les débris ligneux au sol étaient généralement deux à trois fois plus décomposés (k = 0,017-0,025) que les chicots (k =0,009). Ceci serait une conséquence directe des plus hauts taux d'humidité chez les débris au sol, *a fortiori* pour ceux ayant une grande surface de contact avec le sol. Cependant, les arbres plus fortement décomposés ayant pu chuter au sol plus rapidement, les taux de décomposition des chicots est probablement sous-estimé alors que celui des débris au sol serait surestimé.

Une influence de la colonisation saproxylique initiale sur les taux de décomposition ?

Tel que mentionné ci-dessus, la colonisation des espèces xylophages serait beaucoup plus importante dans les arbres faiblement brûlés. Est-ce qu'une plus forte colonisation initiale aurait entraîné des taux de décomposition plus élevés chez les débris ligneux d'épinette noire ? Évidemment, cette étude n'a pu vérifier expérimentalement si cette relation est effectivement causale plutôt que simplement corrélative. Toutefois, plusieurs auteurs rapportent que les espèces xylophages pourraient avoir une influence non négligeable sur la vitesse de décomposition du bois mort (Ausmus 1977; Schowalter 1992; Progar et al. 2000). Certaines études expérimentales simulant la pénétration des insectes dans le phloème et le xylème (Edmonds et Eglitis 1989, Marra et Edmonds 1996; Barker 2008) rapportent des taux de décomposition plus élevés chez les débris fortement « colonisés ». Ainsi, les espèces xylophages accéléreraient la décomposition en fournissant un accès à la matière ligneuse et des conditions micro-environnementales adéquates pour la croissance fongique. De plus, bien que le phénomène n'ait été que très peu investigué, il demeure possible que les adultes soient des vecteurs passifs ou actifs de propagules fongiques (Garcia et Morrell 1999) ce qui pourrait aussi influencer le processus de décomposition. Une étude plus approfondie de ce lien serait nécessaire afin de clarifier l'impact présumé de la colonisation saproxylique postfeu.

Un impact sur la succession saproxylique ?

D'aucuns pourraient stipuler que l'impact de la sévérité du feu sur les taux de décomposition pourrait se traduire sur d'autres processus écologiques associés aux débris ligneux. Dans le cas présent, nous nous sommes concentrés sur la phase initiale de colonisation des arbres brûlés. Ces espèces colonisent le bois mort très tôt après feu (Saint-Germain et al. 2004b; Muona et Rutanen 1994; Hjältén et al. 2007) alors que leur abondance diminue rapidement durant les années subséquentes (Boulanger et Sirois 2007). D'autres assemblages saproxyliques succèdent aux espèces colonisatrices initiales à mesure que les propriétés physiques (ex. : humidité, colonisation fongique, densité du bois) des débris ligneux changent en fonction du temps après feu (Økland et al. 1996; Boulanger et Sirois 2006, 2007). Cette succession est donc très dépendante du stade de décomposition des débris ligneux (Howden et Vogt 1951; Økland et al. 1996; Saint-Germain et al. 2007a). En raison de la quasi-absence de décomposition chez les chicots sévèrement brûlés, Boulanger et Sirois (2007) ont démontré que la succession saproxylique ne s'effectuait qu'une fois le débris au sol. Ainsi, de par son influence sur les taux de décomposition, on pourrait s'attendre à ce que le processus de succession soit particulièrement différent en fonction de la sévérité du feu. Une faible sévérité du feu pourrait accélérer le processus de succession saproxylique en amenant plus rapidement le débris ligneux aux stades de décomposition appropriés à chacun des assemblages. Considérant que le processus de décomposition s'amorce rapidement dans les chicots faiblement brûlés, cette succession pourrait débuter avant même que ces derniers ne tombent au sol, contrairement à ce qui est observé dans les arbres sévèrement brûlés. D'un autre côté, la chute rapide des chicots faiblement brûlés devrait donner un accès plus rapide à la matière ligneuse aux espèces endogées. Parallèlement, cette succession rapide des espèces pourrait elle-même accélérer le processus de minéralisation des débris ligneux (Edmonds et Eglitis 1989). Ainsi, bien que très importante dans le processus initial de colonisation, la sévérité du feu pourrait influencer l'entomofaune saproxylique sur une très longue période.

CONCLUSIONS ET PERSPECTIVES D'AVENIR

Cette étude est la seule à ce jour traitant à la fois de la décomposition du bois et de la colonisation saproxylique dans un contexte postfeu. Elle met en lumière deux éléments d'importance concernant les processus écologiques liés au bois mort après feu à savoir l'importance de la sévérité du feu dans la structuration des patrons de colonisation de ces insectes mais aussi sur le processus de décomposition de la matière ligneuse. De plus, les résultats suggèrent que l'isolement des habitats à coloniser n'a que peu ou pas d'impact sur les espèces saproxyliques. Ce serait plutôt les caractéristiques de l'habitat brûlé, *a fortiori* la sévérité du feu, qui auraient la plus grande influence sur le patron de colonisation et ce, à la fois à l'échelle de l'arbre, du peuplement et du paysage. En retour, l'influence de la sévérité du feu sur la colonisation des espèces xylophages pourrait être partiellement responsable des taux de décomposition plus rapides enregistrés chez les arbres faiblement brûlés.

Cette étude apporte un éclairage supplémentaire sur les connaissances amassées au cours des dernières décennies sur les questions touchant le bois mort. Malgré que ses objectifs demeurent limités à une problématique bien circonscrite, il n'en demeure pas moins qu'elle soulève des interrogations supplémentaires. De plus, elle suggère des interprétations pouvant être généralisées aux processus concernant les débris ligneux produits en forêt verte.

Colonisation postfeu comparativement à celle en forêt verte

La dissection du patron de colonisation des espèces saproxyliques initiales suggère que ce processus est profondément différent de celui prévalant en forêt non-brûlée (Økland et al 1996; Saint-Germain et al 2007a). Dans les deux cas, la colonisation fait intervenir des déterminants pouvant se mesurer à des échelles spatiales multiples (voir aussi Holland et al. 2004). Toutefois, cette étude met en lumière que le contexte postfeu *nécessite* la considération d'échelles spatiales beaucoup plus grandes. Contrairement aux individus colonisant les débris ligneux produits en forêt non brûlée, ceux retrouvés après feu doivent se disperser sur des distances beaucoup plus considérables afin d'atteindre le substrat.

Changement dans la récurrence des feux et colonisation saproxylique

D'autre part, il y a de plus en plus d'évidences indiquant que cycle de récurrence du feu dans le nord-ouest du Québec s'est considérablement réduit depuis la fin du petit âge glaciaire (Parisien et Sirois 2003; Arseneault et Sirois 2004; Héon et al. en préparation), une tendance qui devrait s'accentuer au cours du XXI^{e} siècle (Stocks et al. 1998; Flannigan et al. 2005; Le Goff et al. 2009). Durant cette période, plusieurs grands feux (1922, 1941, 1989) auraient couvert plusieurs milliers de kilomètres carrés (Couturier et Saint-Martin 1990; D. Arseneault comm. pers). Considérant cet état de fait, on pourrait être en mesure de s'interroger sur l'impact de ces changements récents et futurs du cycle de récurrence des feux sur le niveau local des populations d'insectes colonisateurs initiaux. Saint-Germain et al. (2008) mentionnent que la présence de débris ligneux dans la matrice forestière, plus particulièrement dans les peuplements matures et surannés, est d'une importance capitale afin de maintenir à long terme les populations d'insectes saproxyliques qualifiés de « pyrophiles ». Ces espèces pourraient ainsi maintenir des niveaux de populations plus élevés (et constants) dans les paysages où le cycle de récurrence des feux est long. Dans ces paysages, le volume de débris ligneux adéquat pour la reproduction (c'est-à-dire, d'arbres morts très récemment) aurait davantage tendance à demeurer constant dans le temps et dans l'espace. Ainsi, ces territoires seraient moins susceptibles d'offrir de mauvaises conditions reproductives durant une fenêtre temporelle donnée, lesquelles pourraient autrement mener vers l'extinction locale des espèces colonisatrices. La plus évidente des conséquences d'une telle augmentation de la récurrence des feux de forêts, *a fortiori* des très grands feux, serait la diminution de la surface et l'isolement progressif de l'habitat, notamment des peuplements matures et surannés. Le tout pourrait se traduit par une instabilité spatiotemporelle croissante dans la production de substrat reproductif, augmentant les risques d'extinction locale.

Toutefois, cet isolement de l'habitat est fortement dépendant de l'échelle spatiale, et donc de l'estimation des capacités de dispersion des espèces, considérée lors des analyses. Ainsi, dans l'optique d'une dynamique de métacommunautés (Leibold et al. 2004), où la dispersion entre les communautés est très importante, d'aucuns pourraient envisager que l'abondance des brulis dans un contexte de forte récurrence des feux participe à maintenir des populations saproxyliques régionales très élevées. Ce maintien pourrait se faire via des processus source-puits (Pulliam 1988) où les brulis récents constituent eux-mêmes des sources participant à fournir des individus aux parcelles plus fragmentées ou de plus faible qualité. Par conséquent, l'augmentation du risque d'extinction locale pourrait être moindre qu'envisagé précédemment si les capacités de dispersion des individus sont suffisantes afin de maintenir une grande connectivité entre les habitats de qualité, incluant les brulis et les peuplements matures et surannés, à chaque année.

Changements climatiques et taux de décomposition

Les récents modèles climatiques canadiens (CRCM 3.6.1 et CGCM2) prévoient une augmentation progressive de la température moyenne annuelle (TMA) d'environ 3°C d'ici 2041-2060 pour le nord-ouest du Québec (Environnement Canada 2010). Ainsi, d'aucuns pourraient suggérer que l'augmentation de la température aurait un impact direct sur les taux de décomposition de la matière ligneuse. De façon générale, pour chaque tranche de 10°C (Q10), les taux de décomposition du bois devraient être multipliés par un facteur 2,4 (Chambers et al. 2000, Yatskov et al. 2003). Chez l'épinette noire, ce facteur s'élèverait à 2,5 (Wang et al. 2002). En assumant un tel facteur Q10 ainsi qu'une augmentation de la TMA de 3°C, les taux de décomposition moyens (k_m) après feu passeraient de 0,013 (chapitre 4) à 0,017 en 2041-2061, soit une augmentation de 30,8%. Ceci se traduirait évidemment par une augmentation équivalente des émissions de carbone provenant des débris ligneux produits après feu. Il est cependant difficile d'établir si cette augmentation des taux de décomposition du bois mort (mais aussi de la respiration de l'écosystème en général), se traduira par une augmentation nette des émissions de carbone à long terme dans l'écosystème. En effet, la productivité primaire nette devrait aussi augmenter concurremment avec une hausse de la TMA (Keyser et al. 2000, Barr et al. 2002, mais voir Dunn et al. [2007] pour des résultats opposés). Néanmoins, l'augmentation de la récurrence des feux, notamment de très grands feux, amènerait à court terme de larges territoires à émettre de grandes quantités de carbone stockées sous forme de débris ligneux (Kasischke 2000, Kasischke et Stocks 2002). De plus, à moyen terme, la balance décomposition-production ligneuse pourrait être grandement affectée par une diminution graduelle du couvert forestier suite à une augmentation de la récurrence des feux dans cette région (Payette et al. 1989). Le changement dans le régime des feux au Canada est d'ailleurs considéré comme étant le facteur ayant le plus modifié la balance du carbone en forêt boréale entre 1948 et 2005 (Bond-Lamberty et al. 2007). Les effets à long terme de ces changements environnementaux (modifications du régime des feux et hausse de la température moyenne) sur le bilan global du carbone ligneux demeurent toutefois inconnus et mériteraient une investigation plus poussée (Kurz et al. 1995).

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APPENDICE A

MATÉRIEL SUPPLÉMENTAIRE AU CHAPITRE I

Appendix A1. Abundance of potential saproxylic beetle taxa of different trophic guilds collected during two sampling periods in the 66 plots used in the present study.

Family	Taxa	Codes used in RDA	Trophic guild[a]	Number 7-31 days after fire	 32-66 days after fire
Anobiidae	Dorcatominae sp.		x	1	0
Boridae	*Boros unicolor* Say		uw	15	33
Buprestidae	*Anthaxia inornata* (Randall)		x	3	0
	Buprestis nuttalli (Kirby)	BupNut	x	0	9
	Chrysobothris trinerva (Kirby)	ChrTri	x	3	7
	Melanophila fulvoguttata (Harris)	MelFul	x	13	11
	Oxypteris acuminata (DeGeer)	OxyAcu	x	27	46
Byrrhidae	*Arctobyrrhus subcanus* (LeConte)		o	0	2
	Cytilus alternans (Say)		o	1	0
Cantharidae	Cantharidae sp.		o	38	14
Carabidae	*Bembidion grapei* Gyllenhal		p	2	1
	Carabidae sp.		p	0	1
	Platynus mannerheimii (Dejean)	PlaMan	p	0	9
	Sericoda obsoleta (Say)	SerObs	p	125	202
	Sericoda quadripunctata (DeGeer)	SerQua	p	18	37
	Syntomus americanus (Dejean)	SynAme	p	4	6

Taxa		Codes used	Trophic guild[a]	Number	
	Tachyta angulata Kirby		p	1	1
Cerambycidae	*Acanthocinus pusillus* (Kirby)		x	0	2
	Acmaeops proteus (Kirby)	AcmPro	x	265	540
	Anastrangalia sanguinea (LeConte)		x	3	0
	Arhopalus foveicollis Haldeman	ArhFov	x	6	767
	Asemum striatum (L.)		x	1	0
	Gnathacmaeops pratensis (Laicharting)	GnaPra	x	21	21
	Judolia sexmaculata (L.)		x	1	0
	Monochamus scutellatus (Say)	MonScu	x	33	155
	Neoclytus muricatulus (Kirby)		x	0	3
	Pachyta lamed liturata Kirby	PacLam	x	8	3
	Pogonocherus mixtus Haldeman	PogMix	x	0	28
	Pogonocherus pennicillatus LeConte		x	2	1
	Pygoleptura nigrella (Say)		x	0	2
	Tetropium cinnamopterum (Kirby)		x	1	2
	Trachysida aspera brevifrons Howden		x	2	0
	Xylotrechus undulatus (Say)		x	0	1
Ciidae	*Cis striolatus* Casey	CisStr	m	13	8
	Ciidae sp. 2		m	0	1
Clambidae		ClaSp.	m	16	22
Cleridae	*Thanasimus dubius* (F.)		p	2	0
	Thanasimus undatulus nubilus Klug	ThaUnd	p	1065	2497
Coccinellidae	*Hyperaspis* sp.		o	1	0
Colydiidae	*Lasconotus* sp.		m	0	1

	Taxa	Codes used	Trophic guild[a]	Number	
Corylophidae	*Clypastraea fusca* Harold	ClyFus	m	1006	624
Cryptophagidae	*Atomaria* sp.	AtoSp.	m	123	52
	Caenoscelis sp.	CaeSp	m	169	115
	Cryptophagus corticinus Thomson		m	0	1
	Cryptophagus scanicus (L.)		m	0	1
	Henoticus serratus (Gyllenhal)	HenSer	m	22	19
	Pteryngium crenatum Gyllenhal		m	1	0
Cucujidae	*Pediacus fuscus* Erichson	PedFus	p	45	81
Curculionidae	*Crypturgus borealis* Swaine	CryBor	x	3	5
	Dryocoetes affaber (Mannerheim)		x	0	1
	Dryocoetes autographus (Ratzeburg)	DryAut	x	100	34
	Hylobius congener Dalle Torre and Hustache	HylCon	x	129	61
	Hylobius warrenii Wood		x	3	0
	Ips latidens (LeConte)	IpsLat	x	4	4
	Ips pini (Say)	IpsPin	x	22	6
	Orthotomicus caelatus (Eichhoff)	OrtCae	x	19	7
	Pissodes nemorensis Germar		x	1	0
	Pissodes sp. (*fiskei*?)		x	1	1
	Pityophtorus sp.	PitSp.	x	5	8
	Polygraphus rufipennis (Kirby)		x	3	3
	Rhyncolus macrops Buchanan		x	0	1
	Scolytus piceae Swaine		x	2	0
	Trypodendron lineatum (Olivier)		x	1	0

	Taxa	Codes used	Trophic guild[a]	Number	
Elateridae	*Agriotes limosus* (LeConte)		o	6	1
	Ampedus sp.		s?	3	2
	Ampedus luctuosus (LeConte)		s?	1	0
	Ampedus pullus Germar		s?	5	0
	Ctenicera triundulata (Randall)		o	14	2
	Eanus decoratus (Mannerheim)		o	3	0
	Selatosomus splendens (Ziegler)		o	1	0
	Sericus incongruus (LeConte)		o	5	0
	Setasoma arata (LeConte)		o	1	0
Eucinetidae	*Eucinetus* sp. (*punctulatus* ?)		m	0	1
Histeridae	*Platysoma* sp.		p	0	1
Hydrophilidae	Hydrophilidae sp.		o	1	0
Lampyridae	*Ellychnia corrusca* (L.)		p	1	0
Lathridiidae	*Cartodere constrictus* (Gyllenhal)	CarCon	m	626	205
	Corticaria dentigera LeConte	CorDen	m	482	375
	Corticaria sp. 2	CorSp2	m	2293	558
	Corticarina sp.		m	2	1
	Cortinicara gibbosa (Herbst)		m	0	2
	Melanophtalma sp.	MelSp	m	0	5
Leiodidae	*Agathidium* sp.		m	2	1
	Leiodes sp. (valida?)		m	0	1
Lycidae	*Dictyopterus aurora* (Herbst)		p	1	0
	Plateros sp.		p	2	0

	Taxa	Codes used	Trophic guild[a]	Number	
Melandryidae	*Serropalpus coxalis* Mank	SerCox	x	0	5
	Serropalpus substriatus Haldeman	SerSub	x	0	31
	Xylita laevigata (Hellenius)	XylLae	x	4	2
	Xylita livida Sahlberg		x	0	1
Melyridae	*Hoppingiana hudsonicus* LeConte		o	0	2
Mordellidae	*Tomoxia borealis* (LeConte)		uw	3	2
Nitidulidae	*Epuraea* sp.	EpuSp	m	89	61
	Glischrochilus vittatus (Say)		m	1	0
Ptilidae	*Acrotrichis* sp.		m	2	1
Salpingidae	*Sphaeriestes virescens* (LeConte)	SphVir	p	247	494
Scarabeidae	*Aphodus* sp.		o	0	1
	Phyllophaga sp.		o	0	1
	Serica sp.		o	1	0
Scirtidae	*Cyphon variabilis* (Thunberg)		o	1	6
Scraptidae	*Canifa* sp. (*pallipes*?)		uw	6	11
Scydmanidae	*Euconnus* (*Napochus*) sp.		p	0	1
	Microscymnus (*Delius*) *robustulus* Casey		p	0	1
	Parascymnus corpusculum	ParCor	p	2	4
	Stenichnus sp. (*badius*?)		p	1	0
Silphidae	*Nicrophorus vespilloides* Herbst		o	3	0
Staphylinidae	*Acrotona* sp.		p?	4	0
	Acidota crenata (F.)	AciCre	p	4	4
	Atheta (*Dimetrota*) *campbelli* (Lohse)		p	2	2
	Atheta (*Microdota*) *pennsylvanica*		p	1	0

Taxa	Codes used	Trophic guild[a]	Number	
Bernhauer				
Atheta sp. 1		p	1	0
Atheta sp. 2		p	0	1
Athetini Gen.sp. near *Boreophilia*?		p	2	2
Bibloplectus integer (LeConte)		p	1	0
Boreophilia sp.		p	0	1
Boreostiba sp.		p	0	2
Bryoporus rufescens LeConte		P	0	1
Carpelimus sp.		s?	1	1
Carphacis intrusus (Horn)		p	2	2
Carphacis nepigonensis Camp.		p	0	2
Euaesthetus sp.		p?	1	0
Euplectus sp.	EupSp	p	2	11
Eusphalerum fenyesi (Bernhauer)		o	0	4
Gabrius subnigritulus Smet.		p	0	1
Gyrophaena sp. 1		m	1	0
Gyrophaena sp. 2		m	0	1
Heterothops minor Smet.	HetMin	p	32	22
Homalota plana (Gyllenhal)	HomPla	p	3	4
Leptusa jucunda Klimaszewski & Majka		p+m?	3	2
Lordithon sp.		m	1	0
Megarthrus incisus LeConte		m or s	0	1
Micropeplus tesserula Curtis		m	1	0
Mocyta breviscula (Mäklin)		p	3	0

Taxa	Codes used	Trophic guild[a]	Number	
Nudobius cephalus (Say)		p	1	0
Omaliinae sp.		o	0	1
Omalium rivulare (Paykull)		p	1	0
Omalium sp.		p	1	0
Oxypoda amica Casey	OxyAmi	p	1	10
Oxypoda demissa Casey		p?	1	0
Oxypoda frigida Bernhauer		p?	1	0
Oxypoda lacustris Casey		p	1	0
Oxypoda pseudolacustris Klimaszewski		p	0	3
Phloeopora sp.		uw	2	0
Phloeostiba lapponica (Zett.)		p or s?	122	122
Placusa tacomae Casey	PlaTac	m	7	7
Placusa vaga Casey	Plavag	m	3	6
Porrhodites fenestralis (Zetterstedt)		p?	0	1
Pselaphrus fustifer Casey		p	1	0
Quedius frigidus Smetana		p	0	1
Quedius brunnipennis Mannerheim		p	1	1
Reichenbachia spatulifer Casey	ReiSpa	p	8	12
Scaphidiinae sp.		m	1	0
Siagonum stacesmithi		s	1	0
Stenus sp.	SteSp	p	2	6
Syntomium grahami Hatch		s?	1	0
Tachyporus borealis Campell		p	1	0
Tyrus humeralis Aubé		p	1	0

[a] x: xylophagous, uw: unknown but in wood, m: mycophagous, p: predaceous, s: saprophagous, o: others.

Appendix A2. Candidate models used to relate abundance of common post-fire saproxylic beetle taxa to burned habitat quality and source habitat variables at different scales in burned black spruce stands of the northern boreal forest in Québec. Independent variables used in the models are defined in Table 1.1.

No	Model type	Predictors included in models
1	[Fire – Plot]a	Fire_plot
2	[Fire – Plot]b	Fire_plot Fire_plot^2
3	[Fire + substrate – Plot] a	Fire_plot Dtwt Bas_area Dmean
4	[Fire + substrate – Plot] b	Fire_plot Fire_plot^2 Dtwt Bas_area Dmean
5	[Substrate – Plot]	Dtwt Bas_area Dmean
6	[Fire – Plot + nearby]a	Fire_plot Fire_250
7	[Fire – Plot + nearby]b	Fire_plot Fire_plot^2 Fire_250 Fire_250^2
8	[Substrate – Plot + nearby]	Dtwt Bas_area Dmean Dens_250
9	[Fire + Substrate – Plot + nearby]a	Fire_plot Fire_250m Dtwt Bas_area Dmean Dens_250
10	[Fire + Substrate – Plot + nearby]b	Fire_plot Fire_plot^2 Fire_250 Fire_250^2 Dtwt Bas_area Dmean Dens_250
11	[Pre-fire CWD - recent]	Snag12 Log12
12	[Pre-fire CWD - total]	All_logs All_snags
13	Distance_2002	Dist_2002
14	Distance unburned	Dist_edge Dist_10ha

No	Model type	Predictors included in models
15	Distance specific source habitat	Dist_edge Dist_10ha Dist_2002
16	[Distance specific source habitat + (Pre-fire CWD – recent + total)]	Dist_edge Dist_10ha Dist_2002 Snag12 Log12 All_logs All_snags
17	[Distance specific source habitat + Fire – Plot]a	Dist_edge Dist_10ha Dist_2002 Fire_plot
18	[Distance specific source habitat + Fire – Plot]b	Dist_edge Dist_10ha Dist_2002 Fire_plot Fire_plot^2
19	[Distance specific source habitat + Substrate – Plot]	Dist_edge Dist_10ha Dist_2002 Dtwt Bas_area Dmean
20	[Distance specific source habitat + (Substrate + Fire – Plot)]a	Dist_edge Dist_10ha Dist_2002 Dtwt Bas_area Dmean Fire_plot
21	[Distance specific source habitat + (Substrate + Fire – Plot)]b	Dist_edge Dist_10ha Dist_2002 Dtwt Bas_area Dmean Fire_plot Fire_plot^2
22	[Distance specific source habitat + Substrate – nearby]	Dist_edge Dist_10ha Dist_2002 Dens_250
23	[Distance specific source habitat + Fire – nearby]a	Dist_edge Dist_10ha Dist_2002 Fire_250
24	[Distance specific source habitat + (Fire – nearby)]b	Dist_edge Dist_10ha Dist_2002 Fire_250 Fire_250^2
25	[Distance specific source habitat + (substrate – plot + nearby)]	Dist_edge Dist_10ha Dist_2002 Dtwt Bas_area Dmean Dens_250
26	[Distance specific source habitat + (Fire – plot +	Dist_edge Dist_10ha Dist_2002 Fire_plot Fire_250

No	Model type	Predictors included in models
	nearby)]a	
27	[Distance specific source habitat + (Fire – plot + nearby)]b	Dist_edge Dist_10ha Dist_2002 Fire_plot Fire_plot^2 Fire_250 Fire_250^2
28	[Distance specific source habitat + (Fire +substrate – plot + nearby)]a	Dist_edge Dist_10ha Dist_2002 Fire_plot Fire_250 Dtwt Bas_area Dmean Dens_250
29	[Distance specific source habitat + (Fire +substrate – plot + nearby)]b	Dist_edge Dist_10ha Dist_2002 Fire_plot Fire_plot^2 Fire_250 Fire_250^2 Dtwt Bas_area Dmean Dens_250
30	[Full]a	Dist_edge Dist_10ha Dist_2002 Fire_plot Fire_250 Dtwt Bas_area Dmean Dens_250 Snag12 Log12 All_logs All_snags
31	[Full]b	Dist_edge Dist_10ha Dist_2002 Fire_plot Fire_plot^2 Fire_250 Fire_250^2 Dtwt Bas_area Dmean Dens_250 Snag12 Log12 All_logs All_snags

Appendix A3. Best regression models predicting the abundance of 13 common saproxylic beetle taxa in 66 burned black spruce stands of the northern boreal forest of Québec, according to the corrected Akaike's Information Criterion. Only models with ΔAICc < 4.0 are shown. See Appendix A2 for model description.

Taxa	Model Type	K^a	AICc	ΔAICc	*wt*	Cum. *wt*	R^2_a
A) Xylophages							
Acmaeops p. proteus	[Distance specific source habitat + Fire – Plot]b	6	4.53	0	.717	.717	.434
	Distance unburned	2	8.38	3.85	.105	.821	.349
Arhopalus foveicollis	[Distance specific source habitat + (Fire +substrate – plot + nearby)]a	10	43.15	0	.364	.364	.511
	[Fire + Substrate – Plot + nearby]a	7	43.42	.27	.317	.681	.471
	[Distance specific source habitat + (substrate – plot + nearby)]	8	44.17	1.03	.218	.899	.478
Hylobius congener	[Distance specific source habitat + (Substrate + Fire – Plot)]b	9	-40.02	0	.566	.566	.586
	[Distance specific source habitat + (Fire +substrate – plot + nearby)]b	12	-38.16	1.86	.223	.789	.608

Taxa	Model Type	K^a	AICc	ΔAICc	*wt*	Cum. *wt*	R^2_a
	[Distance specific source habitat + (Substrate + Fire – Plot)]a	8	-37.25	2.77	.142	.930	.558
Monochamus s. scutellatus	[Substrate – Plot + nearby]	5	42.30	0	.397	.397	.300
	[Fire + Substrate – Plot + nearby]b	9	43.00	.70	.279	.676	.355
	[Fire + substrate – Plot] b	6	44.67	2.37	.121	.797	.290
	[Fire + Substrate – Plot + nearby]a	7	45.06	2.76	.100	.897	.301
B) Mycophages							
Atomaria sp.	Distance specific source habitat	4	26.69	0	.179	.179	.151
	[Distance specific source habitat + Substrate – Plot]	7	27.36	.68	.128	.307	.196
	[Distance specific source habitat + (substrate – plot + nearby)]	8	27.69	1.00	.108	.415	.211
	Distance_2002	2	27.78	1.09	.104	.519	.104
	[Distance specific source habitat + Fire – nearby]a	5	27.78	1.10	.104	.622	.155

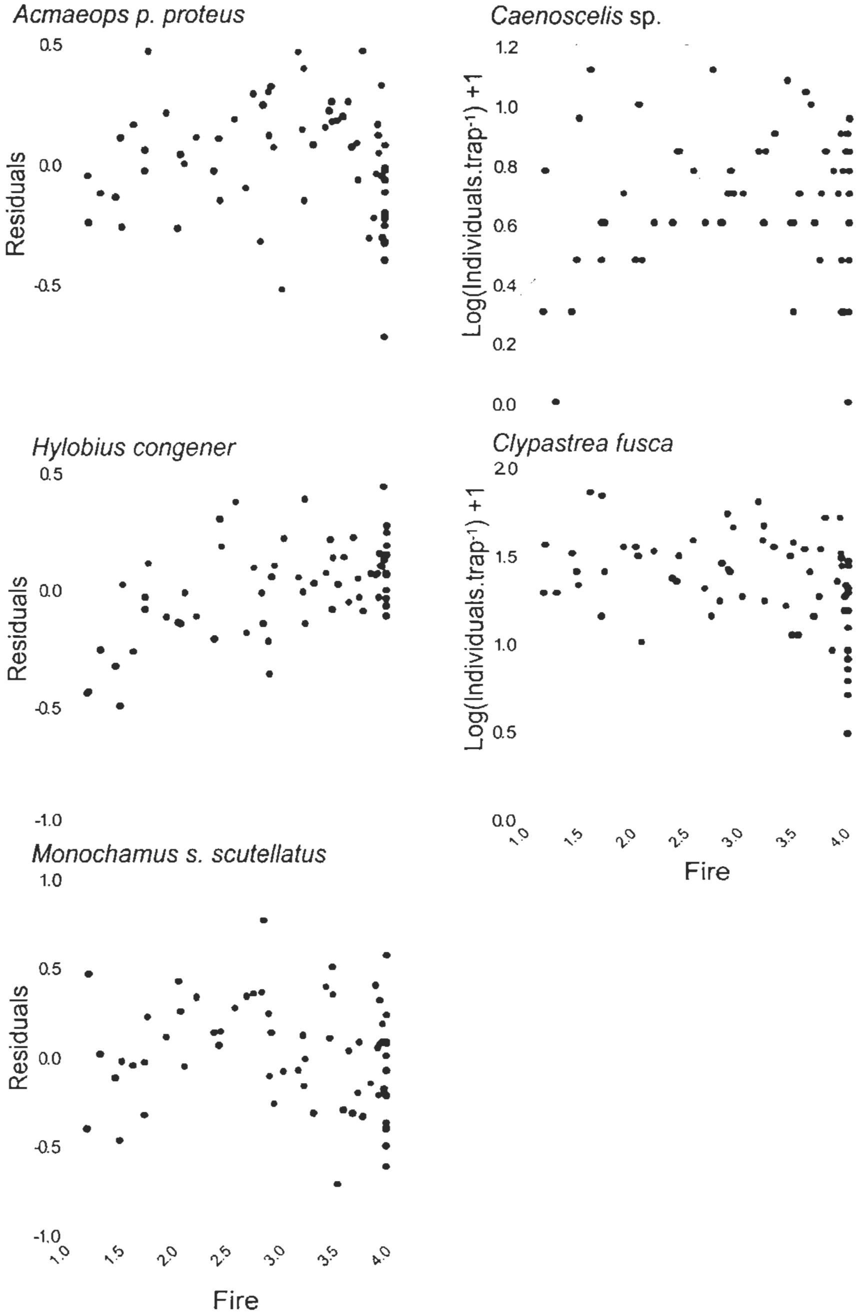
Taxa	Model Type	K^a	AICc	ΔAICc	*wt*	Cum. *wt*	R^2_a
	[Distance specific source habitat + Fire – Plot]a	5	28.42	1.73	.075	.698	.147
	[Distance specific source habitat + Substrate – nearby]	5	29.11	2.42	.053	.751	.138
	[Distance specific source habitat + (Substrate + Fire – Plot)]a	8	29.16	2.47	.052	.803	.193
	[Substrate – Plot + nearby]	5	29.47	2.78	.044	.848	.133
	[Distance specific source habitat + (Fire – nearby)]b	6	30.10	3.42	.032	.880	.143
	[Distance specific source habitat + (Fire – plot + nearby)]a	6	30.19	3.50	.031	.911	.142
Caenoscelis sp.	[Fire – Plot]b	3	6.28	0	.391	.391	.065
	[Pre-fire CWD - recent]	3	9.15	2.87	.093	.484	.024
	[Fire – Plot + nearby]b	5	9.25	2.97	.088	.573	.060
	Distance_2002	2	9.27	2.99	.088	.660	.004
Cartodere	[Distance specific source habitat +	5	-17.85	0	.550	.550	.230

Taxa	**Model Type**	**K**[a]	**AICc**	**ΔAICc**	***wt***	**Cum. *wt***	R^2_a
constrictus	Substrate – nearby]						
	[Substrate – Plot + nearby]	5	-15.78	2.06	.196	.745	.206
	[Fire + Substrate – Plot + nearby]a	7	-15.41	2.43	.163	.908	.236
Clypastrea fusca	[Fire – Plot]b	3	10.03	0	.376	.376	.164
	[Fire – Plot + nearby]b	5	10.56	.53	.288	.664	.191
	[Fire – Plot + nearby]a	3	12.51	2.48	.109	.773	.132
	[Fire – Plot]a	2	13.01	2.98	.084	.858	.109
Corticaria dentigera	[Distance specific source habitat + (substrate – plot + nearby)]	8	-48.36	0	.509	.509	.254
	[Distance specific source habitat + Substrate – Plot]	7	-46.34	2.02	.185	.694	.212
	[Distance specific source habitat + (Substrate + Fire – Plot)]a	8	-44.47	3.89	.073	.767	.209
Corticaria sp.2	[Fire + Substrate – Plot + nearby]b	9	-51.01	0	.890	.890	.372
C) Predators							
Sericoda obsoleta	[Fire + Substrate – Plot + nearby]a	7	37.23	0	0.803	.803	.434

Taxa	**Model Type**	**K**[a]	**AICc**	**ΔAICc**	***wt***	**Cum. *wt***	**R^2_a**
Sphaeriestes virescens	[Distance specific source habitat + (Fire +substrate – plot + nearby)]a	10	20.35	0	.494	.494	.466
	[Fire + Substrate – Plot + nearby]a	7	21.52	1.17	.275	.769	.414
	[Fire + substrate – Plot] a	5	24.14	3.79	.074	.843	.246
Thanasimus u. nubilus	[Distance specific source habitat + (Fire – plot + nearby)]a	6	10.14	0	.348	.348	.637
	[Fire + Substrate – Plot + nearby]a	7	10.31	.17	.319	.667	.644
	[Fire – Plot + nearby]a	3	11.42	1.28	.184	.851	.607
	[Distance specific source habitat + (Fire +substrate – plot + nearby)]a	10	13.99	3.85	.051	.902	.651

[a] Includes the intercept

Appendix A4. Effect of local fire severity for common species where the quadratic term of this variable was significant. Residuals were computed by removing the quadratic term of local fire severity in the best model according to the AICc (see supplementary material C) where this variable was included.



APPENDICE B

MATÉRIEL SUPPLÉMENTAIRE AU CHAPITRE II

Appendix B1. Description of the environmental variables included in this study and identification of the three sets (partitions) to which they belong. Variables produced using buffers of a given radius were used only in analyses associated with the spatial scale they encompassed (either small, medium or large) and the geographical linear or planar trend (XY data).

Variable	Description	Partition*	Scale
Dtwt	Diameter at stump height (DHS) of the tree on which the trap was attached (cm)	P	All
Fire1	Low fire severity (FireIndex < 2.5) in the plot (dummy variable)	P	All
Fire2	Moderate fire severity (FireIndex (2.5-3.5) in the plot (dummy variable)	P	All
Dmean	Mean diameter of burned trees > 10cm of DSH (cm)	P	All
Bas_area	Total basal area in the plot ($m^2.ha^{-1}$)	P	All
Nd25	Number of burned stems between 2 and 5 cm of DSH ($n.ha^{-1}$)	P	All
Nd510	Number of burned stems between 5 and 10 cm of DSH ($n.ha^{-1}$)	P	All
Log12	Volume of unburned downed woody debris (>5cm of maximum diameter) of decay classes 1 and 2 ($m^3.ha^{-1}$)	S	All
Snag12	Basal area data of unburned snags (>5cm of diameter) of decay classes 1 and 2 ($m^2.ha^{-1}$)	S	All
BurnResLiF	Total area of conifer-dominated forest lightly burned (FireIndex<2.5) in a 661m radius around the plot (%)	B	Small + XY data
BurnResMoF	Total area of conifer-dominated forest moderately burned (FireIndex :2.5-3.5) in a 661m radius around the plot (%)	B	Small + XY data
BurnResSevF	Total area of conifer-dominated forest severely burned (FireIndex >3.5) in a 661m radius around the plot (%)	B	Small + XY data
BurnResLiM	Total area of conifer-dominated forest lightly burned (FireIndex<2.5) in a 1322m radius around the plot (%)	B	Medium + XY data

Variable	Description	Partition*	Scale
BurnResMoM	Total area of conifer-dominated forest moderately burned (FireIndex :2.5-3.5) in a 1322m radius around the plot (%)	B	Medium + XY data
BurnResSevM	Total area of conifer-dominated forest severely burned (FireIndex >3.5) in a 1322m radius around the plot (%)	B	Medium + XY data
BurnResLiL	Total area of conifer-dominated forest lightly burned (FireIndex<2.5) in a 2644m radius around the plot (%)	B	Large + XY data
BurnResMoL	Total area of conifer-dominated forest moderately burned (FireIndex :2.5-3.5) in a 2644m radius around the plot (%)	B	Large + XY data
BurnResSevL	Total area of conifer-dominated forest severely burned (FireIndex >3.5) in a 2644m radius around the plot (%)	B	Large + XY data
Log12	Volume of unburned downed woody debris (>5cm of maximum diameter) of decay classes 1 and 2 ($m^3.ha^{-1}$)	S	All
Snag12	Basal area of unburned snags (>5cm of diameter) of decay classes 1 and 2 ($m^2.ha^{-1}$)	S	All
UnbF	Total area of unburned conifer-dominated forest in a 661m radius around the plot (%)	SH	Small + XY data
UnbM	Total area of unburned conifer-dominated forest in a 1322m radius around the plot (%)	SH	Medium + XY data
UnbL	Total area of unburned conifer-dominated forest in a 2644m radius around the plot (%)	SH	Large + XY data
Dist_edge	Minimum distance to the edge of the 2005 fire patch (m)	SH	All
Dist_2002	Minimum distance to the 2002 fire patch (km)	SH	All
Dist_10ha	Minimum distance to unburned conifer-dominated forest of >10ha (m)	SH	All

[*] P: plot-level attributes; B: burned habitat characteristics measured in buffers; SH: variables associated with dispersal from source habitats.

Appendix B2. Total abundance of common taxa considered in the separate analyses. The trophic guild to which each taxa belongs is also indicated.

Taxa	**Trophic guild**	**Total number of individuals**
Acmaeops proteus (Kirby)	Xylophage	805
Arhopalus foveicollis Haldeman	Xylophage	773
Hylobius congener Dalle Torre and Hustache	Xylophage	190
Monochamus scutellatus (Say)	Xylophage	188
Atomaria sp.	Mycophage	175
Caenoscelis sp.	Mycophage	284
Cartodere constritus (Gyllenhal)	Mycophage	831
Clypastrea fusca Harold	Mycophage	1030
Corticaria dentigera LeConte	Mycophage	857
Corticaria sp.2	Mycophage	2851
Sericoda obsoleta (DeGeer)	Predator	327
Sphariestes virescens (LeConte)	Predator	741
Thanasimus undatulus nubilus Klug	Predator	3562

Appendix B3. Production of PCNM variables and scale assessment

Production of PCNM variables. The PCNM analysis is a method belonging to the eigenfunction-based spatial analyses (Griffith and Peres-Neto 2006). It relies on a truncated matrix that retains geographic distances between neighbouring sites. In this matrix, the distances larger than the largest distance between two contiguous sites according to the minimum spanning tree method were replaced by a value equal to four times that threshold (Borcard and Legendre 2002). Threshold distances were 1158 and 831 m for PCNM produced in the northern and the southern areas respectively. Afterwards, we computed a principal coordinates analysis by using this truncated distance matrix and we kept only the coordinates of positive eigenvalues. These eigenvectors made up the PCNM variables. Final PCNM variables consist of orthogonal waves, whose wavelengths range across all spatial scales encompassed by the sampling design (Brind'Amour et al. 2005, Jones et al. 2008) (see figure 3.1 for an example). As PCNM variables are completely orthogonal, we can decompose every spatial scale at which an ecological process occurs without overlapping of spatial components (Borcard and Legendre 2002).

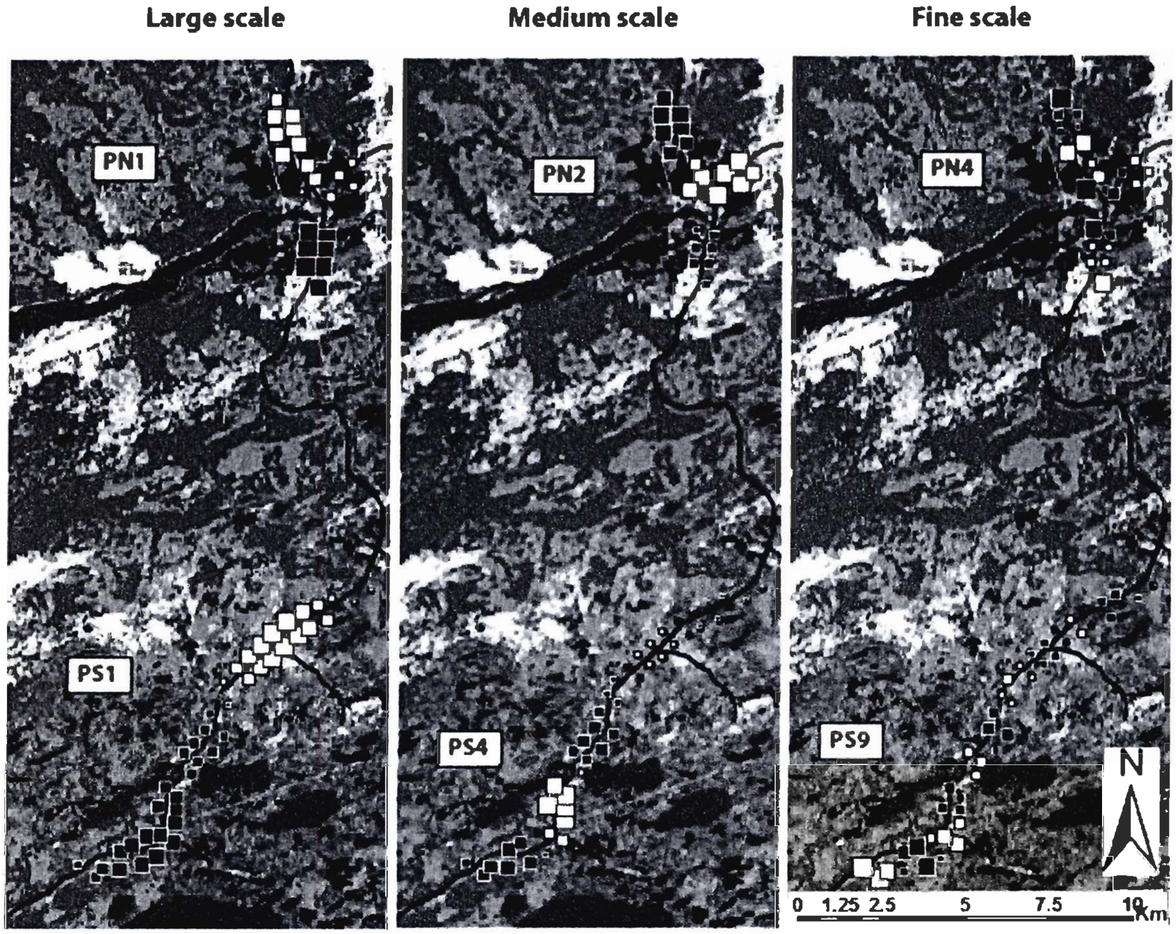


Figure B3.1. Mapped values of some PCNM variables representing different spatial scales. Square size is proportional to the standardized (mean = 0; variance =1) value of the PCNM variable. Filled squares: positive values, open squares: negative values.

Assessing the scale of a PCNM variable. Borcard and Legendre (2002) noticed that it's difficult to assess the corresponding spatial scale of a given PCNM variable when plots are not disposed on a regular sampling scheme. Highly irregular sampling design may produce PCNM variables that bear structures at several scales. However, a quick visual analysis of every PCNM variables showed that the great majority of them were still quite regular (figure 3.1) even though the distances to the nearest neighbour varied between 313 and 661 m (mean = 465 m) according to the minimum spanning tree technique. To know at which scale a PCNM variable is spatially autocorrelated, one can measure the approximate distance between each bump or through (D. Borcard, pers. comm.). Instead, we successively calculated Geary's c at every lag-distance of 661 m (maximum distance between sampling plots) for each PCNM variable. We attributed their spatial scale according to the highest distance at which the Geary's c was significant ($P<0.05$) before the first non significant lag-distance (Legendre and Legendre 1998). Scale of PCNM variables corresponded respectively to 3 to 5-, 2- and 1-fold the maximum distance between nearest neighbour according to the minimum spanning tree technique. Statistical significance of Geary's c was estimated after 999 Monte Carlo permutations using ROOKCASE (Sawada 1999).

Appendix B4. Justifications for inclusion of environmental variables in each group.

Species distribution may be spatially structured because environment attributes measured in the plots and on which they rely on are themselves spatially autocorrelated (Borcard et al. 2004). Several authors (Hÿvarinen et al. 2005, Hjälten et al. 2007, Boulanger et al. 2009) have shown that local fire severity and other habitat quality components are known to affect the colonization of saproxylic species at the onset of the process. As these environmental characteristics are likely to be patchy at various spatial scales (Fortin and Payette 2002), one should expect that the abundance of saproxylic colonizer species should follow approximately the same spatial pattern.

Variables in the second group (ii) represented habitat characteristics displayed at a larger spatial scale than the mean distance between sampling points. If such habitat characteristics are selected by saproxylic species, it should produce measurable spatial patterns at this scale. Although one could assess such a relationship from spatially autocorrelated predictors in the first group, this may be best modelled by including habitat data measured in buffers around the sampling point. Relying solely on spatially structured plot-level attributes to assess this process may overlook the effect of habitat characteristics between sampling points on the local abundance of saproxylic species (see chapter 1, figure 1.1). Only burned severity of coniferous stands were included in this group since other computable variables from EOSD (Beaubien et al. 1999) and LandsatTM images (e.g. amount of bogs/fen, amount of shrubby area, index of total amount of burned wood), were highly correlated to either one or several of these variables. Moreover, in a recent analysis, Boulanger et al. (2009) stated that fire severity was the most important variable to predict early post-fire saproxylic assemblages in this area.

Most authors (Holliday 1991, Saint-Germain et al. 2004a, Hyvärinen et al. 2005, Saint-Germain et al. 2008) stated that colonizing specimens converge to the newly burned habitat mainly from external sources as most insect species are temporarily excluded (Wikars 1997, Gandhi et al. 2001, Wikars and Schimmel 2001) or killed (Paquin and Coderre 1997, McCullough et al. 1998) during the burning. Most species that colonize fresh burned wood are also able to breed in woody debris that were created in "green" forests (e.g. from windthrow, self-thinning). Hence, both unburned forests and other recently burned forest patches located in the vicinity of the 2005 fire were considered as potential source habitats. We considered two distance-based variables associated with unburned source-habitats (distance to fire edge, distance to the nearest >10ha unburned coniferous forest) and one with other recently burned patches (minimum distance to one of the 2002 fire patches) (Table S1.1). We considered 2002 fire patches (see text, figure 1) as a source habitat regarding the relative proximity (minimum distance = 4.8 km) of this burned patch to the study area. Several xylophagous species are known to complete their life cycle in 2-3 years (Haack and Slansky 1987); newly hatched specimens from this fire patch could therefore colonize the closely and newly burned habitat. Furthermore, we considered the amount of unburned coniferous forests in buffers of radius corresponding to each spatial scale investigated, i.e. 650, 1300 and 2650 m (Table 1).

Appendix B5. Variation partitioning in this study

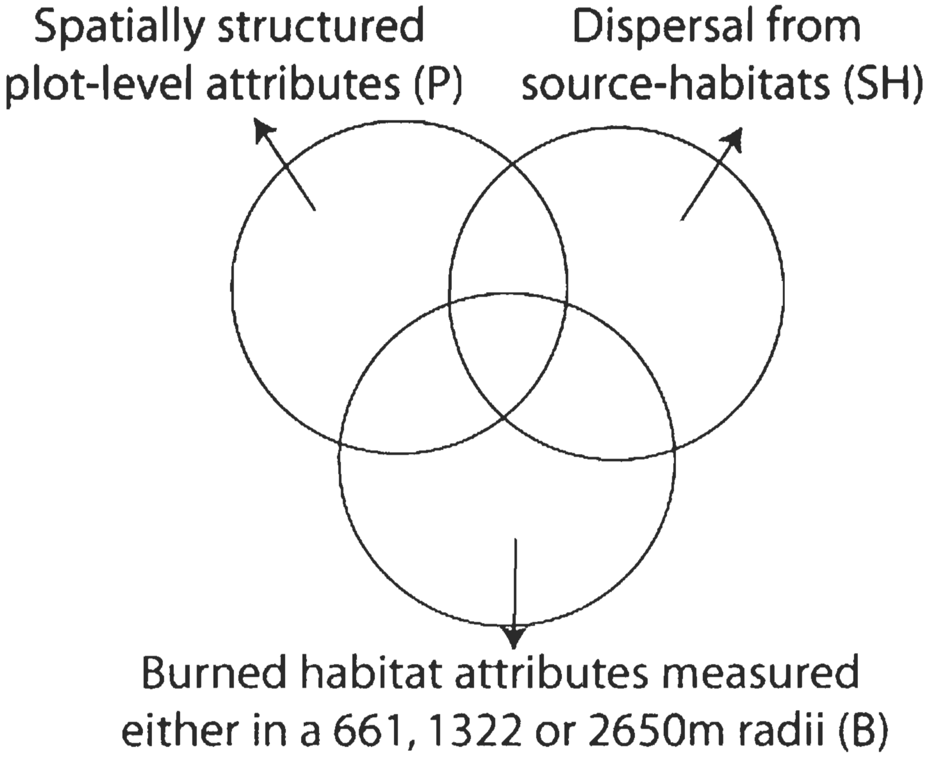


Figure B5.1. Venn diagram showing how the spatial variation at the large, medium and fine scales was partitioned among every saproxylic assemblages. Importance of each partition was obtained using variation partitioning on fitted sample scores on the first axis only from RDA computed on spatial variables. Analyses were repeated for every saproxylic assemblages and spatial scales encompassed by spatial variables.

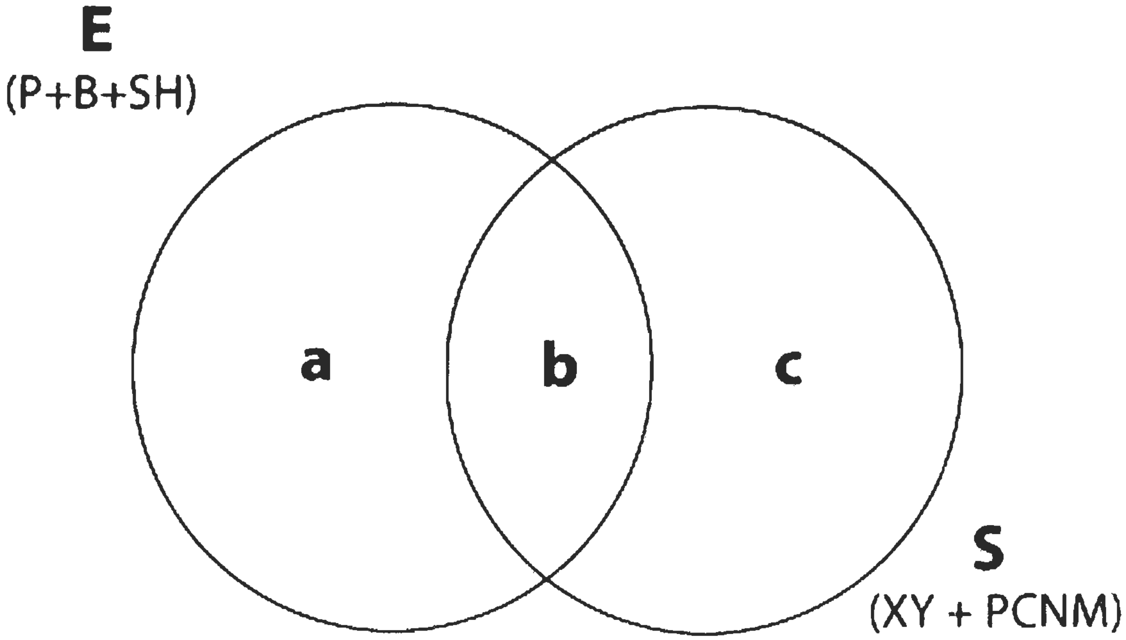


Figure B5.2. Venn diagram showing the partition of the variation between environmental (E) variables (include plot-level, buffers and source-habitat variables) and spatial (PCNM + XY) variables (S). a: Independent effect of environmental variables; b: Unexplained spatial variation; c : variation shared by environmental and spatial variables. See Figure 5.1 for abbreviations.

Appendix B6. References

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APPENDICE C

MATÉRIEL SUPPLÉMENTAIRE AU CHAPITRE III

Appendix C1. Description of the variables used in the present study.

Variable	Type	Scale	Description	Mean	Range
Fire	Substrate	Tree	Fire severity Index on the tree 1 : burned but still alive, 2 : dead with 1-33% of charred bark; 3: dead with 33-66% of charred bark; 4: dead with 66-100% of charred bark.	2.77	1-4
Bark	Substrate	Tree	Bark thickness (mm)	2.40	.66-6.11
Dmax	Substrate	Tree	Maximum diameter of the bole section (cm)	10.8	7.4-19.0
Moisture	Substrate	Tree	Moisture content of bole section (% of dry weight)	43.4	14.6-90.9
Density	Substrate	Tree	Wood density (dry weight.dry volume ($g.cm^{-3}$)	.511	.388-.659
BasArea	BHQ[1]	Local	Plot tree basal area ($m^2.ha^{-1}$)	19.0	3.5-54.9
Firestn	BHQ	Local	Fire severity Index in the plot	3.11	1.21-4.00
BurnLi250	BHQ	Nearby	Total area (ha) of conifer-dominated forest lightly burned (FireIndex<2.5) in a 250m radius	1.68	0-5.56
BurnMo250	BHQ	Nearby	Total area (ha) of conifer-dominated forest moderately burned (FireIndex :2.5-3.5) in a 250m radius	5.56	0.56-13.00
BurnSev250	BHQ	Nearby	Total area (ha) of conifer-dominated forest severely burned (FireIndex >3.5) in a 250m radius	4.31	0-18.06
Log12	SH[2]	Local	Volume ($m^3.ha^{-1}$) of unburned downed CWD (>5cm of diameter) of decay classes 1 and 2	0.2	0-2.5
Snag12	SH	Local	Basal area ($m^2.ha^{-1}$) of unburned snags (>5cm	0.2	0-3.6

			of diameter) of decay classes 1 and 2		
Unb250	SH	Nearby	Total area (ha) of unburned conifer-dominated forest in a 250m radius	2.38	0-11.69
DistEdge	SH	Remote	Minimum distance to the nearest edge of the 2005 fire patch (m)	571	2-2067
Dist2002	SH	Remote	Minimum distance to a 2002 fire patch (m)	13930	4814-23788
Dist10ha	SH	Remote	Minimum distance to unburned conifer-dominated forest of >10ha (m)	661	35-2002

[1] BHQ : Burned habitat quality

[2] SH : Source habitat

Appendix C2. Candidate models tested in this study. Tree level models were only tested for emerging adults and larvae from bole sections. Stand and landscape models were tested for emerging adults and larvae from rearing when considering or not tree-level variables as well as for dispersing adults collected with TWT and for "false positive events" (see text, chapter 3).

Models	Model type
Tree level	
Fire	Substrate quality
Fire Fire^2	Substrate quality
Diam	Substrate quality
Bark	Substrate quality
Bark Fire	Substrate quality
Bark Fire Bark*Fire	Substrate quality
Bark Fire Fire^2	Substrate quality
Bark Fire Fire^2 Bark*Fire	Substrate quality
Density Moisture	Substrate quality
Fire Moisture	Substrate quality
Moisture Bark	Substrate quality
Diam Bark	Substrate quality
Fire Diam	Substrate quality
Fire Fire^2 Diam	Substrate quality
Fire Diam Bark	Substrate quality
Fire Diam Bark Bark*Fire	Substrate quality
Fire Diam Bark Density Moisture	Substrate quality
Fire Fire^2 Diam Bark Density Moisture Bark*Fire	Substrate quality
Stand and landscape levels	
Firestn	Local BHQ[a]
Firestn Firestn^2	Local BHQ
BasArea	Local BHQ
Firestn BasArea	Local BHQ
Firestn Firestn^2 BasArea	Local BHQ
BurnLi250 BurnMo250 BurnSev250	Nearby BHQ
BurnLi250 BurnMo250 BurnSev250 Firestn BasArea	Local + Nearby BHQ
BurnLi250 BurnMo250 BurnSev250 Firestn	Local + Nearby BHQ

Models	Model type
Firestn^2 BasArea	
Snag12 Log12	Local SH[b]
Unb250	Nearby SH
Dist2002 DistEdge Dist10ha	Remote SH
Firestn BasArea Snag12 Log12	Local SH + BHQ
Firestn Firestn^2 BasArea Snag12 Log12	Local SH + BHQ
Firestn BasArea Unb250	Local BHQ + Nearby SH
Firestn Firestn^2 BasArea Unb250	Local BHQ + Nearby SH
Firestn BasArea Dist2002 DistEdge Dist10ha	Local BHQ + Remote SH
Firestn Firestn^2 BasArea Dist2002 DistEdge Dist10ha	Local BHQ + Remote SH
Firestn BasArea Unb250 Dist2002 DistEdge Dist10ha	Local BHQ + Nearby and Remote SH
Firestn Firestn^2 BasArea Unb250 Dist2002 DistEdge Dist10ha	Local BHQ + Nearby and Remote SH
BurnLi250 BurnMo250 BurnSev250 Dist2002 DistEdge Dist10ha	Nearby BHQ + Remote SH
Firestn BasArea BurnLi250 BurnMo250 BurnSev250 Dist2002 DistEdge Dist10ha	Local and Nearby BHQ + Remote SH
Firestn Firestn^2 BasArea BurnLi250 BurnMo250 BurnSev250 Dist2002 DistEdge Dist10ha	Local and Nearby BHQ + Remote SH

a. BHQ : Burned habitat quality

b. SH : Source habitat

Appendix C3. Abundance and frequency of the xylophagous taxa studied in either bole sections (n=141) or trunk-window traps (n=60). Data from rearing concerns emerging adults or falling last-instar larvae that were collected from bole sections sampled 1 year after the fire whereas data from TWT are related to dispersing adults collected the same year as the fire.

	Abundance from bole sections			**Abundance in TWT**	
Species	**Sum (min – max)**	**Frequency among boles (%)**	**Frequency among sites (%)**	**Sum (min – max)**	**N sites with taxa (%)**
Boridae					
Boros unicolor Say	2 (0-1)	2 (1.4)	2 (3.3)	42 (0-7)	26 (43.3)
Buprestidae					
Chrysobothris sp.	1 (0-1)	1	1	8 (0-2)	7 (11.7)
Melanohila fulvoguttata (Harris)[a]	18 (0-3)	12 (8.5)	7 (11.7)	22 (0-7)	8 (13.3)
Cerambycidae					
Acmaeops proteus Kirby [a b]	384 (0-28)	94 (66.7)	55 (91.7)	713 (0-55)	59 (98.3)
Acmaeops pratensis (Laicharting) [a b]	17 (0-3)	12 (8.5)	12 (20.0)	36 (0-4)	21 (35.0)
Meriellum proteus (Kirby)	4 (0-3)	2 (1.4)	2 (3.3)	0 (0)	0 (0)
Monochamus scutellatus (Say) [a]	40 (0-4)	23 (16.3)	21 (35.0)	161 (0-25)	40 (66.7)
Pogonocherus mixtus Haldeman	8 (0-3)	6 (4.3)	6 (10.0)	24 (0-3)	19 (31.7)
Curculionidae					
Crypturgus borealis	137 (0-136)	2 (1.4)	2 (3.3)	8 (0-2)	7 (11.7)
Dryocoetes affaber (Mannerheim)	1 (0-1)	1 (0.7)	1 (1.7)	1 (0-1)	1 (1.7)
Ips spp.	165 (0-139)	7 (5.0)	6 (10.0)	33 (0-11)	14 (23.3)
Orthotomicus caelatus (Eichhofl)	364 (0-113)	7 (5.0)	6 (10.0)	23 (0-3)	18 (30.0)

Species	Abundance from bole sections			Abundance in TWT	
	Sum (min – max)	Frequency among boles (%)	Frequency among sites (%)	Sum (min – max)	N sites with taxa (%)
Pissodes fiskei Hopkins	2 (0-2)	2 (1.4)	2 (3.3)	2 (0-1)	2 (3.3)
Pityophtorus sp.	4 (0-4)	1 (0.7)	1 (1.7)	12 (0-3)	9 (15.0)
Trypodendron lineatum (Olivier)	15 (0-15)	1 (0.7)	1 (1.7)	1 (0-1)	1 (1.7)
Scolytinae spp. – Total[a]	686 (0-143)	13 (9.2)	11 (18.3)	76 (0-11)	33 (55.0)

a. Taxa included in analyses

b. Falling last-instar larvae from bole sections

Appendix C4. Best regression models predicting either the abundance of *A. proteus proteus* (negative binomial regressions) or the occurrence of four other xylophagous taxa (logistic regressions) in bole sections at the tree-level. Best models were ranked according to the corrected Akaike's Information Criterion. Only models with $\Delta_i < 2$ are shown. See Appendix C2 for model description. n=141.

Model	**k**	**Null deviance**	**Residual deviance**	**AIC$_c$**	**ω_i**
***Acmaeops proteus* Kirby**					
Fire Diam Bark Bark*Fire	5	225.20	148.99	538.48	.727
***Acmaeops pratensis* Laicharting**					
Density Moisture	3	82.08	75.36	77.53	.179
Fire Moisture	3		75.68	77.85	.153
Moisture Bark	3		76.20	78.37	.118
***Melanophila fulvoguttata* (Harris)**					
Fire Diam Bark	4	82.08	50.74	54.03	.268
Fire Diam Bark Bark*Fire	5		50.68	55.11	.156
Bark Fire	3		53.11	55.28	.143
***Monochamus scutellatus* (Say)**					
Fire Fire^2 Diam Bark Density Moisture Bark*Fire	8	125.44	92.19	100.22	.947
Scolytinae spp.					
Bark Fire Fire^2	5	86.74	56.54	60.97	.244
Bark Fire Bark*Fire	4		57.96	61.24	.213
Fire Fire^2 Diam Bark Density Moisture Bark*Fire	8		54.10	62.13	.137

Appendix C5. Best regression models predicting either the abundance or the occurrence of the five studied taxa in bole sections as a function of plot- and landscape-scale variables. Effects were estimated by linear regression on log (x+1) transformed mean abundance per plot for *A. proteus proteus* whereas logistic regressions were used to model the occurrence of the remaining taxa. Best models were ranked according to the corrected Akaike's Information Criterion. Only models with $\Delta_i < 2$ are shown. See Appendix C2 for model description. n=60.

Model	**k**	**AIC$_c$**	**ω_i**			
Linear regression models				**R^2_a**	**P^c**	
***Acmaeops p. proteus* Kirby**						
Firestn	2	-137.68	.105	<.000	n.s.	
BurnLi250 BurnMo250 BurnSev250 Firestn BasArea	6	-137.56	.100	.013	n.s.	
Snag12 Log12	3	-137.47	.096	<.000	n.s.	
Logistic regressions models				**Null deviance**	**Residual deviance**	**P (null model)**
***Acmaeops pratensis* Laicharting**						
BurnLi250 BurnMo250 BurnSev250 Firestn BasArea	6	42.69	.474	60.05	36.29	***
BurnLi250 BurnMo250 BurnSev250 Firestn Firestn^2 BasArea	7	43.62	.297		35.76	***
***Melanophila fulvoguttata* (Harris)**						
Firestn BasArea Snag12 Log12	5	18.74	.250	35.68	13.74	***
Firestn Firestn^2 BasArea Snag12 Log12	6	19.53	.168	34.04	13.13	***
Firestn	2	19.84	.144	38.30	18.64	***
***Monochamus s. scutellatus* (Say)**						
Firestn Firestn^2	3	73.16	.198	77.69	70.76	*

Model	**k**	**AIC$_c$**	**ω_i**			
Linear regression models				**R^2_a**	**P^c**	
BurnLi250 BurnMo250 BurnSev250 Firestn Firestn^2 BasArea	7	73.71	.149		65.85	n.s.
Firestn Firestn^2 BasArea	4	74.34	.109		70.67	n.s.
Scolytinae spp.						
Firestn Firestn^2	3	33.93	.237	57.17	31.53	***
Firestn Firestn^2 BasArea	4	35.11	.131		31.44	***
Firestn Firestn^2 BasArea Dist2002 DistEdge Dist10ha	7	35.59	.103		27.72	***

a. n.s. : not significant, * : $P<0.05$, ** : $P<0.01$, *** : $P<0.001$

Appendix C6. Best regression models predicting either the abundance (negative binomial regressions, *A. proteus proteus, M. scutellatus scutellatus*) or the occurrence (logistic regressions, remaining taxa) of adults in trunk-window traps the same year as the fire as a function of stand- and landscape-scales variables for the five studied taxa. Best models were ranked according to the corrected Akaike's Information Criterion. Only models with $\Delta_i < 2$ are shown. See Appendix C2 for model description. n=60.

Model	**k**	**AIC$_c$**	**ω_i**	**Null deviance**	**Residual deviance**	**P (null model)**
***Acmaeops p. proteus* Kirby**						
Firestn Firestn^2 BasArea Dist2002 DistEdge Dist10ha	7	377.38	.566	118.99	62.15	***
Firestn Firestn^2 BasArea Unb250 Dist2002 DistEdge Dist10ha	8	378.92	.263	118.97	62.14	***
Firestn Firestn^2 BasArea BurnLi250 BurnMo250 BurnSev250 Dist2002 DistEdge Dist10ha	10	380.17	.140	121.32	61.29	***
***Acmaeops pratensis* Laicharting**						
Firestn BasArea BurnLi250 BurnMo250 BurnSev250 Dist2002 DistEdge Dist10ha	9	63.54	.141	58.89	52.54	n.s.
Firestn Firestn^2 BasArea BurnLi250 BurnMo250 BurnSev250 Dist2002 DistEdge Dist10ha	10	63.67	.132	57.37	51.00	n.s.
Firestn BasArea Dist2002 DistEdge	6	64.09	.107	62.91	57.69	n.s.

Model	**k**	**AIC_c**	**ω_i**	**Null deviance**	**Residual deviance**	**P (null model)**
Dist10ha						
***Melanophila fulvoguttata* (Harris)**						
Firestn	2	33.54	.130	47.12	32.34	***
Firestn BasArea Dist2002 DistEdge Dist10ha	6	34.09	.098		27.69	**
Firestn Firestn^2	3	34.18	.094		31.78	***
Monochamus s. scutellatus (Say)						
Firestn Firestn^2 BasArea Snag12 Log12	6	246.02	.272	82.49	63.06	**
Firestn BasArea Unb250	4	247.67	.119	78.66	64.56	**
Firestn Firestn^2 BasArea Unb250	5	247.70	.117	80.76	64.86	**
Scolytinae spp.						
Unb250	2	83.34	.113	82.58	82.14	n.s.
Firestn	2	83.76	.091		82.56	n.s.
BasArea	2	83.78	.091		82.58	n.s.

a. n.s. : not significant, * : $P<0.05$, ** : $P<0.01$, *** : $P<0.001$

APPENDICE D

MATÉRIEL SUPPLÉMENTAIRE AU CHAPITRE IV

Appendix D1. Regression models computed to predict the percentage of wood density loss and moisture content in CWD.

No.	Models
Tree-level	
	Plot Fire
	Plot Contact0 Contact1 Contact2 Contact3
	Plot Contact0 Contact1 Contact2 Contact3 Fire
	Plot Contact0 Contact1 Contact2 Contact3 Fire Contact0*Fire
	Plot Contact0 Contact1 Contact2 Contact3 Dmax
	Plot Contact0 Contact1 Contact2 Contact3 Fire Dmax
	Plot Contact0 Contact1 Contact2 Contact3 Fire InitDens
	Plot Contact0 Contact1 Contact2 Contact3 Fire InitDens Dmax Contact0*Fire
Plot-level	
	Drainage
	Drainage Drainage2
	Slope_north slope_south
	Drainage Drainage2 Slope_north Slope_south Slope_angle
	LivTree
	LivTree Shrub
	Drainage Drainage2 Shrub LivTree
	Drainage Drainage2 Slope_north Slope_south Slope_angle Shrub LivTree

Appendix D2. Parameter estimates for all regression models computed to predict the a) percentage of wood density loss and b) moisture content in CWD at the plot- level. We used the mean residual values per plot from the best model computed at the tree-level (without site as a random effect) to assess plot-level effects. Adjusted r-square values from the best model predicting percentage of wood density loss and moisture content at the tree-level were .291 and .356 respectively. Plot-level models were computed separately for snags, logs with close contact with the ground (contact3 and contact4 = 1) and for all logs. Models are ranked according to the AIC_c.

Model	**k**	**AIC_c**	**ω**	**R^2_a**
a) Wood Density				
Snags				
Slope_north slope_south	3	645.28	.398	.040
Drainage Drainage2 Slope_north Slope_south Slope_angle	6	646.57	.209	.031
Drainage Drainage2 Slope_north Slope_south Slope_angle Shrub LivTree	8	648.12	.096	.018
LivTree Shrub	3	648.75	.070	<.000
Drainage Drainage2	3	648.82	.068	<.000
Drainage	2	649.25	.055	<.000
LivTree	2	649.27	.054	<.000
Drainage Drainage2 Shrub LivTree	5	649.47	.049	<.000
Logs (all)				
LivTree	2	616.72	.378	.053
LivTree Shrub	3	617.31	.281	.047
Drainage Drainage2 Shrub LivTree	5	618.98	.122	.030
Drainage Drainage2 Slope_north Slope_south Slope_angle Shrub LivTree	8	619.27	.106	.035

Slope_north slope_south	3	620.55	.056	.007
Drainage	2	621.96	.027	<.000
Drainage Drainage2	3	623.07	.016	<.000
Drainage Drainage2 Slope_north Slope_south Slope_angle	6	623.07	.016	<.000
Log (Contact3 & Contact4)				
Slope_north slope_south	3	368.31	.282	.029
Drainage	2	369.53	..153	<.000
Drainage Drainage2 Slope_north Slope_south Slope_angle	6	369.72	.139	.004
Drainage Drainage2	3	369.90	.127	<.000
LivTree	2	370.43	.097	<.000
LivTree Shrub	3	370.54	.092	<.000
Drainage Drainage2 Shrub LivTree	5	371.24	.065	<.000
Drainage Drainage2 Slope_north Slope_south Slope_angle Shrub LivTree	8	371.97	.045	<.000
b) Moisture content				
Snags				
Drainage Drainage2 Slope_north Slope_south Slope_angle	6	813.18	.321	.084
Drainage Drainage2 Slope_north Slope_south Slope_angle Shrub LivTree	8	813.59	.261	.085
Drainage Drainage2 Shrub LivTree	5	814.13	.200	.071
Drainage Drainage2	3	814.77	.145	.060
Drainage	2	817.82	.032	.023
Slope_north slope_south	3	818.51	.022	.015
LivTree Shrub	3	820.13	.010	<.000

LivTree	2	820.17	.010	<.000
Logs (all)				
Slope_north slope_south	3	688.37	.283	.011
Drainage	2	688.86	.222	.004
Drainage Drainage2	3	689.82	.137	<.000
LivTree	2	690.17	.115	<.000
LivTree Shrub	3	690.72	.087	<.000
Drainage Drainage2 Shrub LivTree	5	691.20	.069	<.000
Drainage Drainage2 Slope_north Slope_south Slope_angle	6	691.57	.057	<.000
Drainage Drainage2 Slope_north Slope_south Slope_angle Shrub LivTree	8	692.85	.030	<.000
Logs (Contact3 & Contact4)				
Drainage Drainage2 Slope_north Slope_south Slope_angle	6	476.04	.442	.145
Drainage Drainage2 Slope_north Slope_south Slope_angle Shrub LivTree	8	478.10	.158	.108
Drainage	2	478.55	.126	.084
Drainage Drainage2	3	478.86	.108	.079
Drainage Drainage2 Shrub LivTree	5	479.23	.089	.075
Slope_north slope_south	3	480.33	.052	.046
LivTree	2	483.15	.013	<.000
LivTree Shrub	3	483.19	.012	<.000

Appendix D3. Effects of plot-level variables on a) wood density loss and b) moisture content following multimodel inference.

	n	**Drainage**	**Drainage^2**	**Slope_north**	**Slope_south**	**Slope_angle**	**Shrub**	**LivTree**
a) Wood density								
Snags	245			+*				
Logs (all)	229							+
Logs (Contact3 & Contact4)	93							
b) Moisture content								
Snags	245	+						
Logs (all)	229							
Logs (Contact3 & Contact4)	93							

* + : $p<0.05$

Appendix D4. Assessing the initial wood density of fire-killed trees.

Although we could have relied on theoretic values to estimate initial (i.e. at time of death) wood density (Jessome 1977), previous observations in the study area (Boulanger et al., unpublished data) revealed that wood density of living black spruce was greatly variable. Although some reported that growth rate does not have a significant effect on wood density (Harmon et al. 1986), many authors (Zobel and van Buijtenen 1989; Zhang 1995) generally still reported such a significant relationship for black spruce . Age, position along the stem, distance from the pith and site quality were also listed as other factors that may influence wood density in living trees (Harmon et al. 1986; Zobel and van Buijtenen 1989). Consequently, we aimed to build a model predicting the initial wood density of the fire-killed tree from various tree's and site attributes (Naesset 1999; Mäkinen et al. 2006). To do so, increment cores were collected at breast height from 157 living black spruces in the vicinity of the study area and then measured for wood density ($g \cdot cm^{-3}$), age and growth rate. Diameter at 1-m above the ground and the main drainage class of the site (from 1 to 6, see table 1) were also noted. Growth rate was determined to the nearest 1/100th mm using a VELMEX measuring system whereas wood density was measured on ovendried increment cores using its volume and mass (see Methods).

Ten regression models were developed in order to predict wood density in living trees (Table S4.1). Best model was selected according to the lowest AIC_c. Age was not included in models since it would have been impossible to assess it with accuracy because of the decayed growth rings. Moreover, this variable was very strongly related to growth rate (Pearson correlation: -.711).

The regression model that included growth rate as the only independent variable had the lowest AICc (-612.21, w = .424, figure S4.1). Model adding diameter of tree also received high level of support (AICc = -611.71; w = .331) but did not significantly improve the model including growth rate only ($F_{0.05,154,155}$) = 1.588, P = 0.210).

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