UNIVERSITÉ DU QUÉBEC A MONTRÉAL

LE BOIS MORT, LA BIODIVERSITÉ ASSOCIÉE, ET LA DÉCOMPOSITION DE BOIS DANS LES FORÊTS D'EPINETTE NOIRE AMÉNAGÉES ET NON AMÉNAGÉES DU NORD-OUEST DU QUÉBEC

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FOREWORD

This thesis is presented in the form of three scientific articles. The studies presented in this thesis were conducted as part of two larger studies. The first is a natural chronosequence of over 2000 years, which emerged from the work PhD thesis of Nicolas Lecomte. The second is network of partial cutting trials (“*le réseau d’expérimentation de coupes partielles* en *Abitibi*”) initiated by Dr. Yves Bergeron. I was responsible for the experimental design within the larger studies for all three chapters. I was present for the collection of all data, identified 15 604 beetle specimens, preformed all analyses and wrote initial drafts of all three chapters. I have identified those who have contributed to the thesis at the end of each article. Contributions came in the form of help in the field, support with identifications, data analysis, editing of the articles and financial support.

The first chapter is titled “Paludification of boreal soils reduces wood decomposition rates and increases wood based carbon storage”. The co-authors are the director of my research Dr. Tim Work, the director of our larger research group (Chaire-AFD) Dr. Yves Bergeron and a research scientist with the Canadian Forest service, Dr. David Paré. All three co-authors contributed to the initial experimental design and provided valuable comments during the preparation of the manuscript for publication. This article was accepted for publication in the journal Ecosphere.

The second chapter is titled “Linking deadwood-associated beetles and fungi with wood decomposition rates in managed black spruce forests”. The co-author is Dr. Tim Work the director of my thesis. This article was published in 2012 as part of a special issue of *Canadian Journal of Forest Research* (42: 1477-1490) highlighting research presented at the “International Symposium on Dynamics and Ecological Services of Deadwood in Forest Ecosystems”.

The third chapter is titled “Evaluating partial cutting as an ecosystem management tool using deadwood-associated beetles and fungi.” The co-author is Dr. Tim Work, who provided comments on the preparation of the manuscript for publication. This article will be submitted for publication in the journal *Forest Ecology and Management*.

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RÉSUMÉ

Le bois mort est un habitat important pour une grande partie de la biodiversité de la forêt et recèle le potentiel de jouer un rôle essentiel dans le cycle des éléments nutritifs de la forêt. La coupe forestière réduit considérablement la quantité de bois mort et menace de nombreuses espèces adaptées à cette ressource forestière. Plusieurs de ces espèces associées au bois mort sont perçues comme pouvant jouer un rôle prépondérant dans la décomposition de celui-ci. Les stratégies d'exploitation forestière actuelles visent la conservation à grande échelle d'attributs forestiers pour atténuer les effets négatifs sur les fonctions et la biodiversité des écosystèmes. Ainsi, les stratégies d'aménagement écosystémique se basent sur les patrons et processus naturels observés à l'échelle du paysage. Cette thèse vise à approfondir les connaissances en liens avec le bois mort, la biodiversité et les fonctions écosystémiques dans un paysage dominé par l'épinette noire *Picea mariana* (Mill.) BSP. Cette thèse est divisée en trois chapitres.

Le chapitre 1 décrit la dynamique du bois mort dans un écosystème dominé par l'épinette noire. Le développement de la structure des peuplements de pessière noire à mousses est unique. Après un feu de forêt sévère, le peuplement se renouvelle et des épinettes noires de même âge forment une forêt dense après 75 - 100 ans. Ensuite, si la période sans feu se prolonge, la paludification réduit la productivité du peuplement, ce qui résulte à long terme en une forêt de structure hétérogène et éventuellement à une phase de rétrogression. Au cours de ce processus, de grandes quantités de bois mort sont créées sur des échelles de temps relativement courtes. J'ai mesuré l'entrée dans le système et la décomposition du bois mort dans une chronoséquence s'étalant sur plus de 2000 ans à l'aide de peuplements d'épinette noire issus de feu et sujets à la paludification. Les taux d'entrée et de décomposition du bois mort étaient les plus élevés lors du stade d'ouverture de la canopée et décroissaient dans les vieilles forêts paludifiées. J'ai aussi pu démontrer que la décomposition du bois mort était retardée de 6-7 ans. Ce décalage permet une colonisation du bois mort par des organismes décomposeurs, permet un préconditionnement du bois par des décomposeurs spécialisés et permet une réduction de la teneur en humidité dans le bois. Toutefois, une grande quantité du bois mort créé se fait ensevelir au sol par l'épaisse couche de matière organique en croissance dominée par les sphaignes. Bien que ce taux d'ensevelissement par an soit relativement faible par rapport à la quantité de bois décomposé, le fait que ce bois persiste durant des siècles dans la matière organique fait qu'une grande quantité de biomasse de bois mort se retrouve enfouie dans les vieux peuplements, ce qui représente une grande quantité de carbone ligneux stocké dans les peuplements les plus âgés qui compense pour la diminution de la captation de carbone associée à la baisse de productivité du peuplement.

Dans le chapitre 2, je m'efforce de relier les changements de la structure de peuplement avec la dynamique du bois mort et les communautés de coléoptères et de champignons qui y sont associées. J'ai utilisé une série de coupes partielles, de coupes totales et de témoins non coupés qui variaient en termes de microclimat et de disponibilité de bois mort, ce qui s'est traduit par des différences dans les assemblages et les taux de croissance des organismes décomposeurs. Les principaux effets des coupes forestières incluent une augmentation du taux de capture des coléoptères se nourrissant du bois mort

et une présence accrue du champignon *Gloeophyllum sepiarium*. J'ai aussi trouvé des taux significativement plus élevés de décomposition du bois dans les coupes totales, attribués à l'accumulation de beaucoup plus de degrés-jours pour les champignons. J'ai résumé les liens en présentant une série de modèles causaux démontrant les effets des changements de la structure du peuplement sur la composition et l'abondance relative des organismes décomposeurs et les effets subséquents sur les taux de décomposition. Ces modèles ont également démontré les effets directs des changements de la structure du peuplement sur les taux de décomposition , bien que ceux-ci soient probablement aussi le résultat du réchauffement et de la dessiccation du bois mort conduisant à des taux de croissance plus élevés des organismes décomposeurs .

Dans le chapitre 3, j'évalue une stratégie d'aménagement écosystémique quant à sa capacité à imiter les vieilles forêts en utilisant des espèces associées au bois mort en tant qu'indicateurs. Dans les pessière noire à mousses de l'ouest du Québec, les peuplements perdent naturellement environ la moitié de leur biomasse ligneuse vivante sur une période de 50 à 70 ans. J'ai comparé les changements dans les assemblages d'espèces le long d'un gradient naturel de succession avec les changements résultant de la coupe partielle et de la coupe totale, avec l'hypothèse que la récolte par coupe partielle engendrerait des changements analogues à ceux de la succession forestière naturelle. J'ai trouvé des changements clairs et constants chez les assemblages de coléoptères associés au bois mort et les champignons en réponse à la succession naturelle. Les réponses observées face à la coupe partielle n'étaient pas analogues à celles issues de la succession naturelle et se rapprochaient plutôt de la coupe totale. Je décrirais ces nouvelles communautés comme étant un mélange très varié d'espèces : 1) généralistes qui sont restées après la coupe ; 2) colonisatrices d'habitats ouverts, et 3) d'espèces préétablies associées aux vieilles forêts mais en déclin en raison de la coupe. Je conclus ce chapitre avec des recommandations précises sur la façon dont la coupe partielle pourrait émuler les vieilles forêts lors de futurs essais d'aménagement écosystémique.

Les résultats de cette thèse améliorent à la fois notre connaissance de la dynamique du bois mort et celle sur la biodiversité associée au bois mort en pessière noire à mousses en plus de dresser un cadre d'évaluation de stratégies d'aménagement écosystémique en utilisant la biodiversité associée au bois mort. Je démontre clairement que la transition de forêts denses équiennes vers des vieilles forêts hétérogènes représente aussi une période de transition dans la dynamique de bois mort et de la biodiversité qui y est associée. L'émulation de cette transition est le but des stratégies actuelles d'aménagement écosystémique dans la région. Les connaissances issues de cette thèse vont grandement améliorer notre capacité à mettre en œuvre ces stratégies d'aménagement spécifiquement dans les forêts d'épinettes noires et à savoir comment la biodiversité associée au bois mort peut être un indicateur efficace afin de tester d'autres stratégies d'aménagement.

ABSTRACT

Deadwood is an important habitat for a large component of forest biodiversity and has the potential to play vital roles in forest nutrient cycling. Forest harvest drastically reduces the amount of deadwood and threatens many species adapted to this forest resource. Many of these deadwood-associated species are thought to play essential roles in the decomposition of deadwood. Forest harvesting strategies now aim to conserve broader ecosystem features to alleviate negative effects on biodiversity and ecosystem functions. These ecosystem based management strategies target natural landscape patterns and processes to model forest harvest patterns. This thesis seeks to expand current knowledge on how deadwood, biodiversity and ecosystem functioning are linked in a black spruce *Picea mariana* (Mill.) BSP. dominated ecosystem. This thesis is divided into three chapters.

Chapter 1 describes the dynamics of deadwood in a black spruce ecosystem. These black spruce ecosystems have a unique development of stand structure. After a stand replacing wildfire, these stands form a dense even aged forest in 75 – 100 years. Over long time periods, paludification reduces productivity resulting in heterogeneous forest and eventually forest retrogression. During this process large masses of deadwood are created over relatively short time scales. I measured deadwood input and decay across a >2000 year fire-driven chronosequence of black spruce stands undergoing paludification. Rates of deadwood input and decay were highest during the breakup of the canopy and slowing in older, paludified forests. I demonstrated that deadwood experiences a lag before the onset of decomposition of 6-7 years. This lag allows for colonization of decomposer organisms, preconditioning of the wood by specialized decomposer organisms and to allow for a reduction of the initial high moisture in wood. I was found evidence that a large amount of this deadwood created becomes buried by the thickening soil organic layer dominated by Sphagnum mosses. Although the amount of wood burial per year was relatively small compared to the amount of wood decayed, the fact that this wood persists for centuries buried in the organic layer results in a large biomass of buried deadwood in older stands. This large persistent mass of buried deadwood accounts for a major part of the stored woody carbon in older stands, offsetting the woody carbon lost to decrease in aboveground productivity.

In chapter 2, I strive to link the changes in stand structure to the dynamics of deadwood and deadwood-associated beetle and fungal communities. I used a series of partial cuts, clear cuts and uncut controls that affect microclimate and deadwood availability resulting in changes in the composition and growth rates of decomposer organisms. The main effects of harvesting included increases in the catch rate of wood-feeding beetles and higher presence of the fungi *Gloeophyllum sepiarium*. I also found significantly higher rates of wood decay in clearcuts attributed to the accumulation of significantly more fungal degree-days. I summarized the linkages by presenting a series of causal models demonstrating the effects of changes of stand structure on the composition and relative abundance of decomposer organisms and the subsequent effects on decay rates. These models also demonstrated the direct effects of changes of stand structure on decay rates, although these too are likely the result of warming and drying of deadwood leading to higher growth rates of decomposer organisms.

In Chapter 3 I test an ecosystem based management strategy for its ability to emulate old-growth forests using deadwood-associated species as indicators. In black spruce forests of northwestern Quebec, stands naturally lose approximately half of their live woody biomass over a period of 50 to 70 years. I compared changes in the species assemblages along a natural succession al gradient and changes resulting from partial cut and clearcut harvesting, with the hypothesis that partial cut harvesting will invoke analogous changes as natural forest succession. I found clear and consistent changes in the response to natural succession by assemblages of deadwood-associate beetles and fungi. The patterns observed after partial cutting was not analogous to natural succession and instead were more similar to the response observed after clearcutting. I suggest that these new communities are a highly diverse mix of: 1) generalist species that remained post-harvest; 2) recently colonized open-habitat species, and 3) old-growth associated species in decline as a result of the harvesting. I conclude this chapter with specific recommendations of how partial cutting may emulate old-growth forests in future ecosystem management trials.

The results of this thesis both improves our knowledge of deadwood dynamics and deadwood-associated biodiversity in black spruce forests, as well as describes a framework for testing ecosystem management strategies using deadwood-associated biodiversity. I clearly demonstrate that the transition from dense even-aged forests to old-growth heterogeneous forests is also a transition period for deadwood dynamics and deadwood-associated biodiversity. The emulation of this transition is the goal of current ecosystem management strategies in the region. The knowledge gained from this thesis will greatly improve our ability to implement these management strategies in black spruce forests specifically and how deadwood-associated biodiversity can be an effective indicator for testing other ecosystem management strategies.

Key words: Deadwood, saproxylic, wood decay, wood decomposition, black spruce, polypore fungi, beetles, black spruce, *Picea mariana* (Mill.) BSP., paludification, retrogression, ecosystem management.

GENERAL INTRODUCTION

Biodiversity in the boreal forest

Dramatic losses or changes in biodiversity, caused by habitat loss and expanding use of natural resources, has generated increased interest in the consequences of such a loss on ecosystem functioning (Wilson 1988, Pimm et al. 1995). This is the foundation of the biodiversity ecosystem function paradigm as described by Naeem (2002), which initially reiterates the well-accepted idea that biota plays an essential role in ecosystem processes, but continues with a second, more contentious claim, that diversity of biota is required to maintain ecosystem processes. Better stated: what proportion of natural diversity is required to maintain proper ecosystem functioning?

While a fundamental theme within community ecology is describing how patterns of biodiversity are a function of abiotic (physical and chemical conditions) and biotic factors (*e.g.* competition, mutualism), this perspective basically perceives biodiversity as a passive consequence of these features. It is clear that patterns of biodiversity can be described by abiotic and biotic factors but it is becoming increasingly apparent that biodiversity can also affect their environment. The integration of community ecology with ecosystem functioning provides a more holistic understanding of biodiversity (Loreau et al. 2001).

This relatively new approach to biodiversity study has spurred an increase in research between ecosystem function and biodiversity, including the long-standing idea that a higher degree of biotic diversity results in heightened ecosystem stability, or resistance to permanent change (MacArthur 1955, May 1974). Tilman (1996, 1999) renewed this idea by providing experimental evidence demonstrating that more diverse communities in grassland ecosystems are more resistant to drought in terms of total biomass and ultimately have higher primary productivity than less diverse communities. Rekindled interest in diversity-stability relationships and biodiversity ecosystem functioning has inspired several studies on the effects of anthropogenic disturbances on natural ecosystems, impacts to biodiversity and ecosystem functioning (Nyström et al. 2000, Loreau et al. 2001). Insects for example can be important drivers of ecosystem process in boreal forests. For example, spruce budworm (*Choristoneura fumiferana* (Clemens)), forest tent caterpillar (*Malacosoma disstria* Hübner) and mountain pine beetle (*Dendroctonus ponderosae* Hopkins) are insects that have the ability to kill large patches of trees, altering successional processes, reshaping forest age distributions, and contributing to structural heterogeneity (Schowalter et al. 1981, Schowalter et al. 1986, Bergeron and Leduc 1998). Bees and other insect pollinators in the forest are responsible for pollinating many flowering plants species (Carter 2005), and many insects play a significant role in decomposition by reducing the particle size and chemically modifying organic matter during feeding (Manuel 2001, Chapman et al. 2003). Still other insect species influence decomposing organisms by facilitating dispersal and controlling nutrient release rates during grazing on the microorganisms (Harmon et al. 1986, Franklin et al. 1987, Edmonds and Eglitis 1989).

The boreal forest consists of one-third of the world forests and at *c.* 2.6 x 10^6 km^2 and historically, fire, insects, and disease were the main factors determining forest age class distribution, successional pathways and biodiversity in boreal forests (Johnson 1992, Payette 1992, Bergeron 2000, Bergeron et al. 2001, Bergeron et al. 2002, Harvey et al. 2002). However, the Canadian boreal forest has not escaped pressures from increasing demand for forest products and is now being harvested at an unprecedented rate (Schneider 2002). Unlike natural disturbances, forest harvesting can lead to a drastic reduction in the quantity of deadwood in forests (Siitonen et al. 2000). Studies from Finland have documented 90-98% reduction in the quantity of deadwood in managed forests with a much larger decrease in large-diameter pieces than small-diameter pieces (Angelstam 1997, Siitonen et al. 2000, Siitonen et al. 2001). Boreal forests are now becoming the focus of biomass harvesting that will only intensify the loss of deadwood in boreal forests (Work et al. 2014).

A large and important component of forest biodiversity is associated with deadwood and is potentially threatened as this resource diminishes. Siitonen (2001) provides a conservative estimate that 20-25% of forest species in the boreal forest are dependant on deadwood habitats. Speight (1989) drew attention to this group of deadwood-associated organisms and coined the term 'saproxylic'. Since then, several studies from Europe have focused on habitat use, conservation and response to anthropogenic disturbance (Speight 1989, Ahnlund 1996, Bakke 1999, Brustel and Van Meer 1999, Andersen et al. 2000, Eriksson 2000, Ehnström 2001, Siitonen 2001, Gibb et al. 2006). In North America, saproxylic insects have begun to receive more attention; however, much of this work has focused on describing natural patterns of occurrence (Hammond 1997, Hammond et al. 2001, Hammond et al. 2004, Saint-Germain et al. 2004, Boulanger and Sirois 2006, Jacobs et al. 2007a, Saint-Germain et al. 2007b) with relatively few studies examining the response to forest harvesting (Jacobs et al. 2007b, Dollin et al. 2008, Webb et al. 2008, Cobb et al. 2011). Industrial forest harvest has the potential to reduce deadwood-associated species by >50% (Siitonen 2001), exemplifying the need for continued research on both natural and managed forests.

Deadwood in the boreal forest

Deadwood dynamics (*i.e.* rates of input, transition and decay), like many other aspects of boreal forest succession, are dependant on the fire frequency, fire intensity, site productivity, and decomposition rates (Harmon et al. 1986, Bergeron et al. 2004a). General deadwood dynamics in forested ecosystems consistently demonstrate that deadwood volumes are highest just after large-scale disturbance, then decline to the lowest volumes, and slowly build up again in older forests (Sprugel 1984, Agee and Huff 1986, Spies et al. 1988, Lee 1998, Duvall and Grigal 1999, Siitonen 2001). Initial volumes of deadwood after disturbance depend on the quantity of dead and living trees preceding the disturbance event, the proportion of living trees killed by the disturbance and, in the case of fire, the amount of dead trees consumed by the fire event itself. After a disturbance event, the deadwood created by the disturbance decays and inputs of deadwood are generally low, resulting in forests with relatively low volumes of deadwood. In some cases, such as low-severity fire, many trees will survive the disturbance event and maintain a more continual input of deadwood. Competition and self-thinning increases in stands *c.* 75-100 years post-disturbance depending on site characteristics (Harvey et al. 2002) elevating deadwood inputs. Deadwood accumulates in these stands and volumes at any given time are based on the inputs from tree mortality and outputs from wood decay. The average rate of input and decay will sometimes reach equilibrium known as the equilibrium volume, which is approached in many old growth stands (Tyrrell and Crow 1994, Duvall and Grigal 1999).

Decay rates of deadwood are generally dependent on tree species, air temperature and precipitation (Yin 1999). These factors affect the three main types of decay: 1) leaching; 2) fragmentation; and 3) biological transformation (Harmon et al. 1986). Leaching of deadwood is not thought to be an important process on its own. Wood is low in soluble substances, especially early in decay. Leaching increases in importance in later decay stages after microbes and invertebrates transform deadwood into more soluble substances and fragmentation increases surface to area ratios. Fragmentation can take many forms. The activity of wood and bark-boring invertebrates in fresh deadwood loosens bark and reduces the integrity of deadwood. Larger vertebrates can crush deadwood, especially in later decay stages, and gravity can cause well-decayed deadwood to fall apart under its own weight. The final type of decay and arguably the most important is biological transformation. Respiration is indicative of biological transformation and is probably the most well-studied aspect of deadwood decomposition (Progar et al. 2000, Chambers et al. 2001, Wang et al. 2002, Gough et al. 2007, Bond-Lamberty and Gower 2008). Respiration is largely attributed to bacteria and basidiomycete fungi (Swift 1977). The majority of wood is made up of lignin, cellulose and hemicelluloses that are transformed to more usable nutrients by saprotrophic basidiomycetes and to a lesser extend ascomycetes and invertebrates (Swift 1977). Invertebrates can facilitate colonization of microbes and act as dispersal agents transferring bacteria and fungal spores between pieces of deadwood (Progar et al. 2000, Greif and Currah. 2007).

While decomposition is the main process of deadwood leaving forested ecosystems, recent studies have drawn attention to the importance of buried wood (Manies et al. 2005, Hagemann et al. 2009). Wood becomes buried faster with greater contact with the ground, deeper soil organic layer depth, reduced canopy cover and decreased log diameter. High rates of burial in some forest types can result in large volumes of deadwood under the surface. For example, Manies et al. (2005) found that 8% to 20% of woody biomass was buried in black spruce forests in Manitoba. Hagemann et al. (2009) reports that in high-boreal black spruce forests of Newfoundland, buried deadwood volumes exceeded aboveground volumes by 50% in old-growth stands and >400% in 34-35 year old post-harvested stands Furthermore, the cool wet conditions under the moss layer reduce decay rates to the point where buried deadwood may persist until consumed by high-intensity fire (Hagemann et al. 2009). When included, this large and persistent mass of buried deadwood increases total carbon in forest carbon budgets (Moroni et al. 2010).

Deadwood has the potential to play important roles in carbon flow and nutrient cycles in the forest (Harmon et al. 1994, Brais et al. 2006). The current available information on the importance of deadwood to forest nutrient cycles is contradictory and depends upon the extent of nutrient contribution and uptake included in a given model (Hart 1999, Harmon et al. 2000, Laiho and Prescott 2004). Deadwood is typically abundant in natural forests, however it has low nutrient concentrations (Harmon et al. 1986) and when compared to inputs from litter, contributes a minor fraction of nutrients annually produced in boreal forests (Laiho and Prescott 1999, 2004). However, deadwood provides a large proportion of nitrogen, calcium, and potassium required for tree growth (Krankina et al. 1999). For example, Brais et al. (2006) was able to show that jack pine boles provided up to 40% of nitrogen and 26% of phosphorus immobilized annually in living tree biomass. The contribution of deadwood to forest nutrient cycles may increase after catastrophic disturbance where the low nutrient content of deadwood is offset by the large mass of deadwood created or in extremely nutrient-limited forests (Harmon and Chen 1991).

Decaying deadwood is a source of atmospheric carbon. Following massive Mountain Pine Beetle outbreaks in Western Canada, carbon released from dead trees was estimated to be an average of 13.5 megatonnes of carbon per year (Kurz et al. 2008). In the worst year, this can be up to 75% of the average emissions from wildfire for all of Canada (Kurz et al. 2008). However, deadwood can also be an important source of long-term carbon sink, particularly in the boreal forest. The low surface area to volume ratio and high lignin content of wood results in slow decay rates relative to other components of the forest floor (*e.g.* litter fall). In boreal forests, long photoperiods during the growing season promote high rates of plant growth and cold soil temperatures limit annual rates of decomposition. The boreal forest is typically considered a small long-term net sink of carbon between fire events (Kasischke and Stocks 2000). These figures generally ignore buried deadwood, which can persist for centuries (Moroni et al. 2010) and can contribute up to 31% of total organic layer carbon stocks (Hagemann et al. 2012). Clearly, deadwood plays important roles in forest carbon cycles and is a crucial component to forest carbon budgets.

Deadwood supporting biodiversity

Deadwood is recognized as a crucial element for biodiversity (Harmon et al. 1986, Siitonen 2001). Deadwood acts as substrate for the growth of trees (Christy and Mack 1984, Simard et al. 1998) and of other herbaceous plants (McCullough 1948, Falinski 1978). Deadwood supports large communities of mosses (Fenton et al. 2003, Arseneault et al. 2012), lichens (Nascimbene et al. 2008), and fungi (Chapela et al. 1988, Amaranthus et al. 1994, Jonsell and Nordlander 2002, Edman et al. 2004, Lindhe and Lindelow 2004, Nordén et al. 2004). Small mammals are associated with deawood (Bowman et al. 2000, Butts and McComb 2000, Fauteux et al. 2012), and standing deadwood (snags) is important habitat for cavity-nesting birds (Drapeau et al. 2002, Nappi et al. 2003) and bats (Crampton and Barclay 1998, Hogberg et al. 2002, Patriquin and Barclay 2003). There is a large body of literature focusing on the relationship between deadwood and arthropods from Europe (e.g. Speight 1989, Ahnlund 1996, Bakke 1999, Brustel and Van Meer 1999, Andersen et al. 2000, Eriksson 2000, Ehnström 2001, Siitonen 2001, Gibb et al. 2006), Australia (Grove 2000, 2002a, 2002b) and more recently from Canada (Buddle 2001, Hammond et al. 2001, Jacobs et al. 2007a, Saint-Germain et al. 2007a, Saint-Germain et al. 2007b, Dollin et al. 2008).

Siitonen (2001) summarized the main factors affecting which organisms inhabits a given piece of deadwood as: 1) species of deadwood; 2) stage of decay; 3) species of fungi and other species in the deadwood; 4) diameter; 5) quality (snags, logs, stumps); 6) amount of surrounding deadwood and 7) the part of the tree the deadwood originated from (i.e., branches, trunk, bole, roots, etc.). As deadwood decomposes, it is in habited by a succession of organisms (Siitonen 2001), and for many organisms this is an obligatory succession as they rely on the previous occupants to facilitate their own colonization (Hammond et al. 2001).

Ecosystem-based forest management

Traditional forest clear cutting and natural disturbances leave different structures and patterns on the landscape and will likely have different long-term ecological consequences. This fact has prompted forest managers and researchers to adopt an ecosystem-based approach to forest management. The basis of this approach is to study natural ecosystems and implement management strategies that closely resemble the natural patterns and processes on the landscape (Attiwill 1994). Originally this idea was based around mimicking patterns of natural disturbance (ie. wildfire) in harvesting; however it has been expanded to include partial cutting and selective cutting to emulate natural patterns of succession and insect damage (Bergeron et al. 1999, Bergeron et al. 2002). For example, in boreal mixedwood forests that naturally progress from deciduous to coniferous species during succession, an ecosystem-based management approach would use selective cutting to remove the deciduous component of early-successional forests to create forests with a coniferous over-story composition comparable with older stands.

Paludification

Black spruce stands in the claybelt region of Québec and Ontario are prone to paludification. During this process, litter accumulates, moss growth prevents regeneration, and there is an increase in the water table (Lavoie et al. 2005). This generally results in reduced soil temperatures, decomposition rates, nutrient availability and productivity (Taylor et al. 1987, Payette 2001). Decrease in decomposition and accumulation of peat in these stands result in large carbon sinks (Simard et al. 2007). Paludification may also decrease decomposition rates of deadwood in older stands and alter nutrient and carbon cycles in these stands.

Black spruce forests are one of the most nutrient-limited of all boreal ecosystems (Cleve et al. 1983), which may increase the importance of deadwood as a nutrient source. As with other species, nutrients are released slowly after an initial flux of nutrient released when the phloem layer is consumed (Krankina et al. 1999, Brais et al. 2006). Black spruce deadwood has a greater potential in providing nitrogen than other boreal forests, as up to an order of magnitude less nitrogen is recycled from litter fall and the moss uptake is nearly three times greater (Cleve et al. 1983). A similar response is expected for phosphorus as a fraction of the phosphorus from litter fall is recycled compared to more productive hardwood and white spruce ecosystems (Cleve et al. 1983). Inputs of N and P have the potential to provide significant proportions of the nutrient immobilized annually in tree biomass (Brais et al. 2006).

Study of deadwood, associated biodiversity and wood decay – Structure of this thesis and links between the chapters

In this thesis I strive to understand how deadwood enters and leaves a forested ecosystem and what effects that has on deadwood-associated biodiversity and subsequent ecosystem functioning. I have chosen to conduct this study in the black spruce ecosystem of north-western Quebec to 1) to contribute to the knowledge of natural stand development and biodiversity in this ecosystem; 2) to establish linkages between changing stand structure, biodiversity, and wood decay, and 3) to test an ecosystem management strategy using deadwood, associated-biodiversity and wood decay as indicators.

In the first chapter of the thesis, I document the inputs and decay of deadwood across a 2000-year fire-driven chronosequence. This chapter overlooks deadwood-associated biodiversity, and aims at understanding the dynamics of deadwood in these forests first. The methods and analyses presented in this chapter utilize two complementary approaches. The first approach used a series of logs placed in forests that varied in time since death. The second, more novel approach models the changes in living tree biomass, to estimate the creation of deadwood biomass and models deadwood present to estimate the biomass of deadwood decaying. Together these two approaches give an understanding of the rates of deadwood input and decay.

The second chapter introduces deadwood-associated beetles and fungi, and how these communities change in response to large anthropogenic changes in forest structure, specifically partial cut and clearcut harvesting. Deadwood-associated beetles are a large specious group that are relatively easy to collect and identify. Fungi are much harder to sample so I relied on the response of an assemblage of six species that were conspicuous and easy to identify. I measured wood decay using similar methods as chapter one and created causal models to demonstrate the stand structural effects on fungal and beetle biodiversity and subsequent effect on wood decomposition. This chapter begins to draw the linkages between deadwood-associated biodiversity and wood decay.

The third chapter tests an ecosystem management strategy aimed at emulating old-growth, uneven-aged black spruce forests. I measured changes in deadwood-associated biodiversity along a natural 700-year chronosequence of stands. I then compared changes in community composition and relative abundance in response to natural succession and partial cut harvesting. I build upon the knowledge gained about stand development in the first chapter and the response of biodiversity in the second chapter to effectively assess the implication of these management techniques. This chapter demonstrates the strengths of using deadwood-associated biodiversity for evaluating ecosystem management strategies and offers clear recommendation on how to improve these strategies in future trials.

CHAPTER 1

PALUDIFICATION OF BOREAL SOILS REDUCES WOOD DECOMPOSITION RATES AND INCREASES WOOD BASED CARBON STORAGE

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1.1 Résumé

À long terme, la paludification réduit la productivité au-delà de la surface du sol, ce qui résulte en une rétrogression forestière. Les forêts paludifiées sont caractérisées par une importante accumulation de matière organique et par une réduction de la température du sol, de la disponibilité en nutriments et des taux de décomposition de la matière organique. Se dirigeant vers la paludification, les forêts des premiers stades de la succession connaissent d'importantes entrées de biomasse sous forme de bois mort durant la phase d'exclusion compétitive, la plupart étant soupçonnée de se retrouver enfouie dans la couche organique qui croît rapidement.

Ici nous examinons les effets de la paludification sur la décomposition du bois dans des forêts d'épinette noire formant une chronoséquence >2000 ans en utilisant trois approches complémentaires 1) en faisant le suivi de billes au sol individuelles dans le temps; 2) en utilisant une série temporelle de billes au sol qui varient en temps depuis la mort et 3) en estimant la biomasse ligneuse à l'échelle du peuplement lors de sa progression de son état d'arbre vivant vers celui de chicot, de bille au sol et ultimement de bois mort enseveli ou décomposé. Ensemble, ces approches démontrent un délai de 6-7 ans avant que la décomposition ne débute et que de hauts taux de décomposition ne suivent. Nous avons aussi trouvé des preuves évidentes qu'une grande proportion des billes au sol se retrouvent enfouies dans la couche de matière organique. Des modélisations à l'échelle du peuplement indiquent que les plus hauts taux d'enfouissement se produisent à la fin de la phase d'exclusion compétitive, durant l'accumulation la plus rapide de matière organique et lorsque les plus hautes entrées et pertes de bois mort se produisent. Il a été suggéré que la récolte forestière dans ces peuplements devrait se faire avant le début de la phase d'exclusion compétitive pour imiter les processus naturels. Nous avons observé de rapide taux de décomposition et d'enfouissement durant la phase d'exclusion compétitive qui résultent en des temps de résidence réduits du bois mort à la surface, suggérant que le la récolte de matière ligneuse lors d'opérations forestières pourrait émuler la réduction naturelle qui s'observe durant la phase d'exclusion compétitive. Au contraire, récolter la matière ligneuse dans les stades avancés de la succession aurait des impacts beaucoup plus grands puisque le temps de résidence du bois mort y est prolongé. À la fin de la phase d'exclusion compétitive, les peuplements entrent dans un stade de rétrogression dans lequel la productivité continue de diminuer quoique plus lentement. Toutefois, les pertes continues en carbone de la biomasse ligneuse durant ce stade de rétrogression sont compensées par des taux de décomposition plus faibles et une importante quantité de biomasse accumulée sous forme de bois mort enseveli, ce qui stabilise les bilans de carbone ligneux dans ces écosystèmes.

Mots-clés : épinette noire; forêt boréale; chronoséquence; décomposition du bois; bilan de carbone; couche de organique du sol; Québec, Canada.

1.2 Abstract

Over long time periods, paludification reduces aboveground productivity resulting in forest retrogression. Paludified forests are typified by intense accumulation of the soil organic layer and a reduction in soil temperatures and nutrient availability. En route to paludification, early successional forests experience large inputs of deadwood biomass during the senescence of the post-fire cohort, much of which may be entombed in this rapidly growing soil organic layer. Here we examined the effects of paludification across a >2000 year chronosequence of black spruce forests on wood decomposition using three complementary approaches which: 1) follow individual logs through time; 2) utilise a time-series of logs that varied in time since death and 3) estimate woody biomass at the stand level as it progresses from live trees to snags, logs and ultimately to buried or decomposed deadwood. Together these approaches demonstrated a 6-7 year delay before the onset of rapid decomposition. We also found strong evidence that paludification results in a large proportion of logs becoming buried in the soil organic layer. Stand level modelling indicates that the rates of accumulation of buried deadwood were greatest following the senescence of the post-fire cohort when both soil organic layer build-up and creation of deadwood peaked. Following this period of high deadwood creation, stands enter a retrogressive state whereby productivity continues to decline albeit more slowly. Continued losses in woody carbon biomass from trees during this retrogressive state are offset by lower wood decomposition rates and a high biomass of accumulated buried deadwood, essentially stabilizing the wood based carbon budget in these ecosystems. We recommend that partial cutting be conducted prior to or near the senescence of the post-fire cohort to improve emulation of natural forest succession in terms of both live tree and deadwood biomass. Furthermore, deadwood during this period has an extremely short residence time and the dynamics of deadwood should recover much quicker than if harvesting is conducted later in succession when there is less live tree biomass and deadwood has longer residence times.

Keywords: black spruce; boreal forest; chronosequence; wood decomposition; carbon budget; soil organic layer; Quebec, Canada.

1.3 Introduction

In the absence of disturbance, forest ecosystems can enter a retrogressive stage where aboveground productivity declines (Wardle et al. 1997, Richardson et al. 2004, Wardle et al. 2004, Vitousek 2006). In northern forests, declines in productivity can be caused by paludification, whereby a thick soil organic layer, primarily in the form of Sphagnum mosses, accumulates resulting in colder, wetter soils with reduced nutrient availability, which ultimately reduces tree growth rates (Simard et al. 2007). With time, paludified forests develop into forest peatlands. Peatlands in general constitute 3% of global land area and contains 600 gigatons of carbon, more than a third of the world's pool of soil carbon (Woodwell et al. 1989, Yu et al. 2011). However, most of these peatlands are the result of edaphic paludification, where site topography and poor drainage result in peatland formation. Successional paludification, which has received relatively less attention, is the result of forest succession and fire cycles. Forests prone to successional paludification require high intensity fires to reset succession; whereas other disturbances (i.e. low intensity fire, insects and wind) tend to accelerate the paludification process. It is difficult to estimate the area of forest prone to successional paludification across the boreal; however, as the fire return interval in many parts of the boreal continues to lengthen (Bergeron et al. 2004), forest retrogression as a result of successional paludification will become more prevalent. Paludification of forested ecosystems and associated accumulation of soil organic material will increase their importance for carbon storage reservoirs and has the potential to drastically change deadwood dynamics.

Deadwood dynamics, like other aspects of boreal forest succession, are dependent on the frequency and intensity of disturbance events, site productivity and woody decomposition rates (Harmon et al. 1986, Bergeron et al. 2004b). Initial volumes of deadwood are determined by disturbance events that reinitiate succession. For example, Siitonen (2001) reported increasing volumes of deadwood following wildfire (from 110 m^3/ha to over 400m^3/ha) in spruce-dominated stands. These volumes depended on the amount of deadwood consumed by the fire, and the mortality rate of living trees. As initial deadwood decays, deadwood volumes are relatively low, until self-thinning increases the rate of deadwood deposition. In boreal forests, self-thinning usually begins 75-100 years after the disturbance, depending on site characteristics (Harvey et al. 2002, Harper et al. 2005). With time, input and decay rates can stabilize resulting in an equilibrium volume, which is common in many old growth stands (Tyrrell and Crow 1994, Duvall and Grigal 1999).

While our understanding of deadwood dynamics and succession are progressing (Krankina and Harmon 1995, Siitonen 2001, Brais et al. 2005), recent studies have drawn attention to the importance of buried wood (Manies et al. 2005, Hagemann et al. 2009). Rates of deadwood burial are determined by amount of ground contact, organic layer depth, canopy cover, and diameter of the log (Stenbacka et al. 2010). High rates of burial in some forest types can result in large volumes of deadwood under the surface. For example, Manies et al. (2005) found that 8% to 20% of woody biomass was buried in black spruce forests in Manitoba. Hagemann et al. (2009) reports that in high-boreal black spruce forests of Labrador, Canada, buried deadwood volumes exceeded aboveground volumes by 50% in old growth stands and >400% in 34-35 year old post-harvested stands Furthermore, the cool wet conditions under the moss layer reduce decay rates to the point where buried deadwood may persist until consumed by high intensity fire (Hagemann et al. 2009). When included, this large and persistent mass of buried deadwood increases total carbon in forest carbon budgets (Moroni et al. 2010).

Here we studied the effects of paludification on the input and losses of deadwood by measuring changes in biomass of live trees and deadwood across a chronosequence spanning 2375 years of stand development. We used three complimentary approaches to estimate loss from wood decay. We: 1) followed individual logs through time; 2) utilised a time-series of logs that varied in time since death and 3) estimated woody biomass at the stand level as it progresses from live trees to snags, logs and ultimately to buried or decomposed deadwood. We then used these stand-level models to predict long-term woody carbon storage in paludified black spruce stands. We hypothesized that decreased productivity from paludification (Simard et al. 2007) will equate to lower rates of deadwood input, and the cold, wet soils will lower rates of wood decay compared to younger less paludified forests. A significant proportion of deadwood will also be lost to burial in the organic layer and as this buried wood accumulates with time, it will represent a large reservoir of stored carbon.

1.4 Methods

1.4.1 Study sites

The clay-belt region of Ontario and Quebec, Canada, covers ca. 12.5×10^6 ha and forms the second largest peatland in the world (Gorham 1991). It is part of the precambrian shield and is composed primarily of clay deposits left by pro-glacial lakes Barlow and Ojibway (Vincent and Hardy 1977, Veillette 1994). The cold-climate and flat-topography, combined with clay soils, makes this region prone to paludification (Lavoie 2005). Mean annual temperatures in the region are 0°C with average precipitation values of 897mm (33% falling as snow) (Environment Canada 2011).

Our study was conducted along a chronosequence of stands in the northern part of the clay-belt (49°00'–50°00' N; 78°30'–79°30' W) originating from high severity fires and ranging from 60 years to 2360 years in age (Figure 1.1) (Lecomte et al. 2006b). This chronosequence has been well-studied in terms aboveground live biomass (Lecomte et al. 2006b), understory vegetation (Lecomte et al. 2005), diversity of mosses (Fenton and Bergeron 2006a), lichens (Boudreault et al. 2009), litter-dwelling arthropods (Paradis and Work 2011) and forest productivity (Simard et al. 2007). We added three additional stands (*vis.* Pui, Fen, Gau) to this chronosequence which were the uncut controls from a network of partial cuts in the area (Jacobs and Work 2012, Fenton et al. 2013). A total of 15 stands were selected to represent the greatest possible time between stem exclusion (34-96 years), senescence of the post-fire cohort and understory re-initiation (96-164 years) and old growth stages (>164 years) (Harper et al. 2005).

1.4.2 Stand-level deadwood dynamics model

Our approach to determining inputs and losses of deadwood across the chronosequence was based on estimations of biomass of live trees, snags and fallen logs which either decay on the surface or are buried beneath *Sphagnum* mosses where decomposition rates are thought to be greatly reduced (Figure 1.2). Biomass of live trees and deadwood was estimated as the product of wood volume and wood density. Transitions of woody biomass among different deadwood pools were then modelled as a function of time since fire (TSF) using estimates of tree growth (for live trees), tree death rates (for snags), snag fall rates and decomposition rates measured both above- and belowground (for logs).

1.4.3 Estimation of live tree biomass across the chronosequence

To estimate live tree biomass across the chronosequence, we converted individual tree volumes to mass using empirically derived estimates of volume and woody density from the chronosequence. Live tree biomass was assessed using circular plots with a diameter of 11.28 m (400 m^2). We measured each stem over 3 cm diameter at breast height (DBH), and recorded the species and whether the stem was alive or dead. Height of live trees was determined as a function of tree diameter using a calibrated Chapman Richards taper function (Zhao-gang and Feng-ri 2003). Individual parameters for the taper function were based on 107 black spruce trees from nine different stands (Boudreault et al. 2009) and fit using model comparisons with Akaike information criterion corrected for finite sample sizes (AICc). Volume of each individual live tree, in the circular plot, was then calculated as a truncated cone extending from the base of the tree to a height where stem diameter was 5 cm. This necessarily excluded branches and smaller parts of the tree from our estimates of live tree volume that decay at different rates than larger diameter pieces. To convert volume to biomass we modelled wood density. We used measured wood density of living trees from nine stands and fit these densities with generalized linear models (GLM) and AICc to determine the relationship between tree diameter, time since fire (TSF) and wood density. Biomass was then calculated by multiplying predictions from the best-fit GLM model for each tree sampled across the chronosequence by live tree volume.

1.4.4 Estimation of snag biomass across the chronosequence

To characterize stand-level density of standing deadwood (snags) within each plot, we established a rectangular sub-plot (20 m x 10 m) and recorded the diameter of each snag and whether the top was broken. In cases where the breakage was below 5 cm diameter, we estimated the height in the field. Heights of intact snags and snags broken above 5 cm diameter were estimated using the same taper function used for live trees. Snag volume was likewise estimated as truncated cone. Wood density of snags were considered to be equal to the live wood density, as other studies have not found a significant relationship between wood density and time since death in black spruce snags (Boulanger and Sirois 2006, Boulanger et al. 2011, Angers et al. 2012).

1.4.5 Estimation of log biomass across the chronosequence

To estimate total log biomass, we measured volume, decay stage, density and mass of downed deadwood (logs) in two star plots within each stand (Ståhl et al. 2001). Each star plot consisted of three 20 m transects radiating from a common midpoint and separated by 120 degrees. For each log > 5 cm diameter intersecting a transect, we recorded: 1) the decay class using a five class system (modified from Maser et al. 1979); 2) the percentage of moss covering the log as an average of 2 meters on each side of the intersection point, and 3) the diameter with a diameter tape or calliper. Logs were classified as buried if moss cover was greater than 50%. We then cut a 2 to 5 cm cross-section from the log using a chainsaw. We measured the minimum and maximum thickness of each cross-section with a calliper and calculated the volume based on a cylinder. We then dried the cross-sections at 65°C to constant mass and calculated wood density by taking the dry mass divided by the volume. We calculated stand level volumes of downed deadwood using the Van Wagner (1968) formula for overall volume and for each 0.1 g/cm^3 density class.

In two of the stands (N50 and N6, 373 and 710 years since fire, respectively) we excavated a 10 meter by 30 cm trench to the depth of the mineral soil and measured all pieces of deadwood that were missed in the aboveground transects. For each piece, we measured the diameter and depth from the soil surface. We attempted to sample the oldest stands (N16 and N20) using these methods but, due to accessibility issues and weather, it was not possible.

1.4.6 Measurement of organic layer across the chronosequence

We measured the depth of the organic layer along one transect of the star plot conducted for the estimation of log biomass. At one meter intervals along the transect, we pushed a steel rod into the ground until significant resistance was met and recorded the depth.

1.4.7 Estimation of decay rates of logs

Estimation of decay rates was based on changes of wood density of logs with increasing time since death of the tree. We established a sequence of logs varying in time since death in each of eight stands. Stand ages, based on time of sampling (2008), were 60, 94, 133, 134, 183, 373, 718 and 2365 years since the last fire. When possible we sampled the wood density of three age classes of logs: Age classes of logs were 1) zero years since death – freshly cut trees we felled in 2008; 2) four years since death – trees felled during study of Boudreault et al. (2009), and 3) 6-10 years since death – trees felled during the study of Lecomte et al. (2006).

We initially sampled four (94, 134, 373 and 718 years since fire) of the nine stands in July of 2008. We cut multiple cross-sections from each log and prepared 50 cm segments of the youngest and oldest log age classes for later remeasurement. The number of cross-sections for each log age class were as follows: 1) For logs in the youngest age class (0 years), we cut four cross-sections 50 cm apart, starting 50 cm from the base of the tree; 2) in the second age class (4 years), we cut two cross-sections 50 cm apart, starting 50 cm from the base of the tree, and 3) In the oldest age class (6-8 years), we cut between six and ten cross-sections. Some of the trees in this oldest age class had cross-sections previously removed at 1m intervals at time of felling. For these trees we cut two cross-sections for each interval for five corresponding sections. When we could find trees still intact, we cut six cross-sections at 50 cm intervals.

Preliminary analyses indicated that by using additional stands we would decrease the variability in decay estimates; therefore we sampled three additional stands (60, 133, 373 years) in September of the same year. As in the first collection trip we sampled the same three age classes; however, we cut just two cross-sections, 50 cm from the base of each tree separated by 50 cm. Further analysis revealed possible effects of stand age on decomposition rates, which motivated us to add two extremely old stands to the study (1595 and 2365 year since fire). These stands were not sampled by Boudreault et al. (2009), leaving us with only the oldest and youngest age classes for logs. Furthermore, we were unable to find the trees cut by Lecomte et al. (2006) in the 1595 year-old stand, leaving us with only a measure the youngest age class. Although, the addition of these sites prohibit a fully balanced statistical comparisons, these data points for living wood density as well as the logs in the oldest stand add to the overall value of this study. We compensate for these differences within log age classes and between stands by using mixed-effects models which are more robust to unbalanced sampling designs (Pinheiro and Bates 2000).

After measuring wood density for all cross-sections using the methods described above, we sealed both ends of 50 cm segments from the youngest and oldest log age class with paraffin wax to reduce the rate of drying, which simulates the condition of longer logs. Logs were placed on the forest floor in the stand where they were sampled. Two years following initial sampling, we remeasured these log segments, for wood density, moss cover and canopy openness over each one using a Model A spherical densiometer (Lemmon 1956).

1.4.8 Data analysis

We compared changes in wood density of the same logs between years with repeated measures ANOVA (RM-ANOVA), using the aov function in R 2.14.1 (R Development Core Team 2011). Aberrant logs, where measured wood density increased, were removed from the analysis. We analyzed moss growth on these logs using LME with log nested in stand as the random effect and log diameter, stand age and canopy openness as the fixed effects. Interactions were not examined and models were compared with AICc.

We initially modelled changes in our estimation of biomass of live trees, snags and logs, as well as changes in the depth of the organic layer using linear regression with the log (TSF) as the explicative variable. We then tested these models for the presence of a non-constant regression parameter (i.e. break-point) using the Davies test (Davies 1987). When a break-point in the regression was detected, we used segmented linear regression using the function segmented in the segmented library (Muggeo 2008) in R. This analysis estimates unknown break-points (Muggeo 2003) and corresponding regression coefficients. We removed the youngest stand from this analysis, as it was the only stand that was likely still gaining biomass at the time of sampling.

We estimated decay rates of logs by modelling changes in wood density for logs, varying in time since death, using negative exponential models and lag time models (Harmon et al. 1986, Harmon et al. 2000). The basic negative exponential model that includes only time since death (TSD) as a parameter had the form:

$$Y_t = Y_0 e^{-kt} \tag{1}$$

where Y_t is the density at time t, Y_0 is the initial density and k is the decomposition constant. The lag time model includes an additional parameter (n) to account for the time it takes for decomposer organisms to colonize and establish in a piece of newly created deadwood:

$$Y_t = Y_0[1-(1-e^{-kt})^n] \tag{2}$$

where *n* represents the time lag in years. We incorporated TSF and diameter into equation 1 and 2 to by altering initial wood density and/or decay rates (k) to produce a series of competitive decay models (Table 1.3 and 1.4). We compared both linear and power-law functions to assess the effects of TSF and diameter on decay rate (k). We presented the linear function only when it was superior to the power-law function according to the AICc.

1.4.9 Modelling of stand level deadwood dynamics

We expressed the yearly input of deadwood biomass as the difference between the estimated biomass of living trees from the segmented regression models during the previous year and the current year. We estimated annual growth rates by measuring ring widths from growth years 2002 to 2007 of 20 living trees representative of the dominant cohort from the initial 4 stands sampled in 2008. Using these data, we then developed a diameter dependant growth model based on models developed by (Coomes et al. 2005) and G. Sainte-Marie (pers. com.). Our model included an additional parameter for time since fire (Equation 3)

$$rg = \frac{a}{\log(TSF)} \times MaxRG \times e^{-0.5\left(\frac{\log\left(\frac{diam}{xo}\right)}{xb}\right)^2} \tag{3}$$

where *a* was the effect of time since fire (TSF), *diam* was the DBH and *MaxRG*, *xo* and *xb* were all constants (4.45, 9.30 and 0.77 respectively). Model constants were derived from Quebec provincial data by G. Sainte-Marie (*unpublished data*). One year of modelled annual growth was then applied to all stems in each plot and biomass of trees was recalculated. Both previous year biomass and current year biomass (previous year plus growth) were modeled using segmented regression. Current year live tree biomass was always less than previous years biomass plus growth, therefore the difference between the current year and previous year can be interpreted as tree mortality, or newly created deadwood biomass.

Snag fall rate (SFR) in a given year was calculated as the difference of the current years snag biomass and the previous years snag biomass plus the inputs from living biomass (Equation 4)

$$SFR = 1 - \frac{m_{snags_t}}{m_{snags_{t-1}} + m_{inputs_t}} \qquad (4)$$

where m_{snags_t} is the mass of snags at time t and m_{inputs_t} is the mass of inputs from tree death. Note that the snag fall rate includes both snags transitioning to logs and trees that transition directly to logs.

Decay constant of downed deadwood (k) was then calculated based on the negative exponential model of wood decay as the difference in the current year log biomass and the previous year's biomass plus inputs form snags minus logs buried in the organic layer (Equation 5)

$$k = \frac{m_{\log s_t}}{(m_{\log s_{t-1}} + m_{snag.inputs_t})r_{burial_t}} \qquad (5)$$

where m_{logst} was the mass of logs at time t, $m_{snags.inputs}$ was inputs from SFR and $m_{burialt}$ was the current year burial rate. We modelled three different scenarios for the rate of burial of logs on the assumption that burial rate is proportional to the rate of increase of soil organic layer. The yearly organic layer depth was estimated from the regression models and the yearly percent increase was determined as the difference between current and previous years organic layer depth, divided by the previous years biomass, and multiplied by 100.

The first scenario had the percent of biomass of logs buried each year equal to the percent increase of the organic layer. This scenario predicted much more buried log biomass than observed in the two measured stands. The second scenario used the percent increase of the organic layer divided by 5. This scenario predicted levels approximately between the two measured stands. The third scenario divided the increase by 10, which corresponded to the lowest value we observed in the two measure stands. Finally we recalculated wood decomposition rates using a modified lag-time model, where exponential decay was permitted only after a lag period derived from the log decomposition time series.

1.5 Results

General stand characteristics are presented in Table 1.1. Older stands had generally greater organic layer depth, lower basal area and, with the exception of the oldest stand, higher volumes of deadwood. In most stands nearly half of the logs were considered buried based on common designation [surface area of the log covered in > 50% organic layer (Hagemann et al. 2009)]. Additional sampling for buried deadwood using trenches in two plots [N50 (373 years since fire) and N6 (710 years since fire)] revealed an additional 110 m^3/ha and 30 m^3/ha of deadwood, respectively.

We found a significant relationship between height and DBH of trees using the Chapman Richards model (Table 1.2). The best model using the AICc explained 60% of the variation of height in the data and did not include the effect of time since fire (TSF) on any of the coefficients in the model. Both diameter and TSF affected living wood density. Live trees had a mean wood density of 0.40g/cm^3. Wood density of live trees increased with the log of TSF (GLM, β_{TSF}=0.015, t=6.91, P<0.001) and decreased with DBH (GLM, β_{DBH} =-0.0031, t=-5.59, P=<0.001).

1.5.1 Changes of biomass with time since fire

We found strong support for breakpoints in the relation between TSF and biomass of live trees, snags and logs (Davie's test p=0.007, p<0.001, 0.007, respectively), and therefore used a segmented regression to model these variables. Live tree biomass declined at high rates (t=-2.77, p=0.020, Figure 1.3A) until 143 (SE=21) years after fire, after which biomass continued to decline but at a much slower rate (t=-2.36, p=0.040). Initially, we did not observe a significant relationship between snag biomass and TSF. However, following the removal of sites N23 (a young site with a high number of snags) and Gau (an older site with a low number of snags), we found snag biomass significantly increased (t=2.79, P=0.027, Figure 1.3B) until 255 years after fire (se=43), at which point snag biomass significantly decreased (t=-3.07, p=0.015). We chose to remove these two observations as they clearly did not fit the trend observed in the other sites and to allow us to fit a regression line that describes the majority of the sites for our stand dynamics model. We found a similar relationship between TSF and biomass of logs (Figure 1.3C), although before the breakpoint, the increase in biomass was not significant (t=1.90, p=0.087). However, following the breakpoint of 262 years (se=64) since fire, the decrease of the biomass of logs significantly decreased (t=-2.26, p=0.047). Organic layer depth (p=0.162) increased linearly with log (TSF) (t=4.92, P<0.001, Figure 1.3D). We highlighted the trends of the site "Pui" in Figure 1.3 as this site has many characteristics of a much older stand than our data indicated. For example, the relatively low biomass of live trees and the thick depth of the organic layer were much more consistent with an older stand or a stand that arose from a lower intensity fire. Unlike the other stands in the chronosequence, the age of this site was not verified by radiocarbon dating. Differences in stand characteristics of "Pui" may occur because this stand could be older or follow a different successional trajectory from a low intensity fire (Lecomte et al. 2006a).

1.5.2 Estimation of decay rate

We used a total of 488 cross-sections measured from 105 trees across 7 stands to estimate decay rate of logs. Parameter estimates for all GLM models reported in Table 1.4 and 1.6, with the best models displayed in Figure 1.4. The best model using the negative exponential (Table 1.3: model 8) indicates that as stands aged initial wood density increased (e.g. for every 100 year increase in stand age, initial wood density increased by about 1-3%) and decay rates decrease (e.g. for every 100 year increase in stand age, decay rates decreased by 2%). The lag time model greatly outperformed the negative exponential model. The best overall model (Table 1.5: model 9) included the effects of both diameter and TSF. This model had a lag of 6.6 years; for every 1 cm increase in diameter, initial wood density increased by 0.0022 g/cm^3, and for every 100 year increase in TSF, initial density increased by 0.0131 g/cm^3 and the decay rate (k=0.010) decreased from 14%-6% with every 100 year increase of the mean TSF ($\bar{x}$=242 years) over the first 1000 years.

Resampling of wood density of the same logs provided little evidence of decay in the initial two years. We were unable to observe a reduction in wood density in over half of the logs (10/19). In the remaining logs wood density was reduced by an average of 2.4% per year. Resampling of wood density of older logs (5-10 years since death) over a 2-year period revealed marginal evidence of wood decay. Two of the 18 logs could not be found for the re-measurement and again there was no detectable reduction in wood density of four of the logs. Statistics on the remaining 12 logs indicated a significant reduction in wood density (RM-ANOVA, $F_{1,13}$=18.312, P<0.001), with a reduction of an average 3.7% per year. However, limiting statistical analysis to just those samples where mass loss was detectable may be biasing the data to predict a larger mass loss than actually occurring.

We also found that the best predictors of moss growth on re-sampled logs were the diameter of the log itself (LME, t_{30}=-3.41, P=0.002) and canopy openness (LME, t_{30}=1.55, P=0.132). Although, canopy openness was not significant, this model outperformed the model that included just log diameter (AICc=-299 vs -292 respectively).

1.5.3 Transition of biomass from live trees, snags and logs

Tree growth rates (measured as ring widths) across the chronosequence decreased with increasing TSF and decreased with increasing diameter at breast height (Figure 1.5A). Overall biomass of deadwood inputs decreased with TSF (Figure 1.5B). The highest rates of deadwood input were in young stands during the time of highest individual tree growth rates and highest rates of decrease in live tree biomass. Snags fell faster in young stands (<143 years) compared to later in the chronosequence (Figure 1.5C).

Under all three scenarios of burial rate, the predicted volume of buried deadwood fell within a range that could be expected based on the two trenches dug in two of the older stands (N50 and N6, shown in Figure 1.6A as black circles). We used the negative exponential model to determine decomposition rates, based on the inputs of log biomass from snags (Figure 1.5C), the losses to the buried deadwood pool under the three above scenarios (Figure 1.6A) and the observed biomass of logs present across the chronosequence (Figure 1.3C). We found no difference in decomposition rates across the chronosequence under the three scenarios of burial rates (Figure 1.6B). Our model predicted extremely high decomposition rates (k=0.544) during the senescence of the post-fire cohort early in succession, which then decreased to k=0.066 at 290 years post-disturbance, and then slowly increasing to k=0.113 as forests become more paludified. The average across the entire chronosequence was k=0.096.

Comparison of the two approaches (log vs. stand chronosequences) and the two decay models (negative exponential vs. negative exponential with a time lag) revealed that all four predict the highest rates of decomposition in the youngest stands, this rate decreases with stand age with the log chronosequence (Figure 1.7). However, the stand chronosequence approach predicts slightly higher rates of decomposition in the oldest stands (>1000 years) than the intermediate stand ages (100-300 years). We also found that the two approaches which incorporate a time lag have more similar decomposition rates than the approaches that did not include a time lag (Figure 1.7B).

1.5.4 Carbon Storage

Aboveground carbon stored in live coarse woody biomass (>5cm diameter) ranged from 16Mg/ha to 54Mg/ha (Figure 1.8A). The younger stand (<100 years) had on average twice the levels of stored C than the older stands. The carbon stored in dead coarse woody biomass ranged from 2.3Mg/ha to 10.3Mg/ha with older stands having much higher amounts of stored C than younger stands in the dead pool. When estimates of buried coarse woody biomass were included (Figure 1.8B), carbon storage in woody materials in black spruce remained relatively constant, ranging between 40 and 45Mg/ha, throughout the chronosequence.

1.6 Discussion

In this study, we used three complimentary approaches (resampling individual logs, comparing logs with different time since death and stand-level modeling) to estimate deadwood dynamics in black spruce ecosystems undergoing forest retrogression. These approaches corroborate a delay to the onset of decomposition, high rates of deadwood input and decomposition during stem exclusion, and following stem exclusion lower, constant rates of decomposition and burial in the older paludified stands. Together these processes led to a constant mass of stored woody carbon (ca. 40 Mg/ha) following the completion of stem exclusion and continuing at for least 2000 years.

The cause of retrogression in these black spruce ecosystems is largely attributed to the paludification of the forests (Simard et al. 2007). Paludification reduces live woody biomass more rapidly during stem exclusion than in older stands. Previous studies characterized loss of live woody biomass using simple linear regression models comparing tree biomass to a log-transformed stand age (Lecomte and Bergeron 2005, Simard et al. 2007). In our study we found strong evidence of a non-constant regression parameter when using the same regression model, indicating an even higher rate of loss for about 50 years following senescence of the post-fire cohort and a relatively slower rate following the breakpoint at 143 years. These results match closely with conclusions of Harper et al. (2005), who proposed a stabilization of live tree density between 95 and 164 years after fire depending on site productivity. Over this 50-year period we conclude that 50 Mg of living biomass transitions from the living woody pool to the deadwood pool.

However, live trees continue to grow and will contribute to the overall biomass of deadwood. Younger stands had the highest growth rates, adding additional 2.1 Mg/ha of biomass per year, or 105 Mg/ha of biomass over this 50-year period of extreme deadwood input and loss. Our estimates of growth are slightly less and follow a similar trend to Simard et al. (2007). This could be explained by the fact that Simard et al. (2007) used representatives from the 3 height cohorts, where we modelled ring widths across diameters from just the dominant height cohort and extrapolated to all the trees in the plot, or that total stored carbon may be even greater than our models predict.

During stem exclusion our models predict high inputs of deadwood biomass (155 Mg/ha), however these amounts do not readily reflect the observed aboveground biomass of deadwood. We do not observe maximal levels of aboveground deadwood biomass (22 Mg) until 100 years following stem exclusion when rates of deadwood input are lower. We believe that this extreme input of deadwood biomass rapidly leaves the stand through decomposition or is incorporated into belowground carbon stocks.

1.6.1 Decay rates (k)

It is clear our ability to predict decay rates of logs was improved by incorporating time lags into exponential models of decay. In these forests, measurable decomposition begins approximately 6-7 years following tree death. Many studies have found that the single negative exponential curve (Olson 1963) does not adequately describe wood decomposition (Grove et al. 2000, Harmon et al. 2000, Yatskov et al. 2003, Strukelj et al. 2013). Trees are thought to decompose slowly at first because of high initial moisture content, decay resistant heart-wood, or time required for decomposer organisms to become established (Grier 1978, Harmon et al. 2000, Yatskov et al. 2003).

However, not all other studies on black spruce have observed this lag in decomposition. For example, Boulanger et al (2011) reported decay rates of fire-killed black spruce (k=0.027-0.036) similar to ours (k=0.037) using the simple exponential model which did not include a lag period. Although little evidence of decay is reported in black spruce snags (Angers et al. 2012), we believe that when a tree dies and remains standing as a snag for several years that the time lag associated with decomposition of logs is negated. We attribute the lack of a decompositional lag to preconditioning of the snag by colonization of decomposers and loss of the high initial moisture content following death.

1.6.2 Effects of diameter and stand age on decay rates

In our study, there was a clear effect of diameter when using the negative exponential model of wood decay. Diameter effects on wood decomposition rates have a strong theoretical basis, in which the low surface-to-volume ratios are thought to prolong the colonization process and reduce sapwood-to-heartwood ratios (Foster and Lang 1982, Harmon et al. 1986, Rayner and Boddy 1988). Diameter effects have been frequently reported on relatively small diameter pieces (Abbott and Crossley 1982, Barber and Van Lear 1984, Erickson et al. 1985) or between large and small size classes (Brown et al. 1996). Equally, many studies did not find diameter effects on woody decay rates (Foster and Lang 1982, Marra and Edmonds 1996, Bond-Lamberty et al. 2002, Grove et al. 2009). There are only a few studies which have been able to show this relationship across larger diameter pieces. For example, Hérault et al. (2010) found a large effect of diameter on decay rates in Amazonian forests of French Guiana. A study in the Russian boreal by Tarasov (1999) [cited in Yatskov et al (2003)] found a negative correlation between size and decay rates. Chambers et al. (2000) found a significant effect of DBH on decay rates, although this relationship explained little of the variation in the data (r^2_{adj}=0.10).

We did not detect large effects of diameter on decay rates using the lag time model. Instead, time since fire (stand age) had the biggest influence on decay rates. In the range of stand ages (60-710 years) the decay rate decreased 64% from 0.18 in young stands to 0.11. This reduction in decay rates corresponds to low organic matter decomposition rates in paludified stands, which have been explained by colder and wetter environments, partly through the dominance of *Sphagnum* spp. on the forest floor (Gordon and Shugart 1989, Lavoie et al. 2005). These wetter environments in paludified stands could lead to higher wood moisture levels, which is also known to reduce wood decomposition rates (Progar et al. 2000, Barker 2008). Bond-Lamberty et al. (2002) found that wetter black spruce sites had lower decomposition rates when wood moisture was above 43%.

1.6.3 Burial of Deadwood

During forest paludification extremely slow decomposition rates of sphagnum mosses results in a rapidly accumulating soil organic layer (Fenton et al. 2010). We expected that the highest accumulation of mosses on logs would correspond to the highest rates of accumulation of the soil organic layer, typical of the younger stands in our chronosequence. However, we observed that the rate of moss accumulation on logs was dependant on diameter and forest openness, not TSF or organic layer depth. The rapid colonization of logs by mosses in these older more open stands can be explained by a shift in the moss composition. In the older stands (N50 & N6), the moss community on the logs was dominated by both *Sphagnum spp.* and humicolous species, whereas in the younger stands (N23,N18) only humicolous species were present on the logs. Furthermore in the oldest stand examined (718 years since fire) 4 different species of *Sphagnum spp.* were present compared to just a single *Sphagnum sp.* was present in the next youngest stand (373 years since fire).

1.6.4 Carbon budgeting and forest management

Forest management strategies in these forests have focused on either partial cutting to advance forest succession or clearcutting to restart the successional process (Bergeron et al. 2002). Partial cutting has the greatest potential for preserving natural systems if realized at the maximal biomass phase before the onset of stem exclusion (Fenton et al. 2013). We observed rapid rates of wood decomposition and burial during stem exclusion. Thus during this phase of stand development, residence time of surface woody biomass is at its shortest. Partial cutting during this period would also result in reduced woody biomass that would otherwise be rapidly disappearing. Therefore, reducing the amount of deadwood during or just prior to stem exclusion should have relatively short term effects on deadwood dependant organisms. Later in succession when the forests have entered a retrogressive state, deadwood wood and carbon stocks are at a more stable equilibrium and anthropogenic disturbance at this point would have longer lasting effect on the natural dynamics of deadwood.

Our study supports the idea that large pools of deadwood exist under the surface of the organic layer. These pools of buried deadwood have been shown to decay at dramatically slower rates and are thought to represent a longer-term pool of carbon than deadwood found on the surface (Moroni et al. 2010). We also demonstrated a possible mechanism of this process in black spruce stands undergoing paludification. When we combine our buried deadwood model with other measures of woody biomass, we found that these paludified stands maintained a relatively constant biomass of woody carbon following the stem exclusion phase of forest succession. This highlights the importance of belowground deadwood biomass in forest carbon models (Kurz et al. 2009). Although forests that enter this retrogressive state continually decease in productivity and lose woody carbon aboveground to encroaching sphagnum mosses, they are able to continually store more woody carbon belowground as deadwood dynamics remains relatively constant for thousands of years. Management of these old forests then becomes a trade-off between goals of long-term carbon storage and wood production. Presumably the trade-off favours carbon-storage as forests age and that ratio between stored carbon and live woody biomass increases.

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1.9 Tables

Table 1.1– General stand characteristics of the 15 stands along the chronosequence

Stand	Time since fire (years)	Organic matter depth (cm)	Live tree basal area (m^2/ha)	Dead tree basal area (m^2/ha)	Snag volume (m^3/ha)	Total Log volume (m^3/ha)	Percent of logs buried (%)*
N4	60	26.65	39.59	2.49	7.41	7.44	7.36
N23	94	15.15	46	6.64	16.89	19.73	59.56
S1	95	22.4	45.03	3.4	7.41	5.66	33.07
CH75	133	44.7	25.93	1.33	7.36	8.67	29.53
N18	134	46.4	35.55	3.11	9.19	8.53	43.54
POP	183	48.05	13.86	3.39	17.75	63.29	54.77
Pui	183	79.6	18.6	3.24	11.15	15.96	30.54
Fen	183	53	23.24	4.25	12.4	61.31	54.84
N8	183	43.15	34.51	2.55	19.07	24.92	82.83
L22	283	49.45	21.25	4.64	17.22	60.58	50.86
Gau	283	49	23.59	1.3	6.46	24.66	-
N50	373	48.3	19.65	3.73	13.88	49.28	47.34
N6	718	58.75	21.69	4.97	16.25	35.32	22.62
N16	1595	92.75	13.16	4.21	8.28	23.65	63.09
N20	2365	89.85	11.01	1.10	4.03	5.16	54.04

* Buried logs are logs that are >50% covered in moss

Table 1.2 – Chapman-Richards model parameter estimates for tree height based on DBH. The Chapman-Richards formula is $y(t) = a\left(1 - e^{(b \times DBH)}\right)^{c}$

	Estimate	S.E.	t-value	p-value
a	17.33	1.35	12.87	<0.001
b	-0.13	0.06	-2.35	0.02
c	1.46	0.76	1.91	0.06

Table 1.3 – Wood decay models and AICc based on the negative exponential function.

	Models	AICc
(1)	$Y_t = Y_0 e^{-kt}$	-346.82
(2)	$Y_t = (Y_0 + d \times Dia)e^{-kt}$	-346.55
(3)	$Y_t = Y_0 e^{(-k + k_d * Dia)t}$	-348.32
(4)	$Y_t = Y_0 e^{\left(\frac{-k}{Dia^{K_d}}\right)t}$	-348.25
(5)	$Y_t = (Y_0 + d \times Dia)e^{\left(\frac{-k}{Dia^{K_d}}\right)t}$	-347.23
(6)	$Y_t = (Y_0 + f \times \log(TSF))e^{-kt}$	-355.78
(7)	$Y_t = Y_0 e^{\left(\frac{-k}{\log(TSF)^{K_f}}\right)t}$	-346.25
(8)	$Y_t = (Y_0 + f \times \log(TSF))e^{\left(\frac{-k}{\log(TSF)^{K_f}}\right)t}$	**-357.84**
(9)	$Y_t = (Y_0 + d \times Dia + f \times \log(TSF))e^{\left(\frac{-k}{Dia^{k_d} + TSF^{k_f}}\right)t}$	-357.68
(10)	$Y_t = (Y_0 + d \times Dia + f \times \log(TSF))e^{\left(\frac{-k}{\log(TSF)^{k_f}}\right)t}$	-357.03

Table 1.4 – Estimates of coefficients for wood decay models in Table 3. Values in bolded row represent the best model (i.e. lowest AICc).

Model	Y_0	k	d	k_d	f	k_f
(1)	0.39	0.037***	-	-	-	-
(2)	0.39	0.038***	-0.002	-	-	-
(3)	0.39	0.036***	-	0.002 ·	-	
(4)	0.40	0.034	-	0.688 ·	-	-
(5)	0.41	0.035	-0.001	0.627	-	-
(6)	0.39	0.036***	-	-	0.019***	-
(7)	0.39	0.035	-	-	-	0.57
(8)	**0.39**	**0.033**	**-**	**-**	**0.017*****	**0.95·**
(9)	0.40	0.082	-0.001	1.09*	0.0001	0.379*
(10)	0.39	0.034	-0.002	-	0.016***	1.010*

Table 1.5 - AICc and estimates of coefficients of models that include a lag time.

	Models	AICc
(1)	$Y_t = Y_0[1-(1-e^{-kt})^n]$	-351.02
(2)	$Y_t = (Y_0 + d \times Dia)[1-(1-e^{-kt})^n]$	-351.40
(3)	$Y_t = Y_0\left[1-\left(1-e^{\left(\frac{-k}{Dia^{k_d}}\right)t}\right)^n\right]$	-348.91
(4)	$Y_t = (Y_0 + d \times Dia)\left[1-\left(1-e^{\left(\frac{-k}{Dia^{k_d}}\right)t}\right)^n\right]$	-351.92
(5)	$Y_t = (Y_0 + f \times \log(TSF))[1-(1-e^{-kt})^n]$	-367.79
(6)	$Y_t = Y_0\left[1-\left(1-e^{\left(\frac{-k}{\log(TSF)^{k_f}}\right)t}\right)^n\right]$	-376.53
(7)	$Y_t = (Y_0 + f \times \log(TSF))\left[1-\left(1-e^{\left(\frac{-k}{\log(TSF)^{k_f}}\right)t}\right)^n\right]$	-381.08
(8)	$Y_t = (Y_0 + d \times Dia + f \times TSF)\left[1-\left(1-e^{\left(\frac{-k}{Dia^{k_d}+TSF^{k_f}}\right)t}\right)^n\right]$	-381.07
(9)	$Y_t = (Y_0 + d \times Dia + f \times TSF)\left[1-\left(1-e^{\left(\frac{-k}{TSF^{k_f}}\right)t}\right)^n\right]$	**-383.28**

Table 1.6 - Estimates of coefficients for wood decay models in Table 5. Values in bolded row represent the best model (i.e. lowest AICc).

Model	Y_0	k	n	d	k_d	f	k_f
(1)	0.44	0.090**	2.0**	-	-	-	-
(2)	0.44	0.090**	2.0**	-0.002	-	-	-
(3)	0.43	0.089*	2.0**	-	0.033	-	-
(4)	0.49	0.183·	1.90**	-0.0031*	0.337	-	-
(5)	0.44	0.12***	3.0*	-	-	0.022***	-
(6)	0.44	0.001**	3.4**	-	-	-	1.029***
(7)	0.36	0.011**	6.3·	-	-	0.014**	0.655***
(8)	0.40	0.193*	6.5·	-0.0024*	0.158	0.013*	0.883***
(9)	**0.39**	**0.010****	**6.6·**	**-0.0022****	**-**	**0.0131***	**0.675*****

1.10 Figures

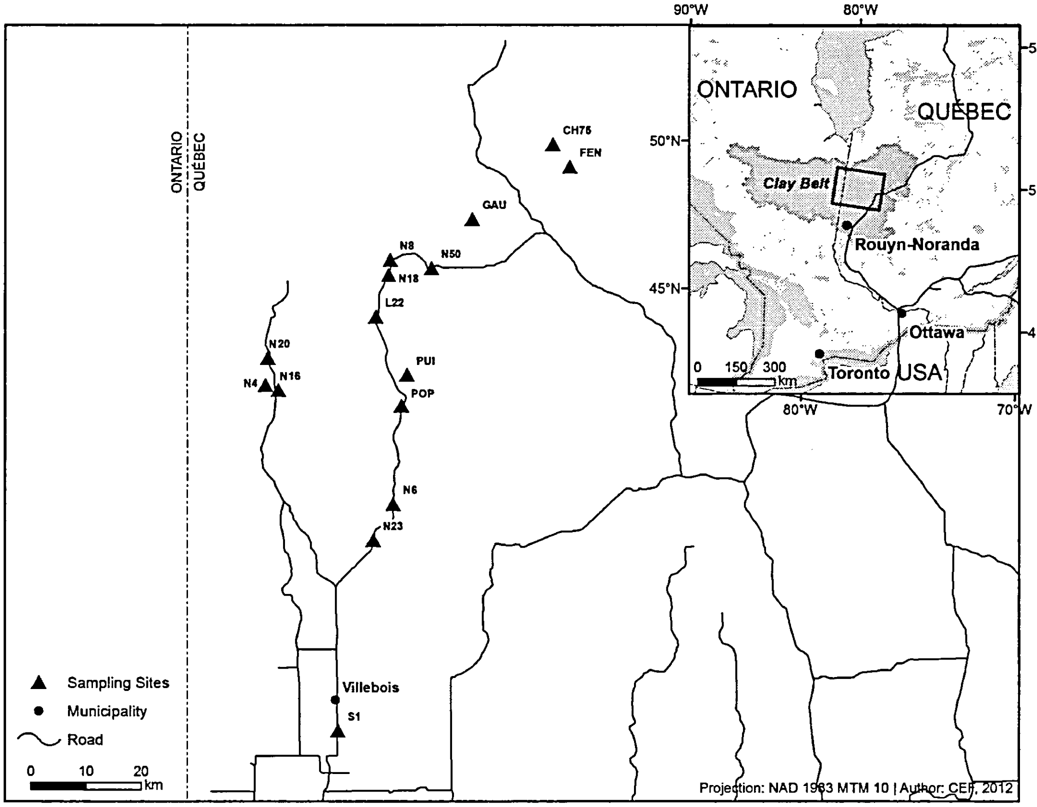

Figure 1.1- Map of the samplings sites in north-western Quebec. Grey area on inset map denotes the Clay Belt region which is prone to paludification.

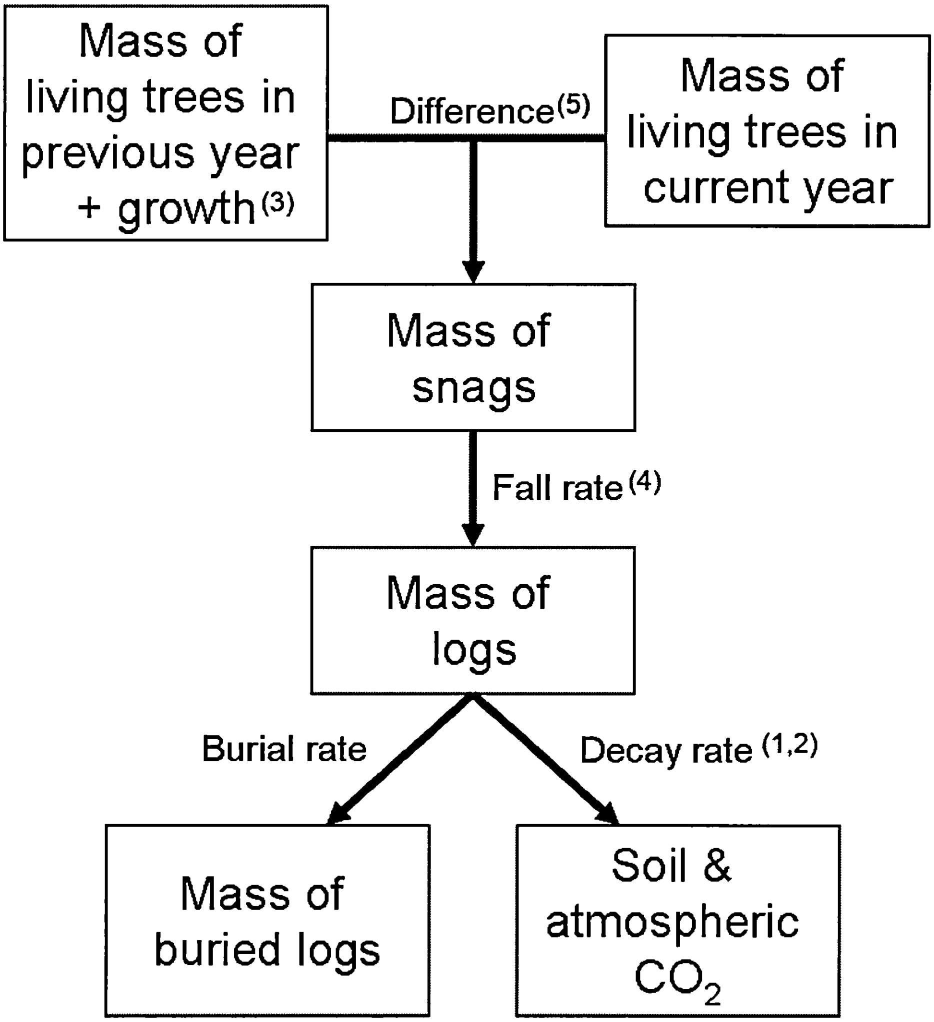

Figure 1.2 – Conceptual model of deadwood dynamics in black spruce forests. With corresponding equation numbers.

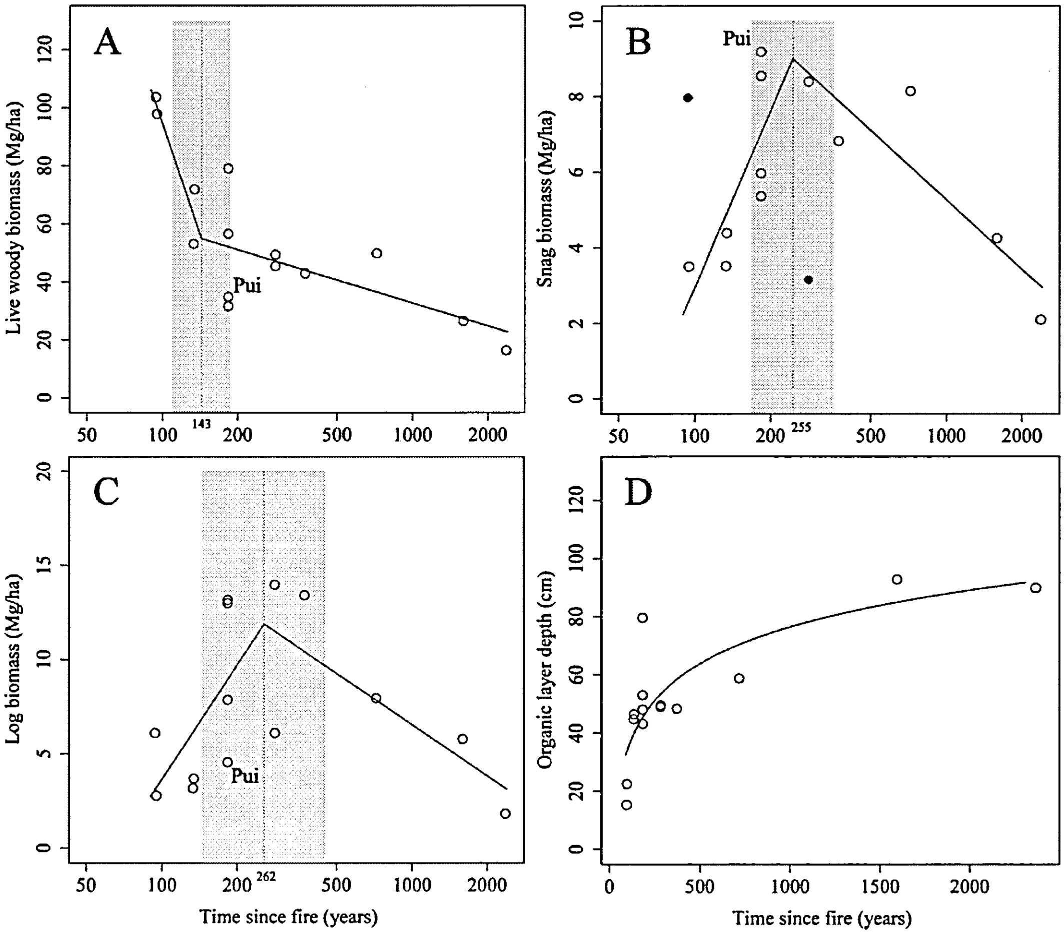

Figure 1.3 – Relationship between time since fire (years) and A) live woody biomass; B) snag biomass; C) log biomass and D) organic layer depth. Lines represented the fitted lines of segmented regression (A,B and C). All lines are significant ($p<0.05$) except for logs (B) before the breakpoint ($p=0.087$). Grey boxes represent 95% confidence interval of the break-points. Black points in graph B represent points removed from analysis. The x-axis is on a log scale in graphs A-C. Points labeled “Pui” are from a site that is appears older than date determined by oldest tree.

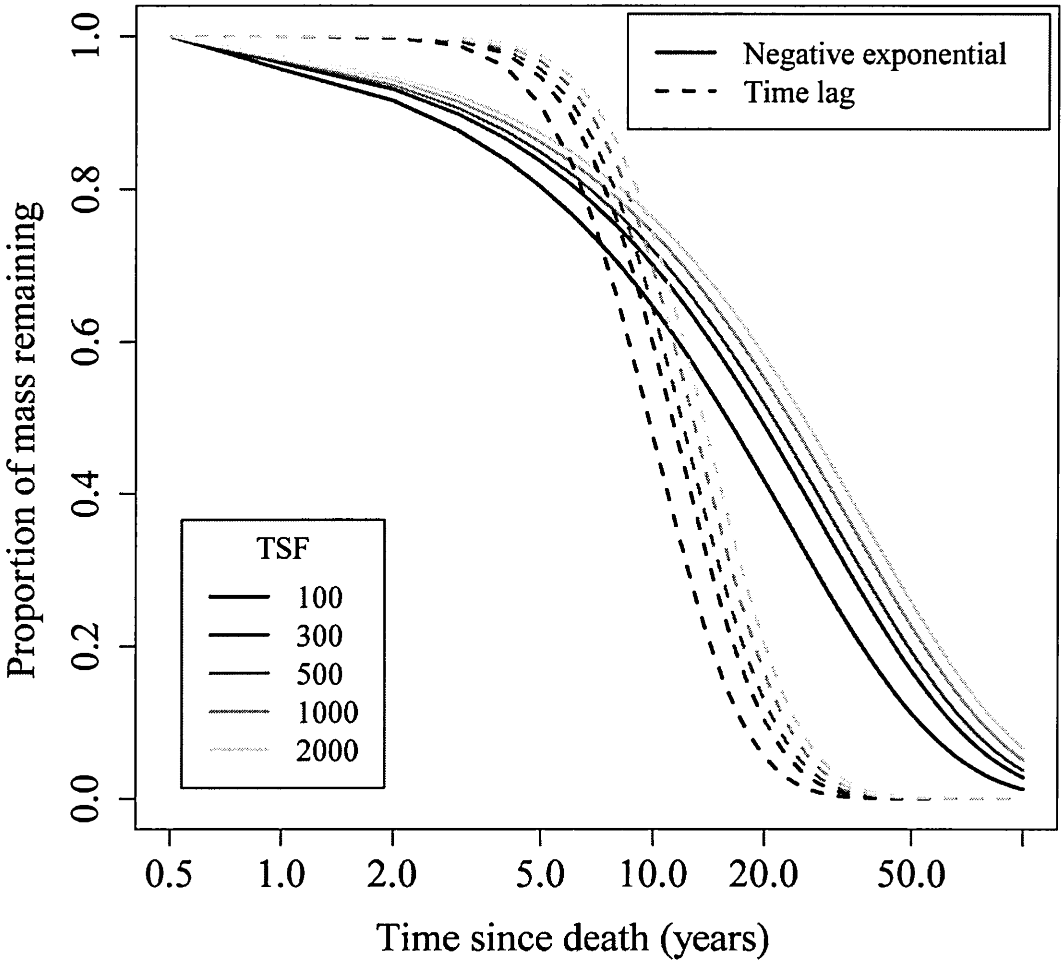

Figure 1.4 – Proportion of mass remaining with increasing time since death for 5 ages of forests.

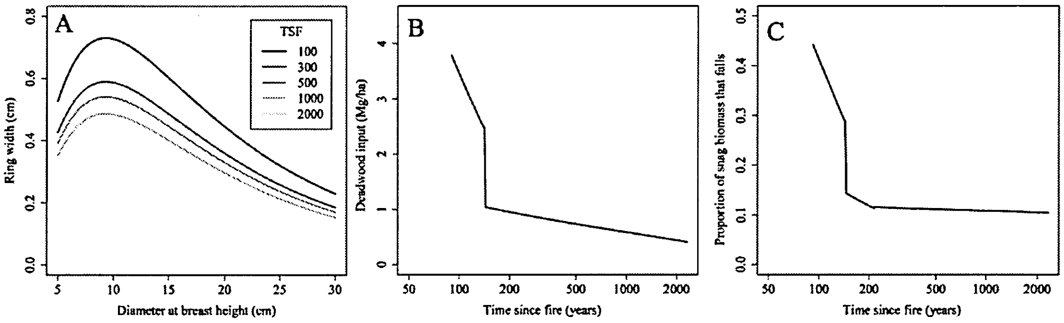

Figure 1.5 – Results from deadwood model based on concept in Figure 1.2: A) modeled growth across tree diameters and TSF, B) inputs into the deadwood pool, C) proportion of snags that falls in a given year across the chronosequence.

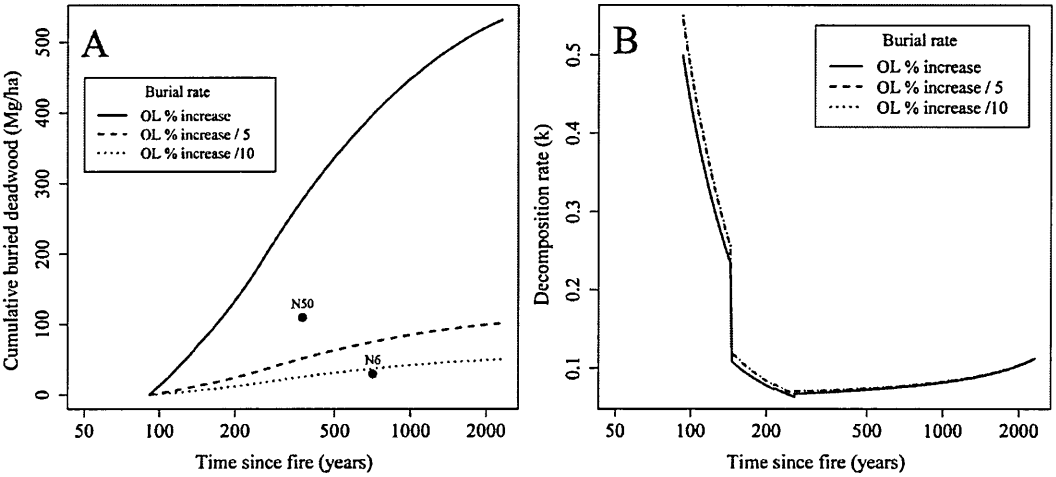

Figure 1.6 - A) cumulative buried deadwood using three rates of burial relative to organic layer (OL) growth rates (Points represent additional buried deadwood found in trenches dug in 2 of the older sites), B) Decomposition rate (k) from negative exponential models under three burial rates.

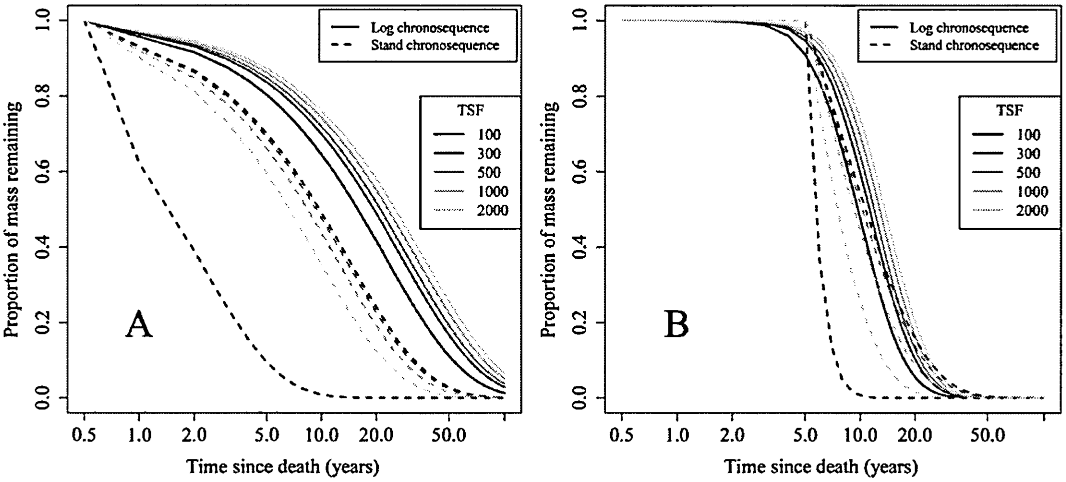

Figure 1.7 – Comparison of the log chronosequence and stand chronosequence approach for estimating decay rates using A) negative exponential models, and B) lag-time models. Both models use a burial rate proportional to a fifth of the organic matter growth rate.

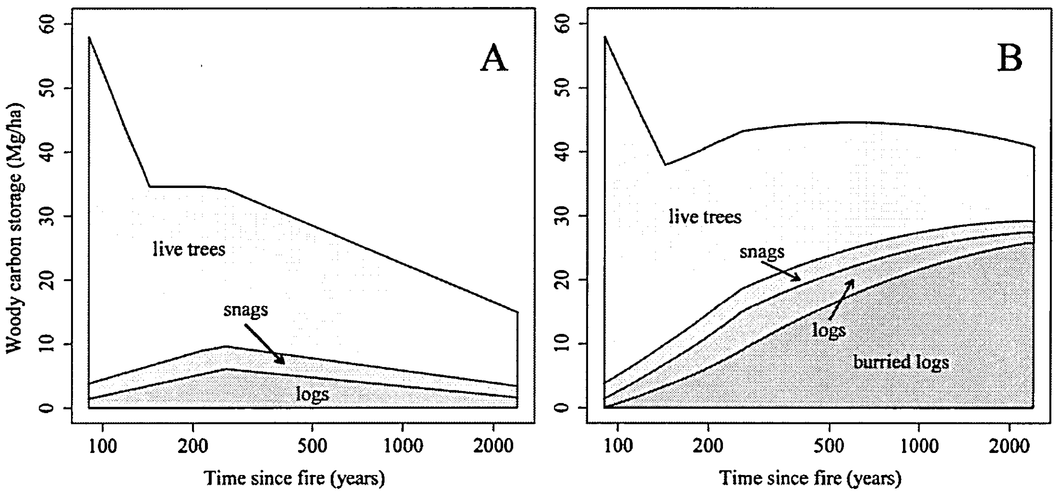

Figure 1.8 – Carbon storage of coarse woody biomass: A) showing the relative levels of woody carbon stored in live trees, snags and logs with diameters above 5cm, and B) the same figure with the inclusion of buried logs using the most conservative scenario of burial rate from figure 1.6A.

CHAPTER 2

LINKING DEADWOOD-ASSOCIATED BEETLES AND FUNGI WITH WOOD DECOMPOSITION RATES IN MANAGED BLACK SPRUCE FORESTS

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2.1 Résumé

Les champignons saprophytes et les insectes associés au bois mort sont les principaux agents de la décomposition du bois dans la forêt boréale. Les traitements sylvicoles qui modifient le microclimat et la disponibilité du bois mort pourraient avoir un impact sur la composition et le taux de croissance des communautés d'insectes et de champignons. Dans cet article, nous mettons en relation les assemblages d'insectes saproxyliques et de polypores dominants avec le taux de décomposition de la matière ligneuse et les variables environnementales dans des coupes expérimentales, partielles ou totales, et des témoins non coupés à l'aide d'une série de modèles causaux, dans le but de déterminer la relation qui existe entre la structure du peuplement, la biodiversité et le fonctionment de l'écosystème (processes de decomposition) dans les forêts d'épinette noire (*Picea mariana* (Mill.) BSP). Dans l'ensemble, la composition des insectes et des champignons était différente selon que les peuplements avaient été coupés ou non. Les principaux effets de la récolte incluaient de fortes augmentations des insectes qui se nourrissent du bois et du champignon *Gloeophyllum sepiarium* (Wul.:Fr.) Karst. Nous croyons que ces espèces étaient favorisées par des modifications spécifiques dans les conditions de microhabitat du bois mort. En particulier dans les coupes totales, les changements dans la composition en espèces et significativement plus de degrés-jours fongiques se traduisaient par des taux de décomposition significativement plus élevés. Nous concluons que les niveaux de coupe partielle dans la gamme de 15%– 20% de rétention n'étaient pas suffisants pour maintenir les communautés présentes avant la perturbation, mais qu'ils étaient suffisants pour maintenir des taux de décomposition du bois semblables à ceux des peuplements non coupés.

2.2 Abstract

Deadwood-associated insects and saprotrophic fungi are principal agents of wood decomposition in boreal forest. Silvicultural treatments that alter microclimate and availability of deadwood likely affect composition and growth rates of both insect and fungal communities, leading to changes in wood decomposition rates. Here we relate both saproxylic beetle and dominant polypore assemblages with woody decomposition rates and environmental variables in experimental partial cuts, clear cuts, and uncut controls using a series of causal models in order to determine the relationship between stand structure, biodiversity and ecosystem function in black spruce forests. Overall beetle and fungal composition differed between uncut stands and harvested stands. Main effects of harvesting included large increases in wood-feeding beetles and the fungi *Gloeophyllum sepiarium.* We suggest that these species were promoted by specific alterations in microhabitat conditions of deadwood. Within clearcuts specifically, changes in species composition and significantly more fungal degree-days resulted in significantly higher decomposition rates. We concluded that levels of partial cutting in the range of 15%-20% retention were not sufficient to maintain pre-disturbance communities, but were sufficient to maintain wood decomposition rates similar to uncut stands.

2.3 Introduction

Dramatic losses in biodiversity have spurred interest in how changes in species composition, specifically those provoked by anthropogenic disturbances, will affect ecosystem functions (Pimm et al. 1995, Loreau et al. 2001). Commercial forest harvesting can induce compositional changes in numerous taxa, including deadwood-associated beetles (Jacobs et al. 2007b, Cobb et al. 2011) and fungi (Penttilä et al. 2004), often resulting in species assemblages with no natural analogue. In areas that have experienced intensive forest management over multiple rotations such as Fennoscandia, the loss of deadwood-associated species is striking (Siitonen 2001). For example, 37% of all wood-inhabiting fungal species in Finland are classified as threatened or near threatened (Rassi et al. 2001) and 20% of species in Sweden are listed as threatened due to modern intensive forestry (Rydin et al. 1997). These losses have been attributed to decreases in both the volume and diversity of residual deadwood in managed forest landscapes (Siitonen 2001). Clearly the close ecological ties between residual deadwood and wood-associated species present conservation challenges within managed forests; however, perhaps more disconcerting are the potential consequences of the loss of wood-associated species on ecosystem functions such as wood decomposition.

Studies linking changes in ecological communities with corresponding changes in ecosystem functions are becoming increasingly common [see review by Hooper et al. (2005)]. Of the studies that have focused on decomposition as an ecosystem process, most have been dominated by comparisons of soil fauna and soil processes in microcosm type experiments (Meier and Bowman 2008). For example, Setälä and McLean (2004) examined diversity effects of saprophytic fungi on decomposition in microcosms and found that under low levels of diversity there was a positive relationship between diversity and decomposition of soil organic matter. The positive relationship between diversity and wood decomposition rates has been demonstrated in at least one field study in tropical forests of Puerto Rico (Torres and González 2005). In this study increased animal diversity, particularly termites, resulted in a 9.25 times increase in the ratio of soft to hardwood, and indicator of wood decay, in swamp cyrilla (*Cyrilla racemiflora* L.), in dry sites compared to wetter sites suggesting that the relationship between faunal diversity and wood decomposition is modified by environmental filters such as changes in microclimatic conditions, which could be particularly evident following disturbances like forest harvesting.

For any given tree species, physical factors determining the rate of deadwood decomposition include temperature, wood moisture, and diameter (Harmon et al. 1986, Boddy 2001). Temperature and wood moisture content generally have positive effects on decomposition rates. For example, Bond-Lamberty et al. (2002) reported that wood respiration rates of black spruce (*Picea mariana* (Mill.) BSP) logs increased with increasing wood moisture at levels below 43.1%, but that above that level, wood moisture was not significant and site type was the best predictor, with drier sites having higher decomposition rates. Larger pieces of deadwood have a higher surface to volume ratio leading to slower decay rates as the ratio of easily decomposable sapwood to recalcitrant heartwood ratio decreases (Harmon et al. 1986).

Factors such as temperature and humidity in deadwood likely serve as significant environmental filters that determine the composition and activity of the wood-associated organisms which in turn may affect decomposition rates (Harmon et al. 1986, Boddy 2001). Temperature and drying regime have both been identified as factors which control the development of wood decay fungi (Boddy 2001). At the community level, species that are growing in their optimal environment could have a competitive advantage over other species. For example, Wikars (2002) observed a decrease in the densities of all basidiomycete fruiting bodies in burned stands except for *Gloeophyllum sepiarium* (Wul.:Fr.) Karst, which thrives under low moisture and high temperature conditions. Furthermore the capacity to decay wood varies among fungal species (Henningsson 1965). For example, Blumenfeld (1984) found that single pine wood blocks varied in the amount of decay from less than 5% to almost complete decay depending on which fungal species were present.

Insects also respond to changes in temperature and wood moisture. Drier and warmer conditions tend to promote abundance and increase growth rates of wood-feeding species leading to higher decomposition rates (Progar et al. 2000, Müller et al. 2002, Jacobs et al. 2007b). For example, Barker (2008) observed that Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) logs sheltered from rain in temperate rainforests in the Pacific Northwest region of USA, reduced wood moisture from 45% to 36% and increased the volume affected by brown rot fungi and wood boring beetles, which resulted in a 20% increase in wood respiration rates. Similarly, Müller et al (2002) found that 20% of the variation of weight loss in Norway spruce was explained by subcortical feeding by insects.

The resulting interaction between such environmental filters and wood-associated species affecting wood decomposition rates has profound implications for forest management. Silvicultural approaches, such as clearcuts, that create drier, warmer microhabitats, have the potential to affect growth rates and composition of wood-associated species, leading to increased decomposition rates of deadwood. These silvicultural approaches also drastically reduces inputs of deadwood until stem exclusion, the point at which the initial cohort of trees following a disturbance begin to die due to high levels of competition (Siitonen 2001). Boreal forests can take 60-100 years to reach this stage, which in some cases coincides with a harvesting rotation (Harper et al. 2005). The combined net effect of accelerated losses and reduced inputs of deadwood is a prolonged gap in deadwood over the course of a rotation.

Alternatively, silvicultural approaches that maintain wood-associated species and environmental conditions consistent with uncut forests may serve to maintain lower decomposition rates and insure the perenniality of ecological legacies such as deadwood. Partial cutting has been widely advocated as a means of coarse filter conservation to maintain both species assemblages and environmental conditions consistent with uncut forests if retention levels of standing green trees are sufficient (Hunter 1990). Partial cutting with high levels of retention (>50%) seem to maintain assemblages of particular leaf litter invertebrates, whereas lower retention levels (<20%) do not (Work et al. 2010). Jacobs et al. (2007b) found that immediately following partial cutting, wood- and bark- feeding insects increased in diversity and abundance with increasing harvesting. These authors further observed some of the largest community-level impacts were limited to specific feeding guilds such as fungivorous and predatory beetles, with several species being restricted to the uncut controls and/or high retention treatments (>50%). In some cases, such as European temperate oak-dominated forests, even high levels of retention of partial cutting (70%-75% retention) reduced species richness of wood-associated basidiomycetes (Nordén et al. 2008). However, the real benefits of partial harvesting on wood-associated communities may be realized over longer time-scales; as retention trees die, they will facilitate a more continuous supply of deadwood into the regenerating stand.

In this study, we examined the how changes in stand structure (*i.e.* basal area, canopy cover and volume of downed deadwood) resulting from clearcut and partial cut harvesting (15% - 20% tree retention) affect climatic variables (*i.e.* temperature and humidity), wood-associated beetle and fungal communities, and ultimately wood decomposition rates. We then tested 5 causal models meant to elaborate the relationships and relative importance of stand structure and the separate biodiversity components of deadwood-associated insects and fungi on decomposition rates of downed deadwood. Our specific objectives were to: 1) determine whether deadwood-associated beetle and fungal communities are linked to changes in stand structure; 2) determine whether decomposition rate related to changes in stand structure and 3) what are the relationships between these ecosystem components. We hypothesized that increased harvest intensity would result in increases in temperature and compositional changes in both wood-associated insect and fungal assemblages. Together these changes would lead to increased growth-rates, provoking higher wood decomposition rates.

2.4 Methods

2.4.1 Study sites

We compared stand structure, beetle and fungal assemblages associated with deadwood, and decomposition rates from experimentally replicated clearcuts, partial cuts and uncut black spruce stands in northwestern Quebec. These stands were part of a larger network of sites dedicated to studying the long-term effects of partial cutting called the RECPA project (*le réseau d'expérimentation de coupes partielles e*n Abitibi). This experiment was located within the Clay belt region of northeastern Ontario and northwestern Quebec (Figure 2.1), a physiographic unit composed primarily of clay deposits left by pro-glacial lakes Barlow and Ojibway. Nearby weather stations (La Sarre, QC, 48° 46'N, 79° 13' W and Matagami, QC, 49° 46'N, 77° 49'W) reported an average precipitation of 889.8mm and 905mm respectively, 28% and 37% falling as snow. Average temperatures of the region ranged from 0.7°C (SD=2.2) in the south to -0.7°C (SD=2.7) in the north (Environment Canada 2011). Fire has been the main disturbance in this region and the fire cycle has lengthened from 101 years before 1810 to 398 years since 1920 (Bergeron et al. 2004a). Many stands in this region, especially those on clay soils, are prone to paludification, an excessive build-up of organic matter leading to the development of peatlands .

Detailed information related to the paludification process in this region has been reported elsewhere (Simard et al. 2007). We chose three sectors from the larger RECPA project (Puiseaux, Fénélon and Gaudet) for this study (Figure 2.1). Each of these sectors was located on clay soils, dominated by *Picea mariana* (Miller) Britton and originated following high intensity fires 180 to 280 years prior to harvesting. Stands were characterized as old-growth based on structural features described by (Harper et al. 2005). Each sector constituted one complete replicate of three silvicultural treatments: 1) clearcut; 2) partial cut, and 3) uncut control. Buffers were retained between cutting treatments, however the partial cut and control treatment in sector Gaudet were contiguous. Each treatment was at least 25 ha in size and retention levels within partial cuts ranged from 15% to 25% of pre-harvest basal area. All cutting treatments were applied during winter months of 2003 (Gaudet) and 2004 when the ground was frozen. Harvesting machinery was restricted to machine corridors in which the trees were delimbed on site, leaving branches and unmerchantable portions of the stem on the machine corridor to reduce the impact on the soil.

2.4.2 Stand structure, microclimate and wood decomposition

Stand structure was characterized one year after harvest based on standard inventory methodology prescribed by the provincial Ministry of Natural Resources (DIF-MRNF 2006)(H. Bescond unpublished data). In each stand, 13 to 18 permanent structural sampling plots were established within each experimental stand by randomly selected grid points from available stand maps (Figure 2.1). Diameter at breast height (DBH) and status (living or dead) of all stems greater than 5cm in diameter were measured within an 11.28m radius circle from the plot center. Canopy cover was also measured at the center of each plot using a spherical convex densiometer. We measured volume of downed deadwood at each plot using three

10m transects. Along these transects, we recorded diameter of fallen wood for each piece of deadwood greater than 5cm in diameter. We calculated stand level volumes for downed deadwood using the Van Wagner formula (Van Wagner 1968).

In two of the sectors (Puiseaux and Fénélon), three Maxim ibuttons ® (DS1923) data loggers were installed in each treatment to measure temperature and humidity (J. Arseneault unpublished data). Data loggers were suspended approximately 20cm above the forest floor using stiff metal wire to represent environmental conditions of a log and began recording at two-three hour intervals continuously between 11th of December 2009 and November 1st 2010.

We compared decay rates using negative exponential decay models (Harmon et al. 1986), based on wood densities from a sequence of logs from a nearby chronosequence and of logs created during the harvesting treatments. Because we were unable to find logs in the controls where both the time of death and mortality factors were known, we used a nearby chronosequence consisting of seven stands from ranging in age from 60 to 718 years since fire. In each stand we felled five trees, sampled five other trees that were felled four years before sampling by a study on arboreal lichens (Boudreault et al. 2009), and five more trees that were felled six to seven years before sampling for a dendrochronology study (Lecomte et al. 2006b). In the six harvested stands we chose 10 logs that were 1) > 5 cm in diameter, 2) >1m in length and had 3) evidence of cutting at both ends. We cut two cross-sections from each log, measured the diameter using a diameter tape and the maximum and minimum thickness of each cross-section with a digital caliper. We used these measures to calculate volume based on the assumption that cross-sections are solid cylinders. We then dried all cross sections at 65°C to constant mass and calculated wood density based as the dry mass of a cross-section divided by the volume. We averaged the density of the two cross sections for a single estimate of wood density for cut logs.

2.4.3 Sampling of wood-associated biodiversity

2.4.3.1 Polypore fungi

We characterized differences in the abundance of polypore fruiting bodies among all experimental stands the 14 to 18th of September, 2009. Polypore fungi are basidiomyctetes and are the dominant decomposer of dead trees in the boreal forest (Penttilä et al. 2004). We established two biodiversity sampling plots (Figure 2.1) in each stand and randomly chose one for surveys of polypore fungi. We counted and identified polypores on all surfaces of deadwood with a diameter greater than 5cm within an 11.28m radius circular plot ($400m^2$). Within the circular plot, we surveyed the first 100 pieces of deadwood encountered. When unable to find 100 pieces within the plot, we surveyed individual pieces of deadwood outside the plot until 100 total pieces had been inspected. For each piece of deadwood in the survey, we recorded the type of deadwood (1-snag; 2-leaning snag; 3-raised log; 4-log; 5-buried log; 6-natural stump, and 7-cut stump) and decay class based on penetrability of a field knife (1A-knife does not enter, phloem is wet; 1B-knife does not enter, phloem is dry; 2-knife penetrates the wood to a depth up to 0.5cm; 3-knife penetrates the wood less than 10cm or half the diameter of the piece; 4- knife fully penetrates the wood to the handle, piece still intact, and 5- knife fully penetrates the wood, piece breaks apart with minimal force).

2.4.3.2 Beetles

We sampled beetles in the center of both biodiversity plots (Figure 2.1) within each experimental stand using freestanding flight-intercept traps. These traps consisted of two perpendicular black plastic panels (30cm x 122cm) affixed to a 20 liter bucket with the same diameter as the width of the panels. We attached the lid of the bucket to the top of the panels to provide increased structural rigidity and redirect insects that may begin to fly up after contact with the panels. We stabilized each trap with two 122cm pieces of electrical conduit. We also added small drain holes covered by fine mesh on the sides of the buckets to prevent flooding and subsequent loss of specimens. We added approximately 1L of propylene-glycol to each trap and replaced the propylene-glycol when samples were obviously diluted.

We began collecting beetles between 5th to 9th of May, 2008 while snow was present within stands and the ground was frozen below 10 cm. We collected samples at three week intervals until 18th to 22nd of August 2008 resulting in approximately 100 collection days for each stand. Specimens were collected by straining samples through fine mesh cloth which were then placed into 75% EtOH. We then sorted and identified beetles to the finest taxonomic resolution possible using available keys and consultations with taxonomic experts and museum collections.

2.4.4 Data analysis

2.4.4.1 Stand structure, microclimate and wood decomposition rates

We compared structural measurements (vis. basal area, percent cover and volume of downed wood) and environmental measurements (vis. temperature, degree-days and humidity) between stand treatments using linear mixed-effects (LME) models. For all models, assumptions of constant variance and normality of within group errors were verified (Pinheiro and Bates 2000). In these models, we used sector as a random variable and treatment as a fixed effect. For all models we altered the contrast matrix of treatment to find significance of all pair-wise combinations. For basal area, we used the exponential of covariate class of variance function to specify the within-group variance model to improve homoscedasticity (Pinheiro and Bates

2000). Additional models for volume of downed wood were examined to determine if treatment was altering diameter class or decay class distributions. Degree-days, a measurement which relates temperature to the metabolic activity of organisms, were calculated based on reported temperature preferences of wood decay fungi. Degree-day variables corresponded to three ranges of temperatures (Randal 2000): 1) tolerable (-1.1 to 37.8°C); 2) favorable (10 to 32.2°C), and optimum (21.1 to 29.4°C) conditions for fungal growth. These ranges generally agree with finding on temperature effects of wood fungi; for example, Wells and Boddy (1995) found wood decay rates to peak at temperatures between 20 and 25°C, for 2 species of fungi. We also compared values for relative humidity which were both temperature corrected and corrected for saturation drift. We compared relative humidity among the three treatments at temperature ranges corresponding to tolerable, favorable, and optimal ranges of fungi using the same linear mixed-effects models. We used the lme function in the nlme library (Pinheiro et al. 2010) in R 2.12.1 (R Development Core Team 2010) for all LME models.

2.4.4.2 Estimating decay rates

We modeled wood density in unharvested stands using a generalized linear model (GLM) based on sequences of logs in a chronosequence of mature fire-origin stands. This model had a log link function (ie. logged the dependant variable) and explanatory variables included 1) time since death of the tree, 2) time since stand replacing fire, 3) log diameter and 4) interaction between time since death and log diameter. We interpreted the parameter estimate for time since death of the tree as the decay constant (k) for uncut controls.

We estimated decay rates in harvested stands based on changes in wood density using a series of GLMs. Because we were unable to cut trees to estimate initial densities in the harvested stands, we first needed to simulate the initial density of 10 logs in each experimental stand. To accomplish this, we first used a GLM that was based on the densities of freshly felled logs from the seven uncut stands and included time since fire and diameter as the explanatory variables. For each harvested stand we calculated the mean and standard error for the initial density of logs and then simulated the wood density of 10 freshly fallen logs based on a normal distribution. We then used a second GLM to model wood densities across harvested stands based on the simulated initial wood densities and measured wood densities. This model had a log link function and explanatory variables included 1) time since death of the tree, 2) log diameter, 3) harvesting treatment, 4) sector, 5) interaction between time since death and diameter, 6) interaction between time since death and harvesting treatment, 7) interaction between harvesting treatment and sector and 8) interaction between time since death, harvesting treatment and sector. We interpreted parameter estimates for time since death combined with the relevant interactions with harvesting treatment and sector as the decay constant (k) for each stand.

2.4.4.3 Responses of polypore assemblages to harvesting

We focused our analysis of fungal composition on six dominant species which were reliably identifiable and sufficiently abundant for statistical analysis (*vis. Gloeophyllum sepiarium*, *Fomitopsis pinicola* (Sw.:Fr.) P. Karst., *Fomitopsis cajanderi* (Karst.) Kotl. & Pouz., *Trichaptum abietinum* (Dicks.: Fr.) Ryv., *Trichaptum fuscoviolaceum* (Ehrenb.) Ryv., and *Trichaptum laricinum* (Karst.) Ryv.). By using only six species and not the entire wood-associated fungal community we are likely under representing the total diversity. We used non-metric multidimensional scaling (NMS) ordination with the Bray-Curtis distance measure to compare fungal composition between treatments. For this analysis, we analyzed the relative frequency of a given species of polypore found on the 100 pieces of deadwood sampled in each stand. We then standardized each stand to have the same total. We used the metaMDS function, without the autotransform argument from the vegan library (Oksanen et al. 2008). We quantitatively compared differences in community composition using a permutational multivariate analysis of variance (PERMANOVA) type analysis (Anderson 2001). For this analysis, we used the Adonis function in the vegan library.

We analyzed the probability of presence of fruiting bodies for each species on a given log using generalized linear mixed models with a binomial distribution using the glmmPQL function in the MASS library (Venables and Ripley 2002). Treatment, deadwood quality and decay class were used as independent variables where the random variables were treatment nested in sector.

2.4.4.4 Responses of beetle assemblages to harvesting

We classified all beetle taxa as wood-associated based on available literature (Jacobs et al. 2007a, Dollin et al. 2008). We then classified all beetle taxa into one of four feeding guilds 1) fungivores; 2) wood-feeding (*i.e.* xylophagous and phloeophagous); 3) predators, and 4) other. We analyzed all taxa together and the three dominant feeding guilds: 1) fungivores; 2) wood-feeding, or 3) predators, separately. We calculated catch rates of each species per stand by taking the total abundance of the two traps in the stand and dividing by the total number of days those two traps were operational over the course of the summer. We compared compositional differences of beetle assemblages among harvesting treatments in the same manner as for polypore fungi using (NMS) ordination and PERMANOVA. We also used individual based rarefactions (Simberloff 1972) on raw abundances to estimate changes in species accumulation among all taxa and the three dominant feeding guilds. We created rarefaction curves with the rarefy function from the vegan library (Oksanen et al. 2008) in R. We used LME models with sector as the random variable to analyze differences in beetle abundance for all taxa and the three dominant feeding guilds.

2.4.4.5 Relating stand structure, biodiversity and wood decomposition

We used d-sep tests to evaluate causal acyclic models specifying potential relationships between elements of stand structure (i.e. basal area and percent cover), biodiversity and decay rate (Shipley 2002). We specified d-separation statements for a basis set of each model and converted these statements to conditional probabilities using partial mantel tests. We used partial mantel tests to generate conditional probabilities as two of our variables, beetle and fungal composition, were already multivariate variables and could not be readily compared using partial correlations as is often done in other studies suggesting causal mechanisms related to deadwood decomposition (Brais et al. 2005). We standardized beetle and fungal assemblage matrices by row totals and physical variables (i.e. percent cover and basal area) and decomposition rate were standardized by column total prior to the calculation of distances. Physical variables and decomposition rates were expressed as Euclidean distance matrices, whereas beetle and fungal assemblages were expressed as Bray-Curtis distance matrices. Once the list of d-separation statements have been specified for a given model, we used Fischer's C test to assess whether the specified causal structure must be rejected based on the composite probability of the entire basis set for each model (Shipley 2002).

From the possible set of candidate models we chose five specific models. Each of these models assumes that stand structure will have direct effects on biodiversity and possible direct and indirect effect on decomposition rates. We then separated the beetle communities into trophic groups to examine relationships between individual trophic groups and other elements in the model. We explored many other configurations of the models and present here five, strong, plausible models with increasing in complexity. Our first model is a sequential causal model that presumes a relationship between stand structure and beetles, as well as a facilitative role of beetles on fungi which then determines decay rates. Our second model removes the direct facilitative role of beetles on fungi and presumes that both fungal and beetle communities are important to decay rates. Our third model adds a direct relationship between stand structure and decay rates to our second model. Our fourth model separates and refines our hypothesis on insect biodiversity, and specifies that wood-feeding beetles, specifically, determine decomposition rates whereas fungivores respond to fungal communities. Our fifth model adds insect predator assemblages as a model variable which responds to both wood-feeding and fungivorous composition.

2.5 Results

2.5.1 Harvesting effects on stand structure, microclimate and woody decomposition rates

Basal area was reduced from 15±5.8 m^2/ha in uncut stands to 3.5±3.1 m^2/ha and 0.8±1.8 m^2/ha in partial cut and clear cut stands (LME, $F_{[2,4]}$=79.84, P<0.001, Table 2.1). We observed little variability in basal area between sectors as indicated by the relatively small size of the random effect within the model (σ^2<0.01). Percent cover was significantly lower in partial cuts (23.7%±5.8) and clearcuts (12.5% ±9.0) than in uncut stands (69.3% ± 3.1) (LME, $F_{[2,4]}$=65.50, p<0.001, Table 2.1). In contrast to basal area, differences in percent cover between partial cuts and clearcuts were not significant (Table 2.1) and variability among experimental sectors was greater (σ^2=0.41). Volume of downed wood was not different among harvested and unharvested stands (LME, $F_{[2,4]}$=2.52, p=0.20) (Table 2.1) but variability among experimental sectors was greater (σ^2=0.63) than percent cover or basal area. We observed no difference among treatments when we analyzed volumes of downed wood separately as diameter classes or as decay classes ($p>0.05$).

In the fungal sampling plots, logs were the most common type of deadwood observed (44% ± 7.0) followed by cut stumps (25% ± 20) snags (10% ± 10), buried logs (9% ± 4.1), elevated logs (8% ± 0.73) and leaning snags (4% ± 5.1, Figure 2.2a). There were more standing snags, leaning snags, elevated logs and natural stumps in the uncut controls than the harvested treatments (Figure 2.2a). There was a higher proportion of logs in early decay class 1B in the partial cuts (0.52 ± 0.11) and clearcuts (0.48 ± 0.17) compared to the uncut controls (0.28 ± 0.10) (Figure 2.2b). The pattern was reversed in the next stage of decay (DC2) with a higher proportion in the uncut control (0.48 ± 0.080) than the partial cuts (0.32 ± 0.037) or clearcuts (0.32 ± 0.078) (Figure 2.2b).

Mean temperatures in the sectors Fénélon and Puiseaux were 5.5°C and 5.3°C respectively, and did not differ among treatments (LME, $F_{[2,2]}$=6.14, p=0.140, Table 2.2). However, the number of degree-days within the tolerable range for fungi significantly differed among harvesting treatment (LME, $F_{[2,2]}$=44.76, p=0.02) and were nearly significant for both the favorable range (LME, $F_{[2,2]}$=17.21, p=0.055) and optimum range (LME, $F_{[2,2]}$=16.69, p=0.057, Table 2.2). Clearcuts accumulated significantly more degree-days within the tolerable range than did partial cuts, or uncut controls (Table 2.2). This pattern was similar for the favorable and optimal range, but there was only near significant differences between the partial cuts and clearcuts (Table 2.2). Mean relative humidity was 89% and 88% in Fénélon and Puiseaux respectively, and did not significantly differ among treatments (LME, $F_{[2,2]}$=6.24, P=0.138, Table 2.2). Clearcutting significantly reduced relative humidity compared to partial cutting or uncut stands in the favorable range of temperatures for fungal growth (LME, $F_{[2,2]}$=23.34, p=0.041, Table 2.2). These differences were near significant within the tolerable range of temperatures (LME, $F_{[2,2]}=16.66$, p=0.056) and not significantly different in the range of optimal temperatures for fungal growth (LME, $F_{[2,2]}=10.70$, p=0.090).

Wood density in the uncut stands increased with time since fire and decreased with time since death (Table 2.3). Interaction between time since death and log diameter was also significant indicating that larger logs take longer to decay than smaller logs. The k constant in the uncut stands was -0.040 with a 95% confidence interval of -0.036 to -0.044. Modeling wood densities in harvested stands resulted in a mean k constant of -0.038 in the partial cuts and -0.075 for the clear cuts, representing and almost doubling of the rate of wood decay (Table 2.4, Fig 2.3). In both models we also observed a significant interaction between time since death and log diameter (Tables 2.3 and 2.4). This equated to 0.002 and 0.013 increase in the k constant with every centimeter increase in log diameter (range: 6.4cm-31.6 cm) in the unharvested and harvested stands respectively. Conversely smaller logs decayed faster especially in the harvested stands.

2.5.2 Harvesting effects on wood-associated biodiversity

2.5.2.1 Polypore fungi

We observed large differences in composition of the six dominant species of polypore fungi between the uncut controls and the partial cut and clearcut stands (Fig. 2.4a, PERMANOVA, $F_{[2,6]}=9.76$, $r^2=0.76$, p=0.016). When fungal species were analyzed separately, *G. sepiarium* was the only species that was observed more frequently on deadwood following partial cuts and clearcuts (GLMM, $F_{[2,4]}=8.98$, p=0.033, Table 2.5). *Trichaptum abietinum* was observed less frequently on deadwood following partial cuts and clearcuts (GLMM, $F_{[2,4]}=21.41$, p=0.007, Table 2.5). The frequencies of *Fomitopsis pinicola* (GLMM, $F_{[2,4]}$ =6.10, p=0.061, Table 2.5) and *F. cajanderi* (GLMM, $F_{[2,4]}$ =5.90, p=0.064, Table 2.5) were not significantly effected by harvesting treatment but tended to be less frequent in partial cut stands, but not in clearcuts.

2.5.2.2 Beetles

Overall we collected 295 species from 6865 individuals in 2305 trap days. Two hundred sixty-eight of these species, represented by 5625 individuals, were reported to be associated with deadwood. We found little difference in the abundance of beetles between harvesting treatments (GLMM, $F_{[2,4]}$=0.789, p=0.514). We observed clear differences in the overall composition of beetle assemblages between uncut and harvested stands in the NMS ordination (Fig 2.4b, PERMANOVA, $F_{[2,6]}$=2.66, r^2=0.53, p=0.003). When we compared composition of feeding guilds separately among harvesting treatments, assemblages of wood-feeding and predatory species differed among harvest treatments (wood-feeding PERMANOVA, $F_{[2,6]}$=1.67, r^2=0.36, p=0.035; predators PERMANOVA, $F_{[2,6]}$=1.63, r^2=0.35, p=0.027), but the effects of harvesting were limited on assemblages of fungivores (PERMANOVA, $F_{[2,6]}$=1.36, r^2=0.31, p=0.112).

We observed little difference in the overall rate of species accumulation per individual sampled among any of the treatments using rarefaction (Figure 2.5a). When overall beetle assemblages were compared separately as feeding guild, we found that fungivorous species accumulated much faster in the clearcuts (Figure 2.5b), however this did not result in significant differences in total abundance (LME, $F_{[2,4]}$=1.95, p=0.256). For wood-feeding beetles, species accumulated at similar rates in all treatments (Figure 2.5c). However, abundance of wood-feeding beetles was lower in the uncut stands than either clearcuts (LME, t_4=2.89, p=0.045) or partial cuts (LME, t_4=3.07, p=0.037). We observed a similar pattern in the accumulation of predatory species (Figure 2.5d). Abundance of predators was less in uncut stands than clearcuts (LME, t_4=3.69, p=0.021) or partial cuts (LME, t_4=2.94, p=0.042).

2.5.3 Relating stand structure, biodiversity and wood decomposition

When comparing the five proposed causal models with d-sep tests, we were only able to reject the first model based on the Fischer's C (p= 0.028) (Figure 2.6a). Once the facilitative relationship was removed from between beetles and fungi, the remaining causal models could no longer be rejected under Fisher's C.

Model 2 could not be statistically rejected, but the exact p-value of the test was relatively low (Fischer`s C, p=0.308). This model has relatively high significant partial correlation values between stand structure and the two components of the wood associated assemblages (mantel r=0.77, p=0.013 and r=0.74, p=0.008 for fungi and beetles respectively) and smaller, non-significant, partial correlations, between biodiversity and decomposition (mantel r=0.22, p=0.128 and r=-0.25, p=0.178 for fungi and beetles respectively, Figure 2.6b). This model was consistent with a hypothesis where stand structure would have no direct influence on decomposition rates and all changes in decomposition rate where mediated exclusively by changes in composition of the wood-associated assemblages. Once stand structure was allowed to have direct effects on decomposition rates in Model 3, the exact p-value of the model increased (Fischer`s C, p=0.578) while the partial correlation between fungi and decomposition greatly decreased and remained non-significant (mantel r=0.06, p=0.71) (Figure 2.6c). The negative partial correlations between beetles and decomposition increased albeit slightly (mantel r=-0.31, p=0.096).

In models 4 and 5, the larger assemblage of beetles was expressed as individual feeding guilds (Figure 2.6d-e). The exact p-values for d-sep tests for Model 4 and 5 were p=0.954 and p=0.501 respectively. In these models, the initial relationship between stand structure and beetles was modified to include only the wood-feeding guild. The partial correlation between stand structure and wood-feeding beetles was greater than when all beetles were combined (r=0.86, p=0.005), and the partial correlation coefficient was also higher, and near significant, between wood-feeding beetles and decomposition rates (r=-37, p=0.059). Despite an overall relation with the wood-feeding assemblage, only a single tree feeding beetle had a significant individual partial correlations with changes in decomposition rates in this model (vis. *Ampedus pullus* Germar, r=0.31, p=0.046). The partial correlation coefficient of stand structure to decomposition rates also increased and was near significant when the beetle assemblage was limited to just wood-feeding beetles (r=0.30, p=0.052). Fungivorous insects were included as a separate variable that had a near significant partial correlation to changes in fungal composition (r=0.33, p=0.051). When further examined separately, five fungivores had significant correlations to changes in fungal assemblages (*vis. Corticaria* sp1, *Cryptophagus* spp., *Atheta remulsa* Casey, *Cortinicara gibbosa* (Herbst), *Neothetalia canadiana* Klimaszewski). Model 5 included additional responses of predators to both fungivorous and wood-feeding beetles, however only wood-feeding beetles had a significant and strong partial correlation coefficient with predatory beetles (r=0.86, p=0.003, Figure 2.6e). There were eight predatory beetles with significant partial correlations with changes in the wood-feeding beetle composition (vis. *Pseudanostirus triundulatus* (Randall), *Rhizophagus brunneus* Horn, *Tachinus basalis* Erichson, *Acidota crenata* (Fabricius), *Olisthaerus substriatus* (Gyllenhal), *Quedius criddlei* (Casey), *Quedius plagiatus* Mannerheim, *Zenodosus sanguineus* (Say)). There were no predatory beetles with significant partial correlations with composition of fungivores.

2.6 Discussion

Changes in stand structure resulting from both clearcut and partial cut harvesting have the potential to serve as an environmental filter which determines composition of species assemblages (Jacobs et al. 2007b, Cobb et al. 2011) and modulates activity and growth-rates of those resident assemblages (Barker 2008). In our study, reductions of standing basal area and loss of forest cover were determinant factors in the composition of both wood-feeding beetles and dominant polypore species. Surprisingly, the subsequent changes in wood-feeding beetle composition caused by harvesting had much stronger effects on decomposition rates than the composition of dominant polypore species five to six years after harvesting. Furthermore, after clearcutting, we observed that shifts in stand structure resulted in an increase in degree-days and decrease in relative humidity, both of which has been demonstrated to increase the activity and growth rate of both wood-feeding beetles and wood-decay fungi (Barker 2008). We suggest that the combined effects of changes in species compositions and increased activity and growth rates resulted in higher wood decomposition rates in the clearcuts.

We were also able to reject a causal model whereby polypore composition was facilitated secondarily by beetle composition. This supports the idea that fungal species are primarily wind dispersed and/or omnipresent and further underscores the importance of wood-feeding insect composition as a primary factor determining rates of decomposition. This does not however discount the importance of fungi in the overall process of decomposition; rather it suggests that under field conditions, overall composition of fungal assemblages may be relatively unimportant for determining decomposition rates. One interpretation of this finding is that the dominant polypores in these forests may be largely interchangeable in terms of their net effect on decomposition rates at least initially. It is important to stress that we characterized the relative frequency of six dominant species based on externally visible fruiting structures, a fraction of the total fungal diversity likely present. We have also shown that in our study harvesting significantly increased the presence of *G. sepiarium*, a brown-rot fungi, decreased *T. abietinum*, a white-rot fungi, on deadwood. Clearly long-term compositional changes in the proportion of brown-rot and white-rot fungi may have impacts on decomposition rates however at least initially, changes in fungal composition has not translated to significant effects on decomposition rates.

It is likely that the importance deadwood volume for wood-feeding beetles and polypore fungi will change with time following harvesting. For example in studies from Fennoscandia, where cumulative effects of forest harvesting have occurred, managed stands typically have fewer species with a conspicuous loss of red-listed and threatened species. These losses have been largely attributed to a lack of deadwood volume and diversity (Penttilä et al. 2004, Nordén et al. 2008). Interestingly, we did not observe significant changes in overall volumes of downed dewadwood caused by harvesting nor changes in the distribution of volumes across diameter classes or decay classes among treatments apart from a decrease in snags and increase in cut stumps and early decay class deadwood following harvesting. This suggests that composition of wood-feeding beetles in these forests are extremely sensitive to relatively small changes in the deadwood profile or they are responding more to physical changes such as increased temperature or decreased moisture resulting from harvesting than to availability of host material. The relationship between physical changes in stands following harvesting and beetle composition has been suggested elsewhere. For example, Jacobs et al. (2007b) also found significant effects of harvesting intensity on the composition of wood-feeding beetles the second summer following harvest. However, over time as deadwood in harvested stands decomposes and is not replaced, we expect to have observable differences in deadwood volume and perhaps increased differences in composition and diversity of both beetles and fungi.

In addition to its role as an environmental filter for species composition, stand structure had significant effects on decomposition rates as described by the direct link within the causal models. We interpret this effect as a stimulative effect of increased temperature and decreased wood moisture on activity and growth rates of the overall decomposer community. For example, we observed an increase in the number of degree-days based on the tolerable range of fungal activity within clearcuts but not in partial cuts. In our study, *G. sepiarium*, which increased in harvested stands, has been shown to have high optimal growth rates between 25°C and 35°C (Bjurman and Wadsö 2000) and is common in sun-exposed dry wood (Kotiranta and Niemelä 1981), burned sites (Wikars 2002). Jonsell and Weslien (2003) demonstrated that this species was often associated with drier logs that also harbored high abundances of wood-feeding beetles. Beetle boring activity increases with temperature (Rudinsky and Vite 1956) and has been reported to increase following harvesting, as wood moisture decreases resulting in increased decomposition rates (Müller et al. 2002, Jacobs et al. 2007b, Barker 2008). In some cases feeding activity by wood-feeding beetles can accounts for 20% and 30% increase in decomposition rate (Edmonds and Eglitis 1989, Müller et al. 2002). Our results also correspond to the study of Bond-Lamberty et al. (2002), that found in wood moisture contents above 43.1% drier sites had higher respiration rates. In our study we did not measure wood moisture directly, but lower relative humidity during the growing temperatures of wood-decay fungi and lower percent canopy cover commonly lead to drier sites, which may have higher decomposition rates.

Changes in stand structure extended beyond primary consumers of deadwood to affect secondary consumers, such as fungivores, albeit indirectly through changes in fungal composition. We observed this pattern despite the fact that we used passive sampling, as opposed to collection methods that target specific fungal species.

Limiting our definition of fungivore to just those that fed on polypores could strengthen this relationship between polypores on fungivores. The link between wood-decay fungi and fungivorous beetle communities has been established in Scandanavian boreal forests (Jonsell and Nordlander 1995). For example, Kaila et al. (1994) found distinct beetle assemblages associated with 3 different species when directly sampling polypores. When paired with the known direct effects of stand structure on fungal composition, it is very compelling to presume a cascading effect of stand structure through larger food webs. Our study corroborates this pattern in a North American boreal system.

We observed a similar indirect effect of stand structure on predatory arthropod composition mediated predominately by the composition of wood-feeding insects in our final causal model. While this model was marginally less-well supported than the model that excluded predators, we found the asymmetric response of predators to the composition of wood-feeding beetles rather than fungivores intriguing. One hypothesis for this asymmetry is that the predator assemblage consists of a mix of species that are specialist predators of wood-feeding insects (*e.g. Rhizophagus* spp. and *Thanasimus* spp.) and more generalist subcortical predators that feed on both wood-feeding and fungivorous insects (eg. *Quedius* spp.). Currently, we cannot readily verify fully this hypothesis as detailed prey preferences for many predators of North American species are unavailable. However within the larger guild of predators, we observed two species, *Rhizophagus brunneus* and *Pseudanostirus triundulatus* which were strongly associated with composition of wood-feeding beetles (Mantel's r=0.60 and r=0.77 respectively). Both the larvae and adults of *Rhizophagus brunneus* have been reported to feed on bark beetle larvae (Curculionidae, Scolytinae). In a partial cutting study in Alberta, Canada, this species was found in lower numbers following harvest than in control stands (unpublished data from Jacobs et al 2007b), further indicating that this species may be responding to changes in prey composition than habitat changes. *Pseudanostirus triundulatus* is reported to increase rapidly in response to openings created by fire (Cobb et al. 2011) or harvesting (Thomas 2007), however little evidence for prey associations other sawfly larvae have been reported (Tostowaryk 1972). It is possible, based on our analysis that this species may also feed on specific wood-feeding species. Clearly, the causal models we have proposed would benefit from further study and increased statistical power however data relating diverse groups such as insects and fungi to ecological processes are difficult to generate and require multiple areas of expertise.

2.7 Conclusions

We have demonstrated how changes in stand structure act as an environmental filter determining composition of both wood-feeding beetles and wood-associated polypore fungi as well as changes in stand structure contribute to increased activity of decomposer organisms. We have also shown how reductions in basal area caused by harvesting, through their impacts on the composition of the biota, increases decomposition rates of deadwood and how changes in stand structure extend beyond the primary consumers of deadwood into secondary and tertiary consumers such as fungivorous and predatory beetles. Our results suggest that partial cutting with 15%-20% retention may offer at least some benefit for maintaining decomposition rates similar to uncut stands, whereas clearcutting provoked changes in both the composition of biota and increased decomposition rates. This could result in a more rapid depletion of deadwood in managed landscapes. Partial cutting has the added benefit that, as the retained trees die, they will create a continual input of deadwood into the stands, maintaining at least a reduced volume of deadwood in each stage of decay until the stand starts producing deadwood during stem exclusion. The success of partial cutting will ultimately depend on sufficient levels of retention following harvest.

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2.10 Tables

Table 2.1 – Linear mixed effects models on structural differences among harvested blocks [3 levels (UC- uncut control, PC- partial cut, CC- clearcut), 3 replicates].

Variable	Estimate	S.E.	d.f.	t-value	p
Basal Area					
Intercept	15.37	1.40	4	10.97	**<0.001**
UC-PC	-11.88	1.36	4	-8.74	**<0.001**
UC-CC	-14.56	1.34	4	-10.84	**<0.001**
PC-CC*	-	-	4	-7.45	**0.002**
Percent cover					
Intercept	69.34	3.72	4	18.64	**<0.001**
UC-PC	-45.63	5.26	4	-8.67	**<0.001**
UC-CC	-56.85	5.26	4	-10.80	**<0.001**
PC-CC*	-	-	4	-2.13	0.100
Downed deadwood volume					
Intercept	21.02	4.90	4	4.29	**0.013**
UC-PC	14.59	6.93	4	2.10	0.103
UC-CC	11.99	6.93	4	1.73	0.159
PC-CC*	-	-	4	-0.38	0.726

Table 2.2 – Linear mixed effects models on climatic differences among harvested blocks [3 levels (UC- uncut control, PC- partial cut, CC- clearcut), 2 replicates].

Variable	Estimate	SE	d.f.	t-value	p
Mean temperature					
Intercept	4.93	0.30	2	16.52	**0.004**
UC-PC	0.08	0.42	2	0.19	0.866
UC-CC	1.31	0.42	2	3.13	0.089
PC-CC*	-	-	2	2.93	0.099
Degree-days (tolerable)					
Intercept	2427.87	64.26	2	37.78	**<0.001**
UC-PC	75.79	25.03	2	3.03	0.093
UC-CC	232.19	25.03	2	9.28	**0.011**
PC-CC*	-	-	2	6.25	**0.025**
Degree-days (favorable)					
Intercept	1754.61	70.34	2	24.95	**0.002**
UC-PC	45.11	24.37	2	1.85	0.205
UC-CC	140.03	24.37	2	5.75	**0.029**
PC-CC†	-	-	2	3.90	0.060
Degree-days (optimal)					
Intercept	573.37	40.31	2	14.22	**0.005**
UC-PC	38.88	23.05	2	1.69	0.234
UC-CC	129.73	23.05	2	5.63	0.030
PC-CC*	-	-	2	3.94	0.059
Mean relative humidity					
Intercept	91.07	1.22	2	74.63	**<0.001**
UC-PC	-1.72	1.38	2	-3.56	0.338
UC-CC	-4.90	1.38	2	-1.25	0.071
PC-CC*	-	-	2	2.47	0.132
Relative humidity (tolerable temperature range)					
Intercept	85.89	1.82	2	47.14	**<0.001**
UC-PC	-3.38	1.53	2	-2.21	0.157
UC-CC	-7.30	1.53	2	-4.78	**0.041**
PC-CC†	-	-	2	2.56	0.124
Relative humidity (favorable temperature range)					
Intercept	76.92	1.47	2	52.27	**<0.001**
UC-PC	-3.07	1.27	2	-2.42	0.136
UC-CC	-8.53	1.27	2	-6.74	**0.021**
PC-CC†	-	-	2	-4.32	0.050
Relative humidity (optimal temperature range)					
Intercept	60.57	1.78	2	34.02	**<0.001**
UC-PC	-3.24	1.90	2	-1.71	0.230
UC-CC	-7.64	1.90	2	-4.03	0.057
PC-CC†	-	-	2	-2.82	0.106

Table 2.3 – Generalized linear model of log transformed wood densities of logs in across a chronosequence of mature fire-origin black spruce stands (TSD – time since death of tree, TSF – time since stand replacing fire).

Coefficients	Estimate	S.E.	t-value	p
Intercept	-0.930	0.0118	-79.077	**<0.001**
TSD (centered)	-0.0403	0.00392	-10.27	**<0.001**
TSF (centered)	0.000246	4.98×10^{-05}	4.939	**<0.001**
Diameter (centered)	-0.00499	0.00262	-1.904	0.0598
TSD x Diameter	0.00214	8.51×10^{-04}	2.511	**0.0137**

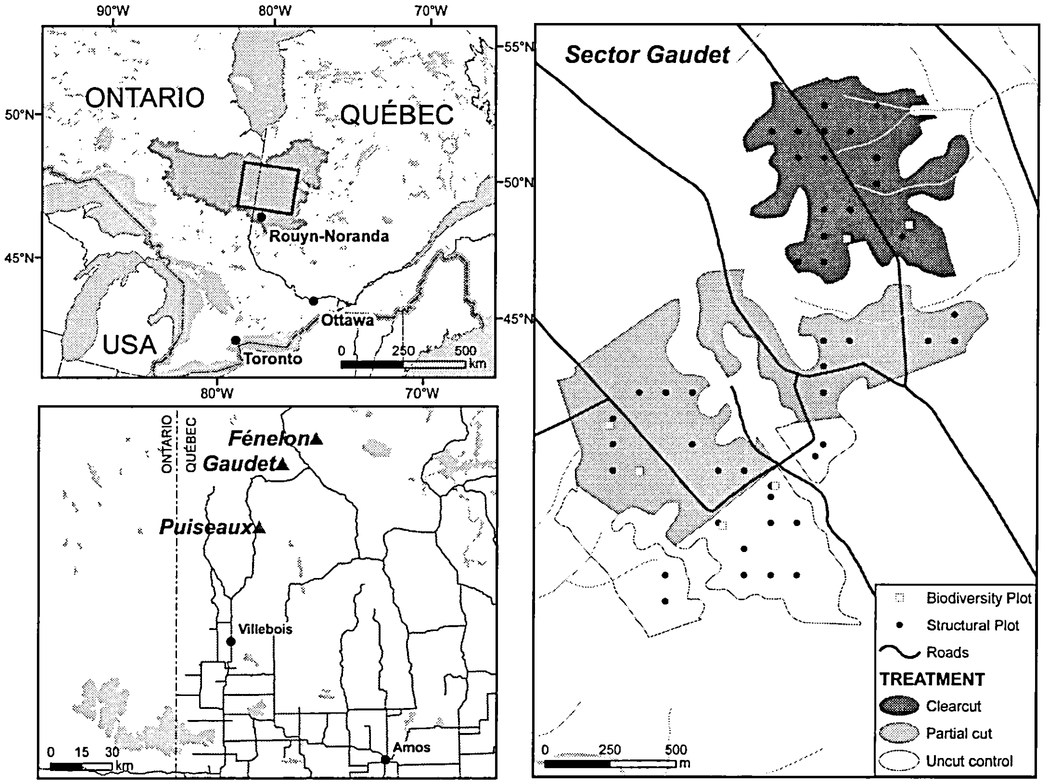
Table 2.4 – Generalized linear model of log transformed wood densities of logs in harvesting treatments. Reference condition is sector Fénélon and treatment partial cut (TSD – Time since death of tree).

Coefficients	Estimate	S.E.	t-value	p
Intercept	-0.826	0.0543	-15.212	**<0.001**
TSD (centered)	-0.0376	0.0116	-3.255	**0.0012**
Diameter (centered)	-0.067	0.0265	-2.526	**0.0119**
Clearcut (CC)	-0.0044	0.0542	-0.081	0.9351
Sector (Gaudet)	0.0019	0.0666	0.029	0.9769
Sector (Puiseaux)	0.0066	0.0664	0.1	0.9206
TSD x Diameter	0.0134	0.0051	2.615	**0.0093**
TSD x CC	-0.0374	0.0129	-2.898	**0.0040**
TSD x Gaudet	-0.0115	0.014	-0.824	0.4105
TSD x Puiseaux	0.0045	0.0144	0.311	0.756
TSD x CC x Gaudet	0.0446	0.0103	4.337	**<0.001**
TSD x CC x Puiseaux	0.0217	0.0093	2.337	**0.0200**

Table 2.5 – Generalized linear mixed models using a binomial distribution on the occurrence of fungal species with significant effects of treatment. Decay stage and type of deadwood (not shown) were also included in the model and held constant as decay class 2 logs for the presentation of the table.

Species	Variable	Estimate	S.E.	d.f.	t-value	P
Gloeophyllum sepiarium						
	Intercept	-1.37	0.29	845	-4.67	**<0.001**
	UC-PC	1.17	0.37	4	3.16	**0.034**
	UC-CC	1.26	0.37	4	3.43	**0.027**
	PC-CC*	-	-	4	-0.28	0.790
Trichaptum abietinum						
	Intercept	-0.94	0.21	845	4.56	**<0.001**
	UC-PC	-0.92	0.26	4	-3.61	**0.023**
	UC-CC	-1.36	0.28	4	4.90	**0.008**
	PC-CC*			4	1.60	0.183
Fomitopsis pinicola						
	Intercept	-2.38	0.53	845	-4.54	**<0.001**
	UC-PC	-1.56	0.55	4	-2.81	**0.049**
	UC-CC	-1.30	0.54	4	-2.40	0.075
	PC-CC*	-		4	-0.46	0.667
Fomitopsis cajanderi						
	Intercept	-1.66	0.25	845	-6.54	**<0.001**
	UC-PC	-1.22	0.37	4	-3.29	**0.030**
	UC-CC	-0.24	0.30	4	-0.82	0.458
	PC-CC*	-	-	4	-2.73	0.052

2.11 Figures



Projection: NAD 1983 MTM 10 | Author: CEF, 2011

Figure 2.1 – Map of the study area showing location in eastern Canada (top right), specific location in north-western Québec (bottom right), and example of the experimental design in one of the three sectors (left).

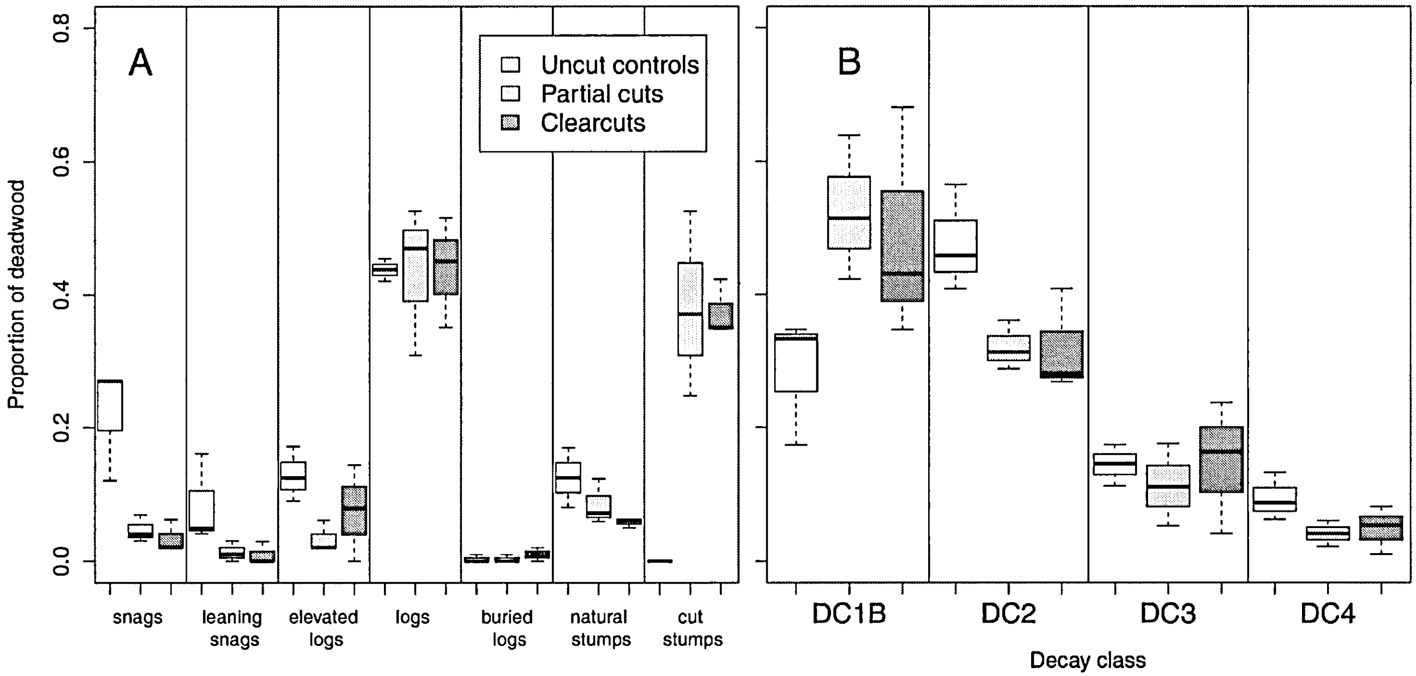


Figure 2.2 – The proportion of deadwood in A) different quality classes and B) different decay classes in uncut controls (white), partial cuts (grey), and operational cuts (dark grey).

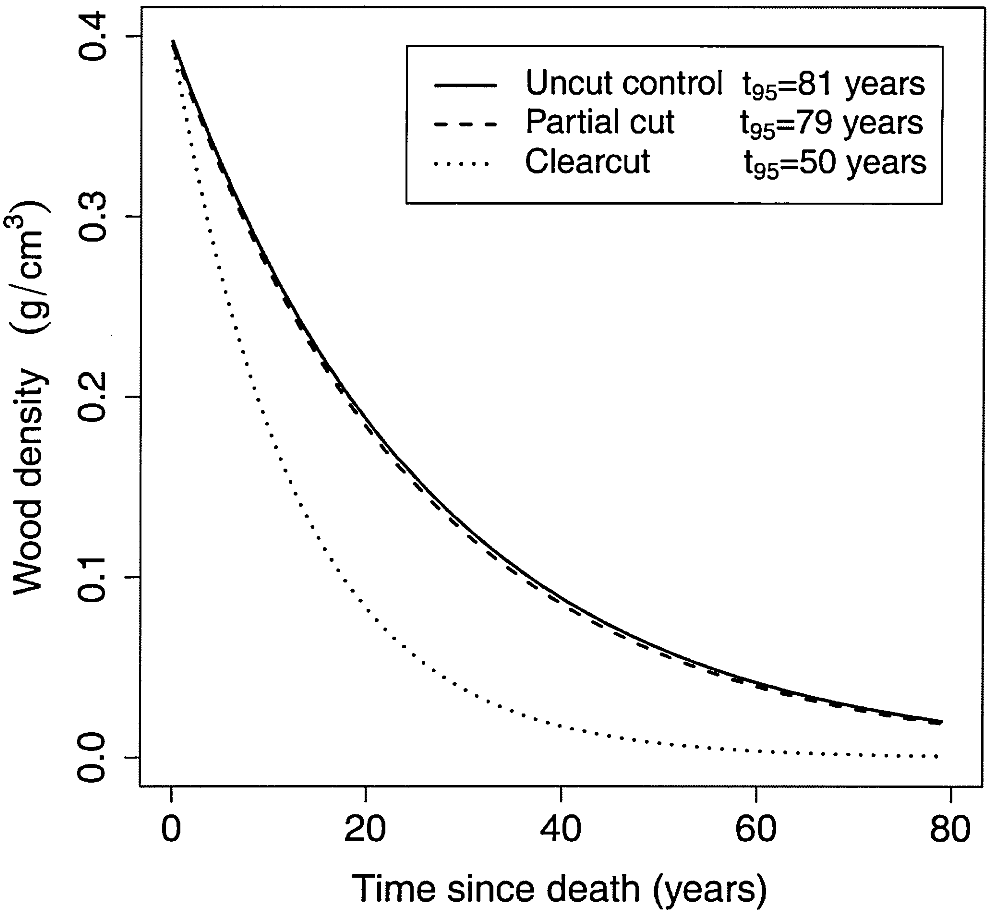


Figure 2.3 – Extrapolated decay curves for the uncut controls, partial cuts and operational cuts. The t_{95} value represents time until 95% density is lost from the logs.

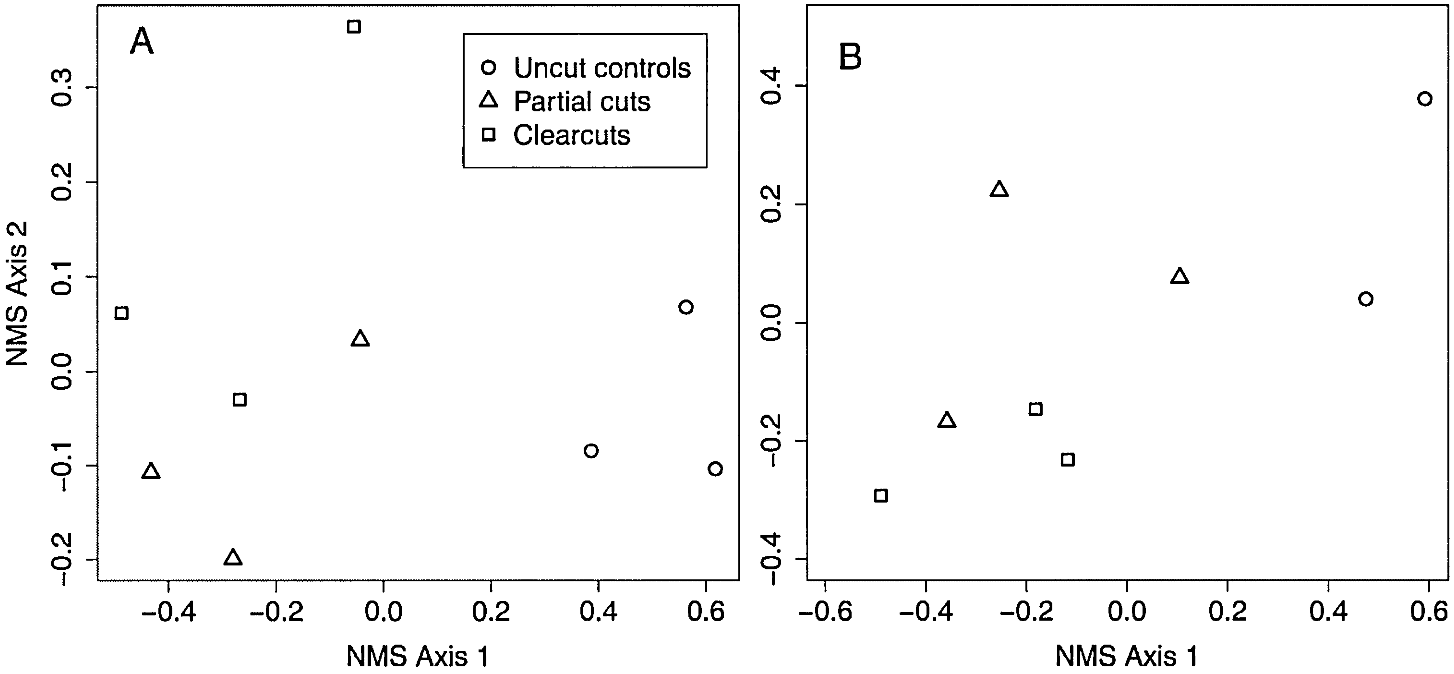


Figure 2.4 - Nonmetric multi-dimensional scaling ordinations for A) 6 dominant species of wood inhabiting fungi, stress=0.15 and for B) 267 species of deadwood-associated beetles, stress=3.52.

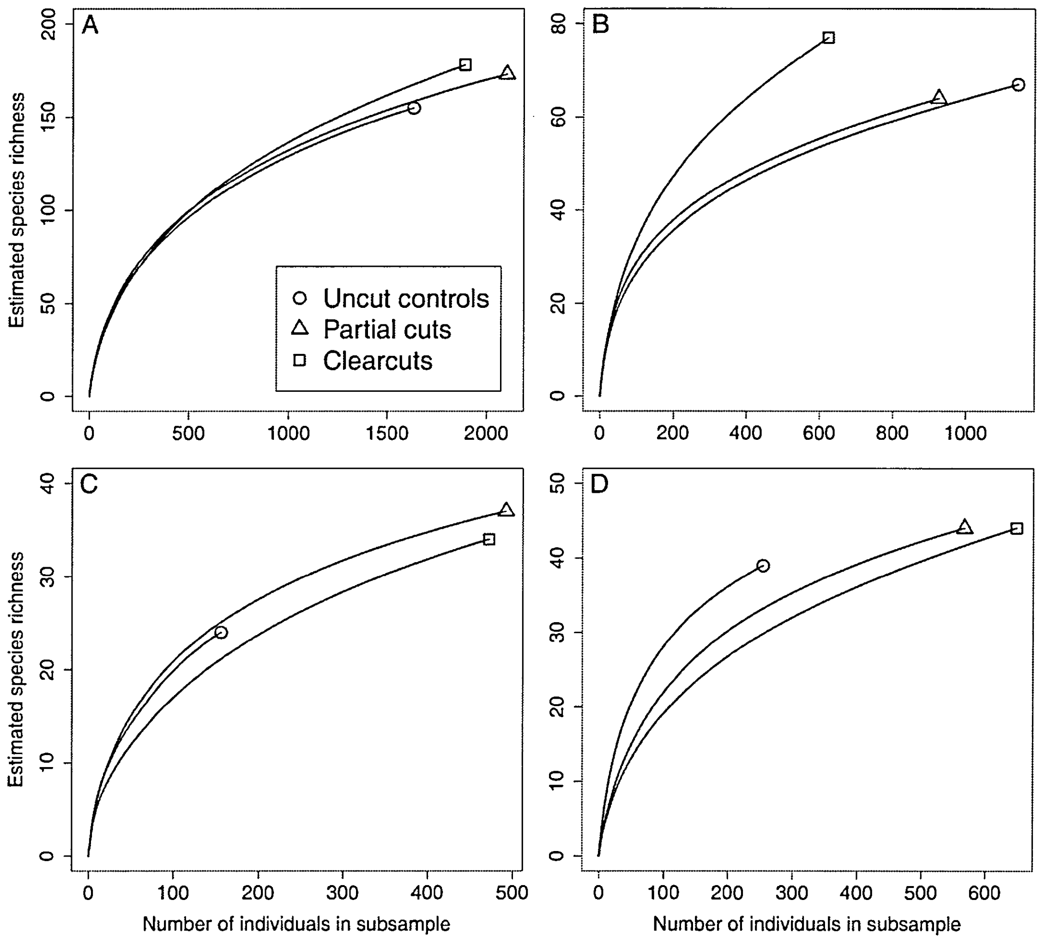


Figure 2.5 – Individual based rarefaction showing the increase in species richness with increases in the number of individuals for: A) all deadwood-associated beetles; B) fungivorous; C) wood-feeding, and D) predatory beetles.

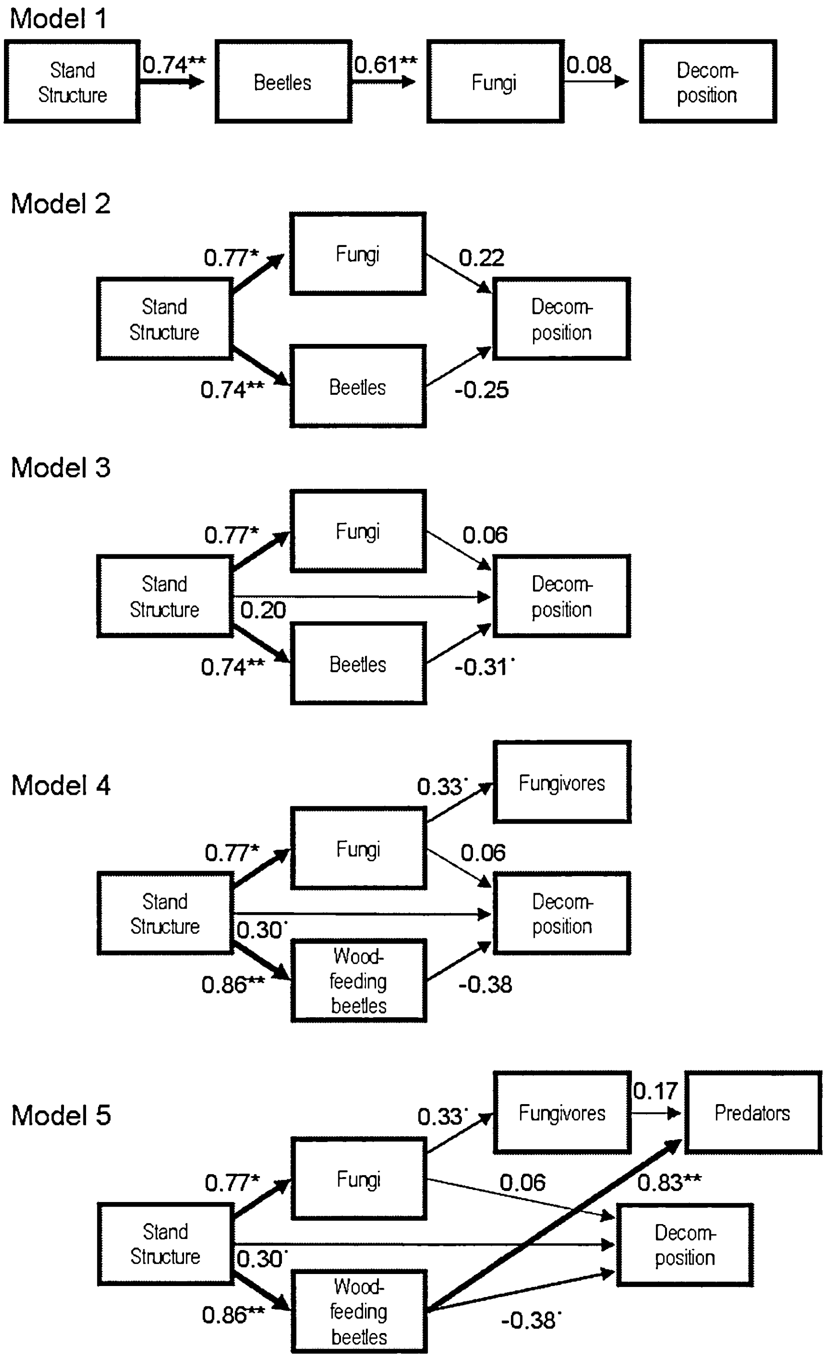


Figure 2.6 – Causal models of stand structural affects on fungal and beetle biodiversity and subsequent effect on wood decomposition.

CHAPTER 3

EVALUATING PARTIAL CUTTING AS AN ECOSYSTEM MANAGEMENT TOOL USING DEADWOOD-ASSOCIATED BEETLES AND FUNGI.

Jenna Jacobs

Article planned for submission in the journal

Forest Ecology and Management

3.1 Résumé

Dans la pessière noire à mousses de l'ouest du Québec, les peuplements issus de coupes partielles ont le potentiel d'émuler la structure de peuplement des vieilles forêts et de fournir une approche en accord avec l'aménagement écosystémique. Nous avons vérifié si les coupes partielles pouvaient maintenir des assemblages d'espèces similaires à ceux des peuplements âgés en comparant les communautés de coléoptères et de champignons associés au bois mort retrouvées dans des coupes partielles, des coupes totales et dans des peuplements issus de feux formant une chronoséquence de 700 ans. Les peuplements non aménagés de cette région subissent une transition dans leur structure allant de dense et équienne à moins dense et inéquienne entre 90 et 150 ans. Les coupes partielles expérimentales de notre étude ont réduit la surface terrière des peuplements à des niveaux que nous n'avons pas rencontrés dans la chronoséquence. Nous avons trouvé des changements clairs et constants autant pour les champignons que pour les assemblages de coléoptères associés au bois mort le long de la chronoséquence, ce qui sert de référence pour l'évaluation des coupes partielles. Toutefois, les assemblages de champignons et de coléoptères associés au bois mort dans les coupes partielles ne sont pas similaires à ceux retrouvés dans les vieux peuplements et se retrouvent à l'extérieur de la gamme de variabilité naturelle observée dans la chronoséquence qui s'étale sur 700 ans. De plus, nous sommes incapables de différencier les assemblages des coupes partielles de ceux des coupes totales, ce qui suggère que les traitements génèrent des communautés sans équivalents naturels observés. Nous en concluons donc que les coupes partielles ont été pratiquées dans des forêts qui avaient déjà perdu une grande partie de leur surface terrière, ce qui a généré des peuplements à surface terrière plus faible que n'importe quel autre de la chronoséquence et dont les communautés d'organismes associés au bois mort étaient différentes. Nous décrivons ces nouvelles communautés retrouvées dans les coupes partielles et les coupes totales comme étant composées d'un mélange très diversifié d'espèces : 1) généralistes qui sont restés après la coupes; 2) d'espèces de milieux ouverts ayant récemment colonisé le milieu et 3) d'espèces associées aux vieilles forêts mais en déclin suite à la coupe. Ces communautés semblent plus similaires à celles de peuplements récemment brûlés qu'à celles des vieilles forêts. Nous déduisons donc que les coupes partielles peuvent émuler des forêts plus vieilles et hétérogènes si : les opérations de récoltes visent des peuplements plus jeunes et équiens; moins de 30 m2/ha de la surface terrière avant coupe est prélevée; et au moins 10m^2/ha de surface terrière est maintenue après coupe.

Mots-clés : Coupes partielles, coupes totales, coléoptères saproxyliques, champignons saprophages, aménagement écosystémique

3.2 Abstract

In boreal black spruce forests of northwestern Quebec, partial cuts have the potential to emulate old growth stand structure, maintain biodiversity and provide a viable approach to ecosystem management. We verified whether partial cuts maintained species assemblages similar to those found in old-growth stands by comparing deadwood-associated beetle and fungal communities in replicated partial cuts, clearcuts and a 700-year chronosequence of uncut stands. After the senescence of the post-fire cohort, unmanaged stands in this region undergo a transition from a dense even-aged to heterogeneous uneven-aged stand structure approximately 90 to150 years after stand initiation. We observed the largest differences along the chronosequence of uncut stands between these dense, even-aged stands and older, heterogeneous stands. However, deadwood-associated biodiversity from partial cuts were not similar to those found in older stands and fell outside the observed range of variability within the 700-year chronosequence. Partial cuts in our study had less basal area (mean=3.5 m^2/ha) than any stand sampled across the chronosequence (min=13.8 m^2/ha). Furthermore, we were unable to differentiate between assemblages in partial cuts and clearcuts suggesting these treatments result in communities with no observed natural analogs. We believe that partial cuts were unable to maintain species assemblages because prior to partial cutting, experimental stands had already lost a large proportion of their basal area resulting in less basal area than any stand observed across the chronosequence. We suggest that these new assemblages found in partial cuts and clearcuts are a highly diverse mix of: 1) generalist species that remained post-harvest; 2) open-habitat species that recently colonized, and 3) closed-forest species in decline as a result of the harvesting. These communities are likely more similar to recently burned stands than to old-growth stands. We propose that partial cutting may emulate older heterogeneous forests if: 1) harvesting operations target younger even-aged stands; 2) at least 10 m^2/ha of post-harvest basal area is retained, and 3) less than 30 m^2/ha of the pre-harvest basal area is removed.

Keywords Partial cuts, clearcuts, saproxylic beetles, saprotrophic fungi, ecosystem - based management

3.3 Introduction

In boreal ecosystems, partial cutting has been widely advocated as a practical means to alter stand composition and/or recreate uneven-aged stand structures characteristic of older stands (Lieffers et al. 1996, Bergeron et al. 2002, Harvey et al. 2002), which could facilitate maintaining biodiversity within the range of natural variability (Work et al. 2010). While selective cutting of deciduous species may speed structural and compositional changes in mixedwood landscapes, this approach may be limited in other forest types such as black spruce. In the black spruce forests in the Clay Belt region of Quebec and Ontario, tree composition does not change with succession; instead, multicohort stands with reduced basal area develop due to paludification, where the organic layer thickens, resulting in reduced stand productivity (Simard et al. 2007). While, partial cuts in early successional black spruce forests have the potential to create stand structure consistent with older, less dense, paludified forests (Bergeron et al. 2002), the impacts on biodiversity are just beginning to be explored (Paradis and Work 2011, Arseneault et al. 2012, Fenton et al. 2013).

In northern black-spruce forests, succession is initiated by an intense stand replacing fire. The initial cohort of black spruce originates from seed and grows into a dense, even-aged forest which persists until approximately 90 years following fire (Bergeron et al. 2002). Following senescence of this post-fire cohort at 100-125 years (Lecomte et al. 2006a), the canopy begins to opens and encourages a mix of different aged black spruce trees originating from the both the initial post-fire cohort and younger regenerating trees. Increased light availability also triggers a shift in the bryophyte community from feather moss to *Sphagnum* species (Fenton and Bergeron 2006b). Increased sphagnum growth initiates paludification, a process whereby the *Sphagnum* mosses and litter accumulates on the forest floor faster than they decompose. What results is a build-up of the organic layer and a consequential rise of the water table, coupled with decreased soil temperatures, nutrient availability and productivity

(Payette 2001, Simard et al. 2007). In the prolonged absence of fire these forests enter a retrogressive state, characterized by an even more open heterogeneous structure with continual decreases in productivity (Simard et al. 2007). Similar reductions in productivity in the prolonged absence of fire have been demonstrated elsewhere and have been coined 'ecosystem retrogression' (e.g. Walker et al. 2001, Wardle et al. 2004, Vitousek 2006).

While ecosystem management strategies including partial cuts, are often evaluated through comparisons of structural attributes or species assemblages among managed and uncut stands, they rarely capture the range of natural variability that occurs as stands undergo long-term changes, such as paludification in black spruce. Instead, uncut stands often reflect pre-harvest forest conditions or a specific stand type (ie. burned stand, old growth stand). Success of a given ecosystem management strategies in stands undergoing long-term changes will thus depend on a strong understanding of natural stand succession.

During succession in these black spruce forests, rates of deadwood input and decay undergo significant changes. Following the senescence of the post-fire cohort stands transition from dense even-aged forests to less –dense forests between 90 and 150 years after disturbance, in which large quantities of deadwood are created and quickly disappear as a result of high rates of wood decay and burial by rapidly growing *Sphagnum* mosses (Jacobs et al. 2015). Approximately 250 years after stand-replacing fire, decomposition rates decrease resulting in the highest biomass of aboveground deadwood in mature forests. In the prolonged absence of fire, overall biomass of aboveground deadwood continues to decrease slowly under a regime of constant but slow decomposition and burial (Jacobs et al. 2015). These, like other black spruce forests have the potential to store large amounts of deadwood below ground in the form of buried deadwood, which is thought to not decompose or provide potential habitat for deadwood-associated species (Hagemann et al. 2009).

Previous study black spruce forests of the Clay Belt region demonstrated that wood decay rates in partial cuts were similar to uncut controls compared to clearcuts where more fungal degree days led to higher rates of wood decomposition (Jacobs and Work 2012). Paradis and Work (2011) concluded that partial cuts were unable to maintain spider assemblages within the natural range of variability observed across a chronosequence of unharvested stands; however, there was some evidence that with sufficiently high levels of retention, partial cutting can maintain pre-disturbance spider assemblages.

Deadwood-associated communities are well suited to evaluate ecosystem-based management strategies (Siitonen 2001, Stokland et al. 2012). Many deadwood-associated groups including beetles, Diptera, fungi and birds have been successfully used to study the impacts of forest management (Harrison et al. 2005, Jacobs et al. 2007b, Work and Hibbert 2011, Kebli et al. 2012, Ranius et al. 2014). For example, Kebli et al. (2012) concluded that partial cuts could be an effective ecosystem-based management strategy for the conservation of fungi in aspen-dominated stands. Deadwood-associated beetles respond to changes in stand composition (Jacobs et al. 2007a), deadwood volume and quality (Siitonen 2001), and are linked to the rates of deadwood decomposition (Jacobs and Work 2012). In Europe, deadwood-associated insects have been identified as a highly threatened group due to modern intensive forestry practices (Nieto and Alexander 2010). Studies from Fennoscandia have established strong links between a long-history of intensive forest management, the reduction of deadwood in forests and losses of deadwood-associated species (Stokland et al. 2012). In Canada, which has a shorter history of forest management, commercial forest harvesting results in rapid community-level changes of both deadwood-associated beetles and fungi (Jacobs and Work 2012, Kebli et al. 2012). For example, Cobb et al. (2011) attributed changes in the composition of saproxylic beetles in mixedwood stands two to three years after harvest to differences in the quantity and quality of deadwood.

In this study we related structural elements of the forest and deadwood-associated beetle and polypore fungal communities across a 700-year chronosequence of black spruce stands and a replicated series of partial cuts and clearcuts. We compared uncut stands from the chronosequence and harvested stands to test whether partial cutting: 1) maintains similar forest structure and deadwood-associated communities as are found in old-growth stands, and 2) maintain structure and deadwood-associated communities within the range of natural variability. We then identified key forest structure elements that differed between old-growth stands and partial cuts and how these elements influence the composition and relative abundance of three major beetle functional groups (*vis.* fungivores, wood and bark feeders (xylophages) & predators). Finally, we use multivariate analysis and individual species' responses to suggest three general species responses in harvested areas. We hypothesized that changes in deadwood-associated beetle and fungal communities will be explained by the degree of canopy opening along the chronosequence rather than the diversity or quantity of deadwood. Therefore, if partial cuts have sufficiently high retention levels, the effects on deadwood-associated communities will be minimized.

3.4 Methods

3.4.1 Study Sites

We sampled deadwood-associated beetle and fungal assemblages along a chronosequence of 12 uncut stands (49°00'–50°00' N; 78°30'–79°30' W). All stands were located in northwestern Quebec, in the northern part of the Clay Belt region of northeastern Ontario and northwestern Quebec (Figure 3.1). The Clay Belt is a physiographic unit composed of primarily clay deposits left by proglacial lakes Barlow and Ojibway (Veillette 1994). Our chronosequence consisted of 9 stands from a previous study (Lecomte et al. 2005) where stand origin and age was verified with paleo-ecological methods. We added three unharvested stands to this chronosequence which also served as paired control stands for experimentally harvested stands. These stands were part of larger network of sites dedicated to studying the long-term effects of partial cutting (Fenton et al. 2013). We classified unharvested stands three stages of stand development (adapted from Harper et al. 2005): Stage 1: Stand initiation - mature, dense, closed canopy forest (34 - 96 years since fire); Stage 2- senescence of the post-fire cohort (96 - 164 years) and Stage 3- uneven-aged, heterogeneous, open stands (>164 years). We then compared the natural range of variability of beetle and fungal assemblages observed in stands along the chronosequence to six experimentally replicated clearcut and partial cut stands (three replicates of each). All harvested stands were cut between the winters of 2003 and 2004. At the time of sampling, mean basal area in the uncut controls paired with the experimental cuts was 21 m^2/ha and the mean basal area in partial cuts and clearcuts was 3.2 m^2/ha and 1.2 m^2/ha respectively. Nearby weather stations (La Sarre, Quebec (48°46′N, 79°13′W) and Matagami, Quebec (49°46′N, 77°49′W)) reported an average precipitation of 889.8 and 905 mm, respectively, 28% and 37% falling as snow. Average temperatures of the region ranged from 0.7 °C (SD = 2.2) in the south to –0.7 °C (SD = 2.7) in the north (Environment Canada 2011). Fire has been the main disturbance in this region and the fire cycle has lengthened from 101 years before 1810 to 398 years since 1920 (Bergeron et al. 2004a).

3.4.2 Measurement of forest structure

In each stand we measured both live and dead basal area, volume and quality (decay class and size class) of downed deadwood (DDW), and volume of snag using two permanent inventory plots. Basal area was measured using circular plots with a radius of 11.28 m (400 m^2). Within each plot we measured the diameter at breast height (DBH) of all stems greater than 5 cm in diameter and classified them as either living or dead. We measured volume of DDW across the chronosequence using star plots consisting of three 20 m transects radiating from a common midpoint and separated by 120 degrees. We used previously measured values for volume of DDW from the RECPA sites which used five 10m transects in each stand. For each piece of intersected deadwood greater than 5 cm diameter, we measured the diameter and the decay class was noted using a five class system (modified from Maser et al. 1979). Three stands were measured using both star plots and 10m transects and no appreciable differences were found.

3.4.3 Survey of polypore fungi

We randomly chose one of the 400 m^2 plots per stand to survey polypore fungi. We counted and identified polypore fruiting bodies on all surfaces of deadwood with a diameter greater than 5 cm. We limited sampling in the plot to the initial 100 pieces of deadwood encountered. When unable to find 100 pieces within the plot, we continued the survey on pieces of deadwood outside the plot until 100 total pieces had been inspected.

3.4.4 Collection of beetles

We sampled beetles in the center of both biodiversity plots in all chronosequence stands and experimentally harvested stands using freestanding flight-intercept traps. These traps consisted of two perpendicular black plastic panels (30 cm x 122 cm) affixed to a 20 L bucket with the same diameter as the width of the panels. We added approximately 1 L of propylene glycol to each trap and replaced the propylene glycol when samples were obviously diluted (Jacobs and Work 2012).

We began collecting beetles from the 5th to 9th of May 2008, at which time snow was present within stands and the ground was frozen below 10 cm. We collected samples at 3-week intervals until the week of the 18th to 22nd of August 2008 resulting in approximately 100 collection days for each stand. Specimens were collected by straining samples through fine-mesh cloth, and were then placed into 75% ethanol. We sorted and identified beetles to the finest taxonomic resolution possible using available keys, consultations with taxonomic experts and comparison with museum collections. For each species or taxa identified we assigned a functional group based on available literature: 1) Fungivore; 2) Xylophage; 3) Predator, and 4) Sap feeder (e.g. Jacobs et al. 2007a, e.g. Dollin et al. 2008).

3.4.5 Data Analysis

We characterized changes in basal area and volume of DDW with stand age using linear regression where the logarithm of time since fire was the explanatory variable. We then tested these models for a non-constant regression parameter (i.e. break-point) using the Davies test (Davies 1987). When a break-point in the regression was detected, we used piecewise linear regression using the function segmented in the segmented library (Muggeo 2008) in R 3.02 (R Development Core Team 2011). This technique estimates unknown breakpoints (Muggeo 2008) of regression. We then evaluated the effect of time since fire and harvesting treatment on basal area and downed woody debris using linear mixed-effects (LME) models. Mixed-effects models are more robust to departures in equal sampling effort among groups than traditional analysis of variance (ANOVA) models (Pinheiro and Bates 2000). We compared models using harvesting treatment (*vis.* uncut, partial cut and clearcut), time since fire and the interaction of these factors as explanatory variables and stand as the random factor using the corrected Akaike information criterion (AICc) (Pinheiro and Bates 2000).

We used individual-based rarefactions (Simberloff 1972) on raw abundances to estimate changes in species accumulation among all beetle taxa among the successional cohorts identified by the multivariate regression tree and harvesting treatments. We created rarefaction curves with the rarefy function from the vegan library (Oksanen et al. 2008) in R.

Abundance data for beetles was transformed into catch rates for community-level analyses. Catch rates were calculated as the abundance of each species of beetles for each trap divided by the total number of days the individual trap was operational over the entire trapping period. Analysis of polypore fungi was limited to six species that were conspicuous and reliably identifiable in the field. For community analyses we analyzed the proportional presence of a given species of fungi. The proportional presence was calculated as the frequency a given species was present on the 100 pieces of deadwood surveyed in each stand.

We tested the effect of time since fire and harvesting treatment on deadwood-associated beetle and polypore fungal assemblages using distance based multivariate regression trees (dbMRT) (De'Ath 2002). Community data was first transformed to remove the influence of sampling effort between stands (ie. uneven catch rates / occurrence rates) by dividing by the stand totals. Data was transformed into a Bray-Curtis distance matrix among all stands, and then the recursive partitioning procedure was performed. We used time since fire and harvesting treatment as the explanatory variables to determine and evaluate the organization of wood-associated biota into previously described cohorts. We produced the trees by running 1000 cross-validations on the two community data sets, each time selecting the best tree based on the 1se rule (the tree that explains the most variance in the data within one SE of the tree that has the lowest cross-validated error) and then used the most frequently selected configuration. We calculated the relative species variance for each split in the dbMRT by using sum of squares variance partitioning for each species and each division of the tree (De'Ath 2002). Regression tree analysis was performed using the mvpart function in the mvpart library (Therneau et al. 2007).

We further analyzed the effect of basal area on beetle and fungal communities using Mantel's tests (vegan library from Oksanen et al. 2008). The community data was again transformed to a Bray-Curtis similarity matrix to create pair-wise comparisons between all stands and correlated against the absolute differences of basal area. We used these same pair-wise comparisons of community similarity and differences of basal area to define the range of natural variability as the pair-wise comparisons among all uncut chronosequence stands. We considered the range of natural variability to be the range of pair-wise distance observed between all the unharvested stands for both community similarity and basal area. We then repeated the dbMRTs and Mantel's test for each major beetle functional group (*vis.* Fungivore, Xylophage and Predator). The procedure for creating the dbMRTs was similar to the procedure described above for all beetles and fungi, however for exploratory purposes, we chose the largest tree that was picked at least 10% of the time according to the `1SE` rule. We also included additional structural variables (*vis.* basal area, total volume of downed deadwood, and volumes of downed deadwood divided into 5 cm size classes and 5 decay classes) into the MRTs.

3.5 Results

3.5.1 Forest structure

We found strong support of a non-constant regression parameter when relating basal area to the log of time since fire (Davies' test, p=0.002, Figure 3.2A). Basal area significantly decreased at a high rate (p=0.012) until an estimated break point of 145 years during the second cohort, at which point it continued to decrease at a lower rate (P=0.013). Harvested stands had significantly less basal area than the uncut stands (LME, $F_{2,17}$=10.32, p=0.012), but no difference was detected between the partial cut and clearcut stands (LME, t_{17}=-0.253, p=0.802).

We also found strong support for a non-constant regression parameter for the volume of DDW (Davies' test, p=0.020, Figure 3.2B). Volume of DDW increased to a break-point of 237 years after disturbance, during the third cohort, at which point it decreases. However, neither of these slopes was significant (p=0.065, p=0.087, respectively). We did not find a significant effect of harvesting on the total volume of DDW (LME, $F_{2,17}$=0.72, p=0.50).

3.5.2 Community Results

We collected 14 972 beetles from 357 species. Of these we determined that 10 723 individuals and 319 species were associated with deadwood. We found 10 species that are potentially new to science, two of which have subsequently been described (Klimaszewski et al. 2013). Using rarefaction analysis of beetle communities we observed generally higher richness of beetles in the harvested stands compared to the unharvested stands (Figure 3.3). There were higher levels of richness as intensity of harvesting increased and as unharvested stands aged (Figure 3.3).

We found that overall, beetle assemblage differed among our three defined forest stages and between cut and uncut stands, as indicated by MRT (Figure 3.4A). This tree was chosen by cross-validation 820/1000 times and explained 70% of the variance in the data. The largest separation observed was between the cut and uncut stands explaining 50% of the variance. Separation of the youngest stands from older stands accounted for an additional 9% of the variance. The final split separating the two older stand stages explained and additional 10% of the variance associated with species assemblages.

Differences in polypore fungal assemblages were similar to beetle assemblages, except the separation between the two oldest groups occurred much later in succession (328 years instead of 160 years) and we see an additional split between the partial cuts and clearcuts (Figure 3.4B). This tree was chosen by cross-validation 871/1000 times and explained 87% of the variance. The first spilt between harvested an unharvested stands explained 66% of the variance. The separation of the youngest stand from older stands explained an additional 18% and the separation of the two older groups of stands explained 14% of the variance. The separation between the partial cut and clearcut stands explained 23% of the variance.

The pair-wise distances of both beetle and fungal assemblages were highly correlated to absolute difference of basal area (Beetles: Mantel's r=0.73, p=0.001, Fungi: Mantel`s r=0.86, p=0.001). For beetles and fungi, 40% and 42% respectively, of pair-wise distances between chronosequence sites and harvested sites fell well outside the range of natural variability (Figure 3.5). This effect is even more obvious for beetles (Figure 3.5A), where beetle assemblages were less similar between chronosequence and harvested stands than between chronosequence stands at comparable differences of basal area. Pair-wise distances between harvested sites were generally highly homogeneous (*i.e.* low dissimilarity distance) in terms of pair-wise distance of both species similarity and absolute difference of basal area (Figure 3.5).

Basal area was important in determining species assemblages for all three major functional groups of beetles, although this relationship was somewhat weaker for fungivores (Figure 3.6). The dbMRT of fungivores separated stands based solely on having more or less than 4.2 m^2/ha, essentially separating all chronosequence stands and one partial cut stands from the remaining 5 harvested stands (30% of the variance explained, picked 959/1000). This tree had a relatively high cross-validated error (1.03), indicating that additional sampling may not follow the same pattern. We also observed a weak but significant correlation between changes in fungivore assemblages and basal area (Mantel's r=0.30, p=0.003). Xylophagous and predatory beetle assemblages were strongly correlated with changes in basal area. The largest difference in xylophagous beetle assemblages were between stands with more or less than 15 m^2/ha of basal area. We also observed additional, albeit weaker changes in xylophagous beetle assemblages among unharvested stands when total basal area dropped below 30m^2/ha. Finally in those late successional old-growth stands (<30 m^2/ha), we detected a divergence in species assemblage based on the quality of deadwood present (DDW5 & DDW2). Overall we observed a strong correlation between changes in xylophagous beetle assemblages and basal area (Mantel's r=0.81, p=0.001). Changes in predatory beetle assemblages follow a similar pattern as xylophagous beetles. Multivariate regression trees indicate that the largest change in the community is between stands with more or less than 9 m^2/ha, which separated all harvested stands from the unharvested stands. As observed in xylophagous beetles, there were weaker changes among unharvested stands when basal area dropped below 30 m^2/ha. In these late successional old-growth stands (<30 m^2/ha) beetles were responding to the amount of fresh deadwood present (DDW1). Interestingly, we also detected a change in the beetle community in harvested stands based on the volume of small diameter (5 cm to 10 cm) logs present. Overall, like xylophagous beetles, we observed a consistent change in predatory beetle assemblages with changes in basal area (Mantel`s r=0.76, p=0.001).

The variances attributable to individual species based on splits in regression trees (Table 3.1) highlighted patterns in species responses and give insight on exactly how the community is changing in response to changes in basal area either through succession or harvesting. However, many species were collected in such low numbers that it was difficult to classify them using MRT. For example, 99% of the individuals are represented by just 6% of the species. We ultimately categorized three major responses by species when sufficient data were present. First, generalist species were typified by catch rates that did not greatly change in response to forest succession or harvesting. These species had little to no variance explained by any of the splits in the regression tree. Second, open-habitat species whose catch rates increased as the forest opened due to either succession or harvesting (Figure 3.7A). These species had a high variance explained by the first split (harvested vs. unharvested, Table 3.1). The third trend, were species whose catch rates remained relatively constant throughout succession and were negatively affected by forest harvesting (Figure 3.7B). Like species in the first group, these species also had higher explained variance by the first split, but the catch rates of individual species decreased instead of increased (Table 3.1).

Polypore fungi had similar trends to the beetles; however, with observations of only six species we observed just two notable responses. The first was that of *Gloeophyllum sepiarium* (Fr.) Karst, which had much higher proportional presence in harvested stands. The other being *Trichaptum abietinum* (Dicks.: Fr.) Ryv., a white rot fungi, had the highest probability of encountering a fruiting body in the early succession al stands, with probabilities decreasing with succession and forest harvesting (Table 3.2).

3.6 Discussion

Deadwood-associated beetles have great potential to evaluate ecosystem-based management strategies in the black spruce forests of the Clay Belt region. We observed significant compositional turnover in both beetle and fungal assemblages following the senescence of the post-fire cohort. This turnover was driven by the recruitment of open-habitat adapted species and the disappearance of closed-canopy species. While we observed a similar influx of open-habitat species after partial cutting as during natural succession, the magnitude of these changes after partial cutting were much greater. In addition, many more closed canopy species were negatively impact by partial cutting, than succession alone. Together, this resulted in species assemblages unlike any we observed throughout our 700-year chronosequence.

3.6.1 Harvesting operations should target younger even-aged stands

We suggest that harvesting operations should target younger even-aged stands if our goals are to accelerate succession to result in stands which emulate old-growth in terms of structure, biodiversity and processes. The partial cuts in our study were conducted later in forest succession when forests had already lost a large proportion of their basal area. While loss of basal area has frequently been reported following succession (e.g. Simard et al. 2007), we now can associate the senescence of the post-fire cohort to major changes in the deadwood-associated communities. Sensence of the post-fire cohort has already been associated with a loss of forest productivity (Simard et al. 2007), a transition in moss communities that leads to forest paludification (Fenton and Bergeron 2006b) and the creation and rapid decay of large amounts of deadwood (Jacobs et al. 2015). Therefore, immediately prior to the senescence is an ideal period for partial cutting or other forest management interventions when the forest is poised to undergo major changes. Partial cutting at this time will likely result in communities similar to those found in older uneven-aged forests.

3.6.2 At least 10 m2/ha of post-harvest basal area should be retained

We were able to demonstrate little immediate advantage of partial cutting with 15% - 25% retention over operational clearcuts for maintaining beetle and fungal assemblages of black spruce forests. The resulting basal area for both these treatments fell below 10 m^2/ha creating profound changes in the deadwood-associated communities. The most commonly collected beetle in our study, a predator (*Pseudanostirus triundulatus*, 966 individuals), was almost exclusively collected in these low basal area habitats. This beetle is commonly collected in open habitats (Légaré et al. 2011) has been identified as an indicator of burned habitats (Cobb et al. 2011) and is known to persist in burned forests of Quebec for at least 10 years after a fire (Hébert 2011). High catch rates of open-habitat predators following cutting can be observed across invertebrate groups. Multiple studies on ground dwelling spiders observed an open-habitat predator, (*Pardosa moesta* Banks) dominate recently harvested and burned habitats (Buddle et al. 2000, Larrivée et al. 2005, Paradis and Work 2011). Similarly, studies on the effects of partial cutting on ground-beetles report that the most commonly collected beetle is the open-habitat predator *Pterostichus adstrictus* Eschscholtz in intensely disturbed and burned habitats (Martikainen et al. 2006, Work et al. 2010).

Another notable response when basal area drops below 10 m^2/ha was the disappearance of small fungivorous beetles from harvested areas(*Melanophthalma pumila* (LeConte) and *Cortinicara gibbosa* (Herbst)). Harvesting below 10 m^2/ha resulted in changes in the relative abundance of fungal fruiting bodies and can invoke larger community changes (Kebli et al. 2012) potentially affecting these small fungivores. Intensive partial cutting also greatly augments generalist predators which may prey upon these species. Together intensive partial cutting resulting in low basal area could create both bottom-up and top-down pressures on these species.. These effects may not ne mutually exclusive nor do they dismiss the possibility declines are related to increasingly warmer microclimates and decreasing habitat suitability (Jacobs et al. 2007b).

We also observed a fungal species, *Gloeophylum sepiarium*, dominating when basal area drops below 10m^2/ha. This species is common in sun-exposed dry wood and has optimal growth rates between 25 °C and 35 °C (Kotiranta and Niemelä 1981, Bjurman and Wadsö 2000) and is also common in burned stands (Wikars 2002). We frequently observed the fruiting bodies of this species on cut surfaces, which were only present in the cut stands. This species is likely ubiquitous in most black-spruce forests, yet the high growth rates in the open, warmer stands results in a larger proportion of deadwood in these habitats with fruiting bodies.

The dominance of *Gloeophylum sepiarium*, and the corresponding decrease of *Trichaptum abietinum* in these highly disturbed stands, could also have large impacts on the ecosystem. *Trichaptum abietinum* is a white-rot species, which unlike brown-rot fungi like *Gloeophylum sepiarium*, are capable of the breakdown of lignin. Clearly, long-term composition changes in the proportion of brown-rot and whit-rot fungi may have impacts on the dynamics of wood decomposition; however, initial evidence does not suggest that changes in fungal composition leads to significant effects on decomposition rates (Jacobs and Work 2012).

3.6.3 Less than 30 m2/ha of the pre-harvest basal area should be removed

The natural range of variability for basal area across our chronosequence had maximum changes of about 30m^2/ha, typically observed over a 100-year period. When changes induced by harvesting began to approach this level, changes in species assemblages were much greater than expected, especially for beetles. This change does not necessarily constitute a threshold, but appears to be a more linear relationship with basal area. Ground-dwelling predators, for example, often respond positively to the degree of canopy opening (Work et al. 2010) and then quickly disappear as regeneration creates closed canopy conditions on the forest floor (Jacobs et al. 2008). Restricting harvest operations to less than 30m^2/ha will help to ensure that species are not pushed into alternative equilibrium and allow for fast recoveries.

3.6.4 Ecosystem-based management in black spruce

We believe that partial cut harvesting may still be used to maintain old-growth structure in the black spruce forests of the Clay Belt region. These forests undergo a natural, well documented transition from dense even-aged stands to more open, heterogeneous stands that could be emulated with partial cut harvesting (Bergeron et al. 2002, Harper et al. 2005). We have many well-documented responses to this transition by different groups of species, including mosses (Fenton and Bergeron 2006b), lichens (Boudreault et al. 2009) and spiders (Paradis and Work 2011), which can be used to evaluate future partial cut harvesting trials in these black spruce forests. There are also ecosystem processes that could be used as indicators of the success of partial cut harvesting in black spruce including stand productivity (Simard et al. 2007) and wood decomposition (Jacobs et al. 2015).

The response of deadwood-associated species observed here has allowed us to develop a set of criteria to improve the chances of success of partial cut harvesting as a tool for ecosystem management. First, the amount of wood that can be effectively removed should be based on the amount of basal area lost along during natural stand development. The largest difference of basal area between two unharvested stands across the chronosequence was *ca.* 30 m^2/ha. This is not drastically different than the amount that was harvested in our study. Secondly, the lowest observed basal area across the chronosequence was about 10 m^2/ha and responses from beetle functional groups suggest that when basal area is less than 10 m^2/ha beetle communities are driven outside the natural range of variability observed in mature forests. Ten square meters per hectare is much higher than any of the basal area measurements for partial cuts in our study. Basal area in partial cut stands ranged from 1.3 m^2/ha to 4.5 m^2/ha. Therefore we propose that if future ecosystem-based management strategies are to be successful, less than 30 m^2/ha of pre-harvest basal area should be removed and at least 10 m^2/ha of post-harvest basal area should remain.

3.7 Conclusions

We identified a key transitional period during forest succession that marked clear changes in deadwood-associated beetles and fungi and coincided with the development from dense even-aged stands to heterogeneous stands. We concluded that in our study harvesting after this transition resulted in a 'double reduction' of basal area and pushed these stands outside the observed range of natural variability in terms of both basal area and deadwood-dependant beetle and fungal communities. The main community responses responsible for these 'new' communities were the colonization and/or augmentation of species adapted to open habitats and the extirpation or near extirpation of old-growth species. We suggest that emulation of this transition is possible with forest harvesting if implemented prior to this natural transition and with adequate amounts of post-harvest retention. However, future monitoring will be required to determine if the deadwood-associated communities respond similarly to harvesting under these guidelines as to natural forest succession.

3.8 Acknowledgements

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3.10 Tables

Table 3.1- Relative percent of variance explained by each beetle species (explaining >1% of total) for divisions based on the multivariate regression tree (Figure 3.4A).

Species	**feeding group**	**split-1**	**split-2**	**split-3**	**tree total**	**species total**
Pseudanostirus triundulatus (Randall)	Predator	36.5	0.1	0.1	36.8	19.9
Glischrochilus sanguinolentus (Olivier)	Sap Feeder	5.2	1.8	2.3	9.4	16.8
Acrotrichis spp.	Fungivore	1.2	2.5	7.2	10.8	11.5
Melanophthalma pumila (LeConte)	Fungivore	5.3	0.3	1.4	7.0	8.6
Ampedus pullus Germar	Xylophage	11.0	0.1	0.0	11.1	6.2
Glischrochilus siepmanni (W. J. Brown)	Sap feeder	2.7	0.8	0.2	3.8	6.0
Melanophthalma villosa (Zimmermann)	Fungivore	1.1	0.7	1.3	3.1	5.3
Corticaria rubripes Mannerheim	Fungivore	0.4	0.8	0.0	1.2	5.0
Cortinicara gibbosa (Herbst)	Fungivore	3.0	0.0	0.6	3.5	3.7
Corticaria spp.	Fungivore	0.4	0.1	0.2	0.6	1.5
Epuraea spp.	Sap feeder	0.3	0.7	0.4	1.4	1.3
TOTAL		**72.2%**	**12.9%**	**14.9%**	**100%**	**100%**

Table 3.2– Relative percent of variance explained by each polypore fungal species for divisions based on the multivariate regression tree (Figure 3.4B).

Species	**rot type**	**split-1**	**split-2**	**tree total**	**species total**
Gloeophyllum sepiarium (Fr.) Karst	brown	50.2	4.6	54.8	50.7
Trichaptum abietinum (Dicks.: Fr.) Ryv.	white	18.8	16.4	35.2	32.8
Fomitopsis pinicola (Sw.:Fr.) P. Karst.	brown	4.3	1.1	5.4	8.8
Fomitopsis cajanderi (Karst.) Kotl. & Pouz.	brown	0.0	2.9	2.9	4.9
Trichaptum laricinum (Karst.) Ryv.)	white	0.4	1.2	1.6	2.2
Trichaptum fuscoviolaceum (Ehrenb.) Ryv.	white	0.0	0.0	0.1	0.5
TOTAL		**73.7%**	**26.3%**	**100%**	**100%**

3.11 Figures

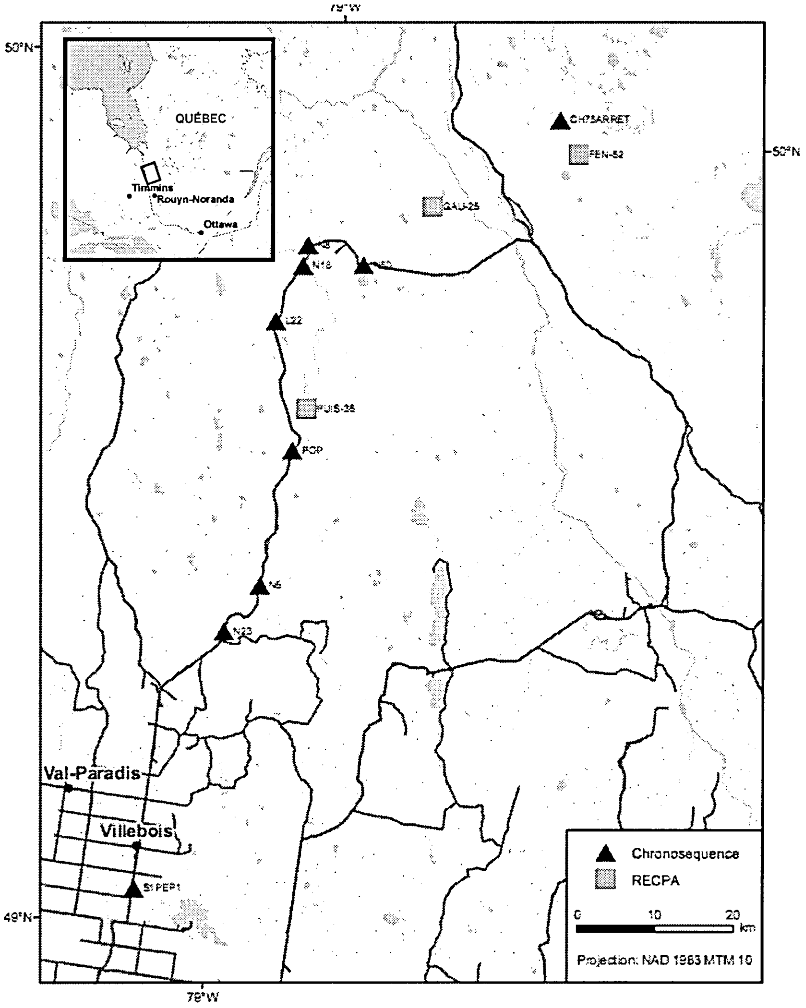


Figure 3.1– map of study site showing the location of chronosequence (triangle) and harvested stands as part of the RECPA network of trial cut (squares).

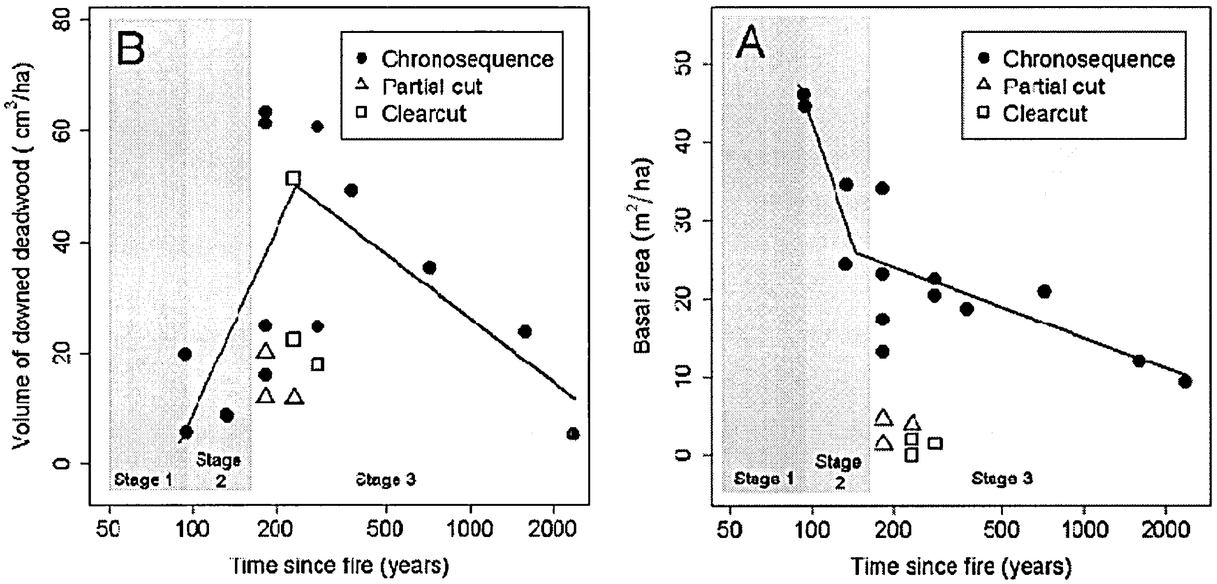


Figure 3.2 – comparison of stand characteristics and defining cohorts from an uncut chronosequence and series of harvested stands: A) declining basal area with time since disturbance, solid line represents results from a segmented regression analysis on chronosequence stands, and B) volume of downed deadwood peaking near the end of the second cohort, the solid line represents the results of the segmented regression on just the chronosequence stands.

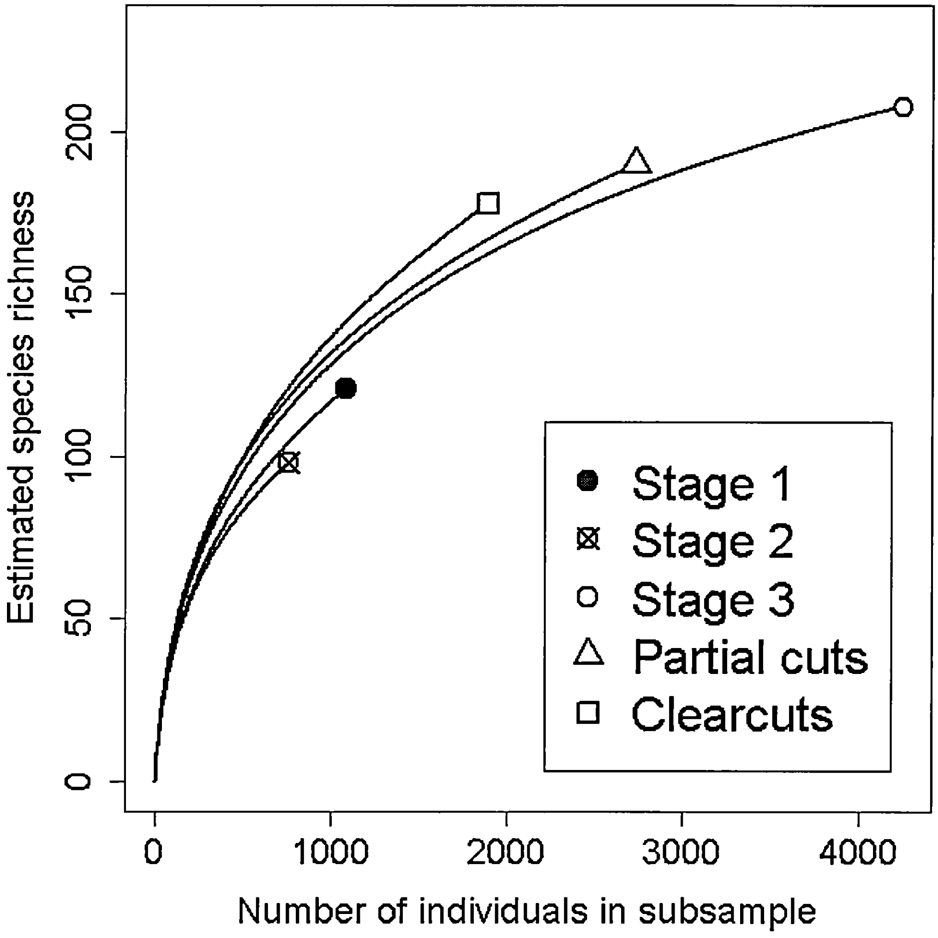


Figure 3.3 – Individual based rarefaction of deadwood-associated beetle assemblages across the successional gradient and in response to two levels of harvesting.

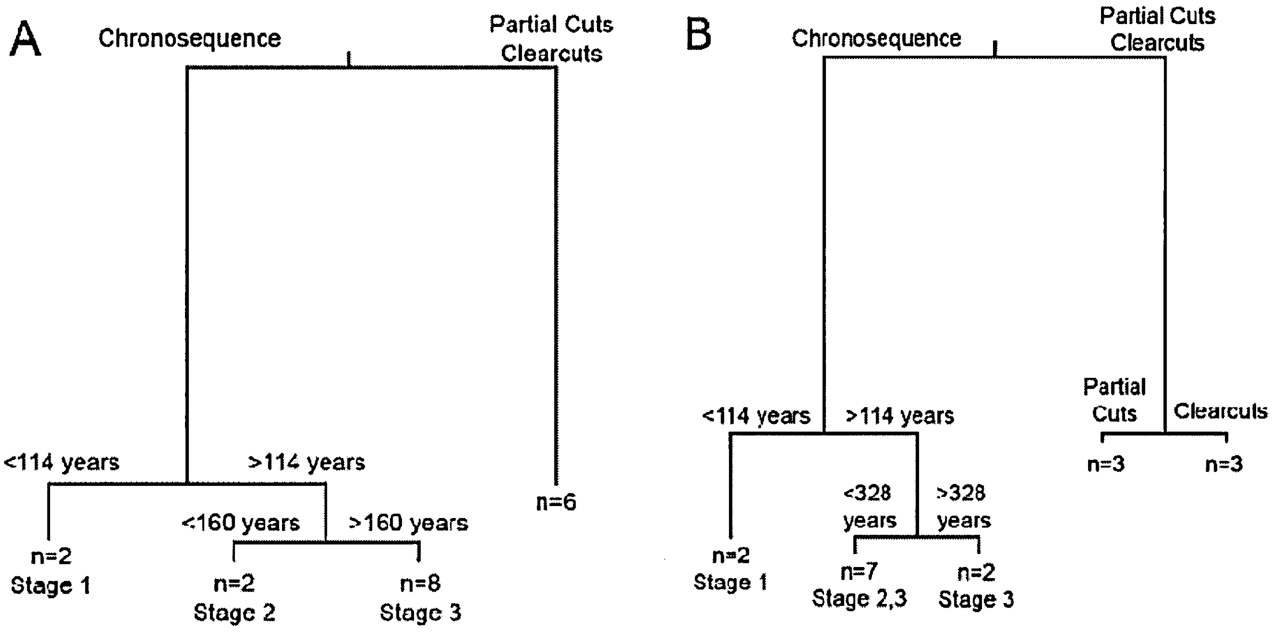


Figure 3.4 – distance based multivariate regression trees of A) beetles (error: 0.30, CV error 0.48, SE: 0.06) and B) dominant fungi (error: 0.13, CV error 0.31, SE: 0.05) using just time since fire and harvesting treatment as explanatory variables.

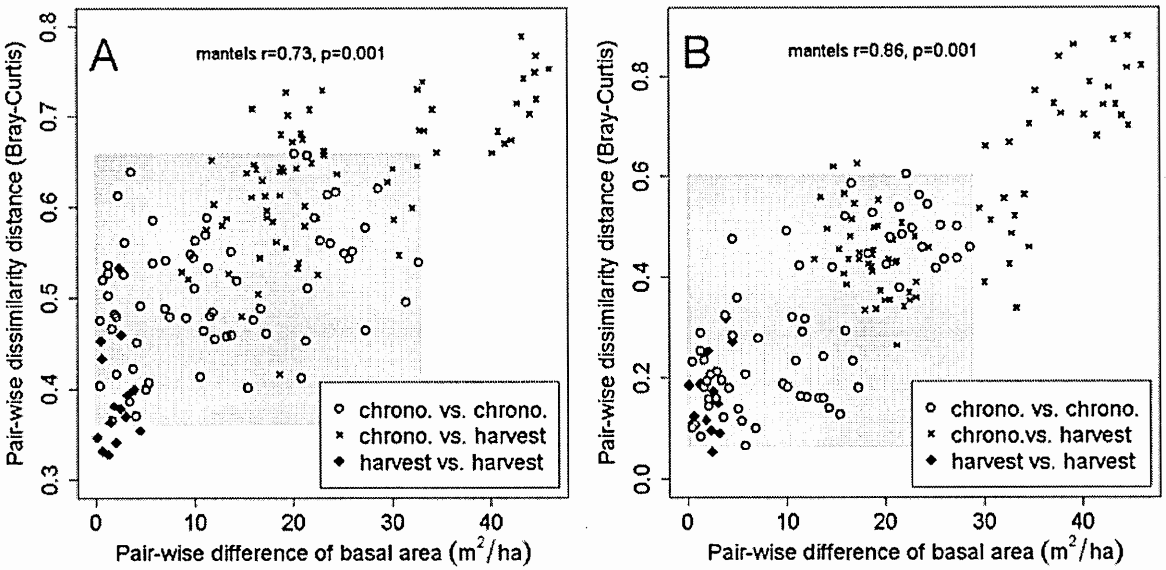
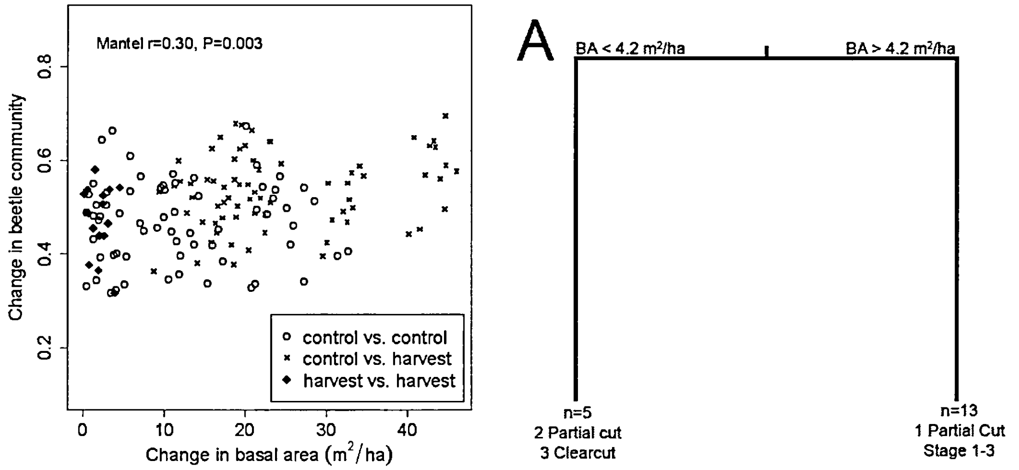
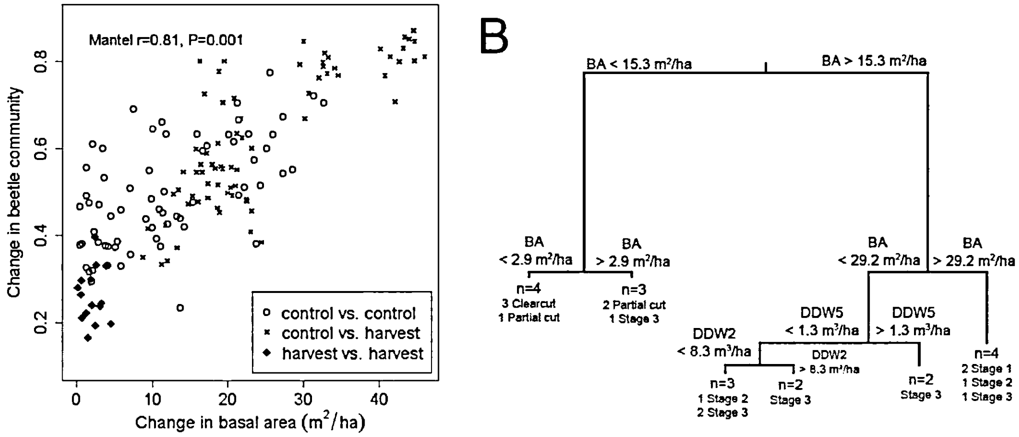


Figure 3.5 – Scatterplot of pairwise Bray-Curtis distances against absolute difference of basal area divided into comparisons between two chronosequence stands (chrono. vs. chrono.), chronosequence stands and harvested stands (chrono. vs. harvest) and two harvested stands (harvest vs. harvest) for both beetles (A) and fungi (B). Greybox denotes range of pairwise comparisons between all uncut chronosequence stands.


Mantel r=0.30, P=0.003
Change in beetle community
0.2
0.4
0.6
0.8
0
10
20
30
40
Change in basal area (m^2/ha)
○ control vs. control
× control vs. harvest
◆ harvest vs. harvest
A
BA < 4.2 m^2/ha
BA > 4.2 m^2/ha
n=5
2 Partial cut
3 Clearcut
n=13
1 Partial Cut
Stage 1-3


Mantel r=0.81, P=0.001
Change in beetle community
0.2
0.4
0.6
0.8
0
10
20
30
40
Change in basal area (m^2/ha)
○ control vs. control
× control vs. harvest
◆ harvest vs. harvest
B
BA < 15.3 m^2/ha
BA > 15.3 m^2/ha
BA
< 2.9 m^2/ha
BA
> 2.9 m^2/ha
n=4
3 Clearcut
1 Partial cut
n=3
2 Partial cut
1 Stage 3
BA
< 29.2 m^2/ha
BA
> 29.2 m^2/ha
DDW5
< 1.3 m^3/ha
DDW5
> 1.3 m^3/ha
DDW2
< 8.3 m^3/ha
DDW2
> 8.3 m^3/ha
n=3
1 Stage 2
2 Stage 3
n=2
Stage 3
n=2
Stage 3
n=4
2 Stage 1
1 Stage 2
1 Stage 3

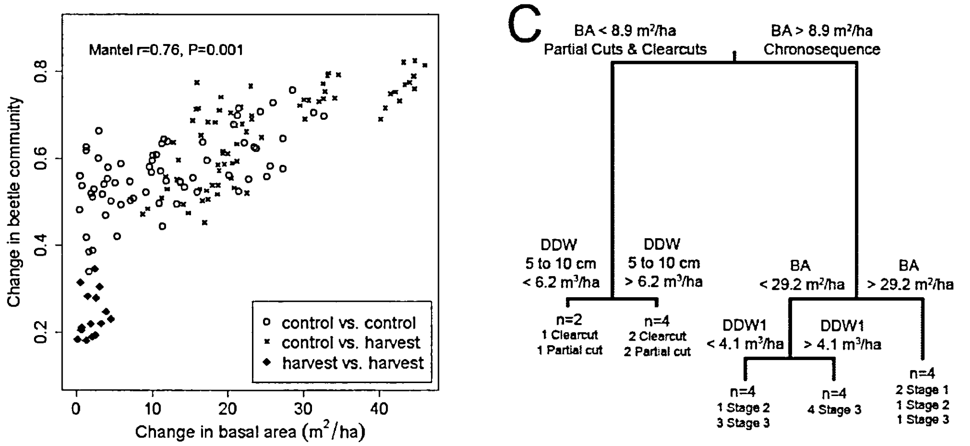
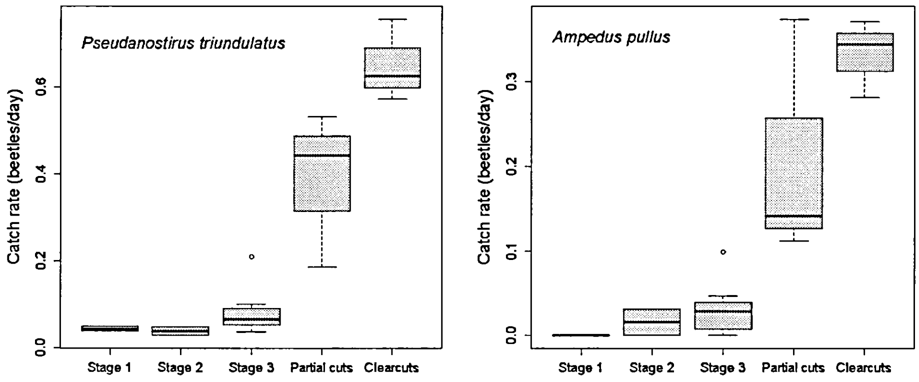

Mantel r=0.76, P=0.001
Change in beetle community
0.2
0.4
0.6
0.8
0
10
20
30
40
Change in basal area (m^2/ha)
○ control vs. control
× control vs. harvest
◆ harvest vs. harvest
C
BA < 8.9 m^2/ha
Partial Cuts & Clearcuts
BA > 8.9 m^2/ha
Chronosequence
DDW
5 to 10 cm
< 6.2 m^3/ha
DDW
5 to 10 cm
> 6.2 m^3/ha
n=2
1 Clearcut
1 Partial cut
n=4
2 Clearcut
2 Partial cut
BA
< 29.2 m^2/ha
BA
> 29.2 m^2/ha
DDW1
< 4.1 m^3/ha
DDW1
> 4.1 m^3/ha
n=4
1 Stage 2
3 Stage 3
n=4
4 Stage 3
n=4
2 Stage 1
1 Stage 2
1 Stage 3

Figure 3.6 – Mantel tests and multivariate regression trees divided by functional groups: A) Fungivores (error=0.701, CV-error=1.03, SE=0.144), B) Xylophages (error=0.134, CV-error=0.589, SE=0.175), C) Predators (error=0.19, CV-error=0.478, SE=0.075).

A) Species whose catch rates increase with succession and harvesting



B) Species whose catch rates a negatively affected by harvesting

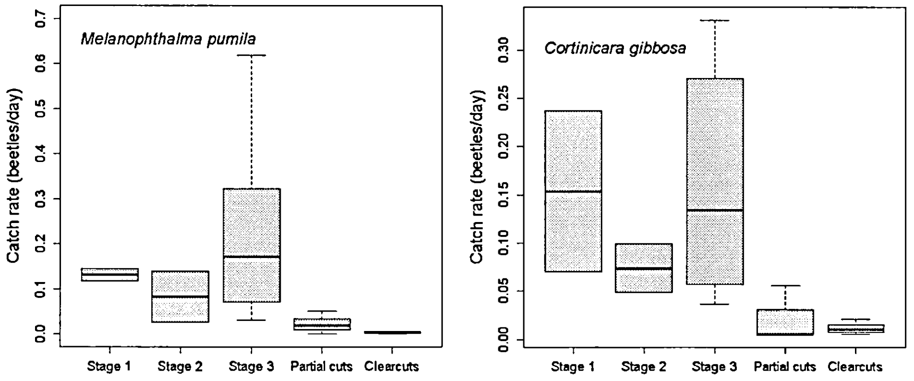


Figure 3.7 – Six individual species responses of beetles that highlight community responses to succession and harvesting.

GENERAL CONCLUSIONS

In this thesis I have conducted an in-depth study on deadwood, associated biodiversity and wood decay in black spruce forests of north-western Quebec. I have also begun to establish links between changes in stand structure, deadwood-associated biodiversity and wood decay. Although many of the results of this thesis are specific to these black spruce forest ecosystems, I believe in addition to improving our understanding of this ecosystem, I have created a framework for future study of deadwood-related ecosystem components in other forested ecosystems. This framework consisted of: 1) the study of inputs and decay of deadwood across a 2000-year chronosequence; 2) describing the corresponding changes in community structure of deadwood-associated organisms across the chronosequence; 3) evaluating the effect of forest management on deadwood, associated biodiversity and wood decay; 4) establishing links between changes in stand structure, deadwood, associated biodiversity and wood decay, and 5) demonstrating how deadwood-associated biodiversity can be used to evaluate an ecosystem management hypothesis.

The first part of this conclusions returns to the main conclusions of the thesis and discusses their implications in a broader context. Following conclusions specific to this thesis, I will discuss some general issues related to the study of deadwood, associated biodiversity and wood decay.

Principal results and conclusions of the thesis

Fast transition from dense to open forests

Stand development in these black spruce forests has already been well described by previous studies (Harper et al. 2005, Lecomte et al. 2006a). The data I collected on stand development along the chronosequence highlighted that the transition from dense even-aged forests to open forests occurs relatively quickly over a 50 to 75 year time period beginning about 90 years after a high intensity fire. This transition results in large amount of deadwood being created during this period, but the highest biomass of deadwood is not observed until well after this transition at about 250 years after fire. These two trends of accumulation and loss of live and dead woody biomass are critical to understanding many of the results presented in this thesis and the reduction in live biomass is the basis of the ecosystem management strategy tested in the third.

I called this period a transition because I feel it divides two very different times in stand development. Prior to the transition, trees are growing relatively uninhibited by soil conditions or competition, during the transition the forest thins due to competition, and following the transition a new equilibrium is reached of constant declining tree productivity due to poor and worsening soil conditions (Simard et al. 2007). Following this transition, old-growth forests are characterized by slow wood decomposition, accumulation of soil organic layer and accumulation of buried deadwood. This stage in forest development characterized by a reduction in productivity in the prolonged absence of fire has been demonstrated globally and is termed 'ecosystem retrogression' (e.g. Walker et al. 2001, Wardle et al. 2004, Vitousek 2006).

Previous studies of stand development have not used segmented regression to describe the transition and as a result describe a more gradual transition from dense even-aged forest to paludified forest (see Lecomte et al. 2006a, Simard et al. 2007), while others describing general characteristics of stand development have (Harper et al. 2005). Although I believe that the transition is not as abrupt as described by the segmented regression models (see Figure 1.3A, Figure 3.2A), there is strong statistical support that the rate of change is much greater during this transition than in old-growth paludified forests. In a similar method of why I did not include stands gaining biomass in this study, because they are developing under different conditions, it did not seem accurate to fit stands undergoing stem-exclusion during this transition with the same regression models of older paludified stands.

Open old-growth forests support a unique community of deadwood-associated species

I demonstrated that the assemblages of deadwood-associated beetles and fungi were different before the transition from dense to open forests. This was the largest difference observed across unharvested forests. Although these changes appear to be gradual over the course of the transition, I found the largest difference in composition and relative abundance in stands with more than 29 m^2/ha compared to those with less than 29 m^2/ha. Overall, several small fungivorous beetles accounted for the largest explained variance for this transition. However, when the analysis was separated into functional groups, the xylophagous beetles, here considered all beetles which feed or bore into the bark or wood of the tree, had the strongest response to the transition, followed by predators. This suggests that within the fungivores, although a few species demonstrated the strongest overall responses to this transition, many did not; whereas, there was a more consistent trend of all species within the xylophagous and predators beetles to this transition to old-growth forests.

I feel it is important to acknowledge that I did not sample early post-fire stands. Based on previous studies on post-fire community dynamics (Jacobs 2004, Saint-Germain et al. 2004, Paquin 2008), I predict that these assemblages would be even more different than the assemblages I sampled in mature dense forest or open old-growth forests. Early post-fire stands typically have a unique assemblage of insects and fungi, specifically adapated to these environments and to open habitats in general. I chose to exclude these stands from my study as it has been established that these communities are relatively ephemeral and are highly related to the intensity and severity of the disturbance itself.

Highest rates of wood decay are during the transition to open forests

I used two complementary approaches to describe the effects of stand age on wood decomposition. Using a time-series analysis on logs that varied in time since death, I found that decay rates were highest in young stands and then slowed as the soil organic layer thickens and paludification proceeds. Stand-level modelling of the inputs and decay of deadwood, found a similar trend, but predicted even higher rates of decomposition early in succession and relatively stable slower rates of decomposition later in stand development. The slow rates of decomposition later in succession can be partly explained by high soil moisture leading to high moisture content in the wood. The extremely high rates of decomposition predicted by the stand-level models are somewhat more interesting. My stand-level models predicted a decay constant as high as k=0.18, or that the deadwood is loosing 18% of its density (or mass, assuming a constant volume) per year. Previous studies on spruce and black spruce have reported decay constants closer to k=0.03 (black spruce, Boulanger et al. 2011) to k=0.038 (white spruce, Brais et al. 2006). This period in stand development is relatively unique during stand development; large masses of deadwood are being created through stem-exculsion annually. These large annual inputs of deadwood biomass could result in shorter dispersal distance for decomposer organisms and larger population sizes than under typical circumstances, resulting in high decomposition rates. It is clear that this deadwood is being created; however, in our study stands we did not observe high levels of deadwood until much later when wood decomposition slows. This period also coincides with the highest rates of increase of the soil organic layer and a transition from a feathermoss- to *Sphagnum*-

dominated moss community. Although a lot of deadwood becomes entombed in this thickening organic layer, it likely represents only a small proportion of the deadwood created annually. Furthermore, our stand-level modelling suggests that because the amount of wood that is buried represents a small proportion of the deadwood produced annually, the rate of burial has little effect on the rate of wood decomposition. Ultimately these large masses of deadwood must either be consumed by decay organisms or buried beneath the thickening soil organic layer.

There is a delay before the onset of decomposition

The time-series approach I used to study specific factors influencing decomposition allowed me to accurately control for important factors, such as how long the tree remained standing before coming in contact with the ground, how the tree died, and when the tree died. A tree that remains standing for several years after death has different decay trajectories than those that immediately come in contact with the forest floor. For example I was able to demonstrate a delay of 6-7 years before the onset of decomposition in logs that immediately come into contact with the ground after death, which likely does not occur in deadwood that remain standing for several years before falling.

The hypothesis of a lag before the onset of decomposition has been speculated at least since the work of Grier (1978) and further described by Harmon et al. (1986). The reason for this lag is thought to be related to the time required for decomposer organisms to colonize the newly created piece of deadwood (Grier 1978) and the high initial moisture content of the wood (Dilworth 1974). Both of these factors become mute when a tree remains standing. When a tree dies and remains standing, much of this initial moisture is lost and there is ample time for the colonization of decomposers, yet little time-dependant decomposition is detected during this period (Angers et al. 2012). Therefore, snags (standing deadwood) are essentially preconditioned for decay while they remain standing, negating the lag observed for deadwood that falls directly to the forest floor.

Larger logs decay more slowly than smaller logs

Using the time-series approach to the study of wood decay I was able to quantify differences in decay rates between larger and smaller logs. Diameter effects have been frequently hypothesized due to the low surface-to-volume ratio which effectively prolongs the colonization process by decomposer organisms and reduces sapwood-to-heartwood ratios (Foster and Lang 1982, Harmon et al. 1986, Rayner and Boddy 1998). The effect of diameter on decay rates is not always found in other studies (e.g. Bond-Lamberty et al. 2002, Grove et al. 2009), and the studies that do find diameter effects are often on relatively small-diameter pieces (e.g. Abbott and Crossley 1982, Erickson et al. 1985) However, as more studies are being conducted on deadwood, more evidence is being amassed that diameter effects on decay rates do exist (Tarasov 1999, Chambers et al. 2000, Hérault et al. 2010). The reasons I was able to detect diameter effects in this study is a result of the accurate dating of deadwood pieces and the knowledge of how the tree died and that it came into contact with the ground directly after tree death.

Like conclusions regarding when a lag time is present, diameter effects could also only be present when trees come into contact with the ground quickly after tree death. Trees that have adequate time standing after tree death will have adequate time for colonization by decomposer organisms regardless of diameter. Once a snag falls, moisture levels of the forest floor and further colonization by decomposer organisms results in the negative exponential decay reported in numerous studies (e.g. Olson 1963, Boulanger et al. 2011).

Wood-based carbon remains relatively constant in old-growth forests

The combination of reduced wood decay rates and large masses of accumulated buried deadwood results in a relatively constant mass of wood-based carbon in old-growth forests (see Figure 1.8). This below-ground pool of woody carbon becomes important when developing forest carbon models (Kurz et al. 2009) and when evaluating goals of forest management plans. In young forests, a large proportion of the wood-based carbon is in the living trees, but with time this proportion shifts first to surface deadwood and ultimately to buried deadwood. Therefore, the trade-off favours carbon storage as stands age as the ratio between stored carbon and live woody biomass increases.

Forest harvesting drastically changes deadwood-associated biodiversity

I found that both partial cuts and clearcuts resulted in significant changes to the composition and relative abundance of deadwood-associated beetles and fungi. Furthermore, I detected little advantage of partial cuts over clearcuts for maintaining species compositions and relative abundances similar to predisturbance conditions or within the range of natural variability established across the chronosequence.

These new post-harvest assemblages consist of: 1) generalist species relatively unaffected by the change in forest structure; 2) open habitat species colonizing and/or flourishing in these new habitats, and 3) species adapted to close canopy forests which and disappearing or struggling in these new habitats.

Partial cuts preserve wood decay rates similar to natural forests

I demonstrated that the decay rates in partial cuts were more similar to control stands representing predisturbance conditions than to operationally harvested clearcuts. I attributed high rates of wood decay in clearcuts to warmer and drier conditions resulting in higher activity levels by wood feeding beetles and higher growth rates by wood decay fungi. Evidence of this is based on relatively high partial correlations between wood feeding beetles and wood decay and the accumulation of significantly more fungal-degree days in clearcuts compared to partial cuts or uncut controls. There is also strong support in the literature that wood decay slows as stands become wetter. These observations agree to slower decomposition rates observed in older paludified stands along the chronosequence.

Deadwood-associated communities are good indicators for evaluating ecosystem management strategies

One of the main goals of this thesis was to gain an understanding of deadwood-associated biodiversity in black spruce forests and to be able to effectively test an ecosystem management hypothesis using deadwood biodiversity as an indicator of success. I believe this thesis demonstrated how these communities are sensitive to environmental change and can be used to test forest management hypotheses. I observed clear changes in community similarity under both: 1) natural stand dynamics and 2) in response to a partial harvesting technique attempting to emulate natural stand dynamics. These responses were not analogous. Instead, the species assemblages after partial harvesting were much more similar to assemblages after operation clearcutting than any assemblage observed during natural stand dynamics. This was true for both the specious beetle community as well as changes in proportional presence of six polypore fungal species on deadwood. I further demonstrated that the beetle communities in partial cut and clearcut harvesting were highly similar to each other, indicating a lack of community diversity, or a simplification of the overall community diversity. Similar to the concept of a decrease in beta diversity (Whittaker 1960).

Deadwood-associated biodiversity also has direct links to wood decomposition. I outlined several causal models in the second chapter of the effects of changes in stand structure on fungal and beetle biodiversity and subsequent effects on wood decomposition. Wood decomposition is an important forest process that is involved in nutrient cycling and the removal of deadwood habitat. Ultimately these groups make good indicators for testing these types of hypotheses because they are both sensitive to environmental change and consistent in their responses.

Research Perspectives

Deadwood-associated versus saproxylic organisms

In this thesis I chose use the term 'deadwood-associated' rather than saproxylic to describe the group of organisms I focus on for the study. In the past I have used the term 'saproxylic' to refer to virtually the same group of organisms I study in this thesis. Speight (1989) first define the term of saproxylic as being "dependent, during some part of their life cycle, upon the dead or dying wood of moribund or dead trees (standing or fallen), or upon wood-inhabiting fungi or upon the presence of other saproxylics". When I have used saproxylic in the past there are many species whose *dependency* on deadwood is hard to prove. For example, many insects that feed on other saproxylic beetles also feed on non-saproxylic insects as well, so it is hard to know how strict this dependency is. The same can be said for many fungivores that will feed on wood-decay fungi, but will also feed on fungi living in the forest floor.

I prefer to use the more general term "deadwood-associated". This reduces the emphasis on dependence and includes any species that is somehow linked to deadwood. The one thing that all of the beetles have in common in this study, is that they all were caught by my trap made to resemble a snag. Any insect that randomly falls in will only subtract from the sensitivity of the group as a whole by adding noise to the data. Alternatively, selecting certain species that are strictly dependant on deadwood increases the chance of adding bias to the dataset. Therefore, the conservative approach is to leave the majority of species in the analysis and utilizing robust analyses to detect underlying trends.

Deadwood versus coarse woody debris (CWD) versus coarse woody material (CWM).

This is another intentional use of words to remove bias in the language. Coarse woody debris was first introduced to refer to pieces of deadwood above a certain diameter (typically 5 cm). Pieces below this were referred to as fine woody debris. As it became more evident that these large pieces of deadwood were important to a large component of forest biodiversity, they were upgraded to coarse woody material. I prefer to use the term deadwood. I feel that deadwood is the most broad and encompassing as well as the most descriptive. It is all wood that is dead. This term is often further specified as standing deadwood (snags) fallen deadwood (logs), leaning deadwood (snogs) or buried deadwood.

The identification dilemma

Deadwood-associated organisms are notoriously difficult to identify, especially in North America where there wasn't a strong culture of naturalists and taxonimists in comparison to Europe. However, I do not feel that this is still a large obstacle to studying this group. Studies on deadwood-associated beetles are becoming more common and there are more studies with impressively large sample sizes (eg. Bouget et al. (2014), 149 419 individuals, 738 species). However, there are still species being discovered. In my thesis I have found at least nine new beetle species to science. Two of them have already been described (Klimaszewski et al. 2013).

The study of deadwood-associated fungi is harder. In this thesis I sampled just the fruiting bodies of a small number of fungi. This was sampling only the presence of this species. I knew that if the fruiting body was present that the species must have been in the piece of wood. I did not know what proportion of the wood was occupied by the species compared to others or the other species present in the wood that were not presently fruiting. However, I believe we added valuable information to this thesis by documenting the relative presence of these species across our treatments. We were able to show generalized trends in both deadwood-associated beetle and fungal communities and start to make linkages between changes in structure, beetle and fungal species compositions and wood decay.

It is also becoming common to use microbiological approaches for the study of wood-inhabiting fungi. A recent study by Kebli et al. (2012) that used a molecular fingerprinting technique found 33 operational taxonomic units (OTUs), from 102 logs. However, these techniques are also criticized for not being able to fully utilize the knowledge that already exists for certain species when they can only be separated by OTUs and not know species.

Creating better linkages between deadwood, associated biodiversity and wood decay

In chapter 2, I created causal models to create linkages between stand structure, associated biodiversity and wood decay. To better establish how diversity can alter wood decomposition there is need for a more experimental approach. During the course of the research for this thesis, I attempted numerous laboratory experiments (see below); however, the elements of this ecosystem do not lend themselves well to laboratory analyses.

This ecosystem of deadwood, associated biodiversity and wood decay exists on a very broad scale. In the study of this ecosystem *in situ* we work with stands of forests and communities of hundreds of beetles. Even the basic habitat requirements for many deadwood-associated organisms are large pieces of deadwood. In attempts to miniaturize deadwood to just its elements, it loses many of it fundamental properties. The rates at which fungi decomposes sawdust (Swift 1977) are not the same as the rates at which fungi decompose intact wood. In my experimental approach, I measured mass loss in small-diameter (2 cm – 5 cm) logs to emulate what might be happening in larger logs. These were sections from small-diameters trees with the bark intact, dried to constant mass, weighed and then rehydrated to similar wood moisture levels to what is found prior to death. These samples, I believe were the most representative of larger logs found in nature. They had similar proportions of bark, xylem and phloem and theoretically should respond to conditions similar to larger diameter pieces.

Next in this ecosystem are deadwood-associated organisms, principally beetles and fungi. I also attempted to live capture, identify and experiment with several species of beetles. One experiment was to allow them to run across a Petri dish and culturing the micro-organisms they were harbouring. I found that there were a large number of microorganisms travelling on these beetles, both fungal and bacterial. I also found it difficult to capture a large number of live individuals for other replicated experimentation. I was able to duplicate the damage caused by important groups of beetles to the miniature logs described above. There are two broad categories of wood boring insects: 1) bark beetles, which bore into the phloem layer just below the bark, and 2) true wood-boring beetles that bore into the heartwood of the tree. To mimic this activity, I used a small diameter drill bit and bored holes either perpendicular or parallel to the miniature logs.

Deadwood-associated fungi were somewhat easier than beetles to culture in the lab. I field sampled all of the species represented by the fruiting bodies surveyed in this thesis, and was able to culture them in the lab. I then introduced these fungi to the miniature logs described above with the goal of measuring mass loss of the wood, which represents wood decomposition. This, I believe, was the most difficult part of this experimental process. The rates of colonization that I was able to obtain were low for all species. This made the data hard to interpret because of so many null results and these absent values made rigorous comparisons hard. Furthermore, wood decay occurs so slowly that I was unable to conduct multiple attempts of colonization during the course of my program.

There are also possibilities for experimental manipulations in the field. This was also undertaken during the course of my research. I cut fresh deadwood, and found deadwood cut during previous research projects and applied three different treatments. In the first trial with fresh deadwood, I applied two different mesh sizes in the attempt to alter decomposition rates by excluding insects of 2 different size classes. However, as was found to be one of the main results of this thesis, there is a lag of 6-7 years in freshly created deadwood before the onset of decomposition. Therefore, even after two years of 'decay' in the forest, I was unable to detect any consistent signs of decomposition. I conducted the same experiment in older logs (5-6 years after tree death). Although, I was able to detect more consistent signs of decomposition in these older logs, decay rates were variable and there were no significant effects of excluding insects of specific size classes. As with laboratory experimental approaches, I feel that additional experimental approaches in the field would greatly enhance our understanding of the relationships between deadwood and deadwood-associated biodiversity.

The study of deadwood-associated organisms

The study of deadwood-associated organisms is both fascinating and necessary. These organisms consume their own habitat, either directly in the case of wood decay fungi and wood feeding beetles, or indirectly like the fungivores who feed on these wood decay fungi. This ecosystem is also based on a resource that is highly threatened by modern forest management practices. It has been clear for many years that one of the main differences between forest harvesting and virtually any natural disturbance is the amount of deadwood remaining. This makes the conservation of deadwood-associated organisms particularly challenging.

I believe that biodiversity is important to conserve for the sake of biodiversity itself. Beyond its intrinsic value, biodiversity is also key to maintaining resilient ecosystems with the ability to evolve under current and future pressures. However, as deadwood-associated researchers, I feel that it is important we start developing other reasons why maintaining diverse communities is important to forest ecosystems as a whole. It still remains to be definitively demonstrated that the cycling of nutrients through deadwood and associated biodiversity is an important aspect to nutrient cycling. There is presently not enough evidence to be able to certify that nutrient-poor, but abundant, deadwood is important to regenerating forests. The relatively nutrient-poor black spruce forests studied in this thesis probably have the best chance at demonstrating that deadwood is important to part of forest nutrient cycles. In these black spruce ecosystems there is a large amount of deadwood that enters the ecosystem right before it transitions to a retrogressive state. This leaves the question: will forest retrogression be even more dramatic under ecosystem-based management strategies, where most of the trees are removed before they have the chance to die, harbour biodiversity and ultimately return to the soil to nurture future generations of trees?

In this thesis, I was able to very clearly show that changing forest structure has large effects on community composition and relative abundances in the black spruce ecosystem of north-western Quebec. I was also able to demonstrate corresponding changes to decay rates in response to natural stand succession and to clearcut forestry practices. I made linkages between changing community composition and changing decay rates using causal models. Ultimately, understanding growth rates in response to changing stand structure, and not just changes in composition and relative abundance, will help us to solidify linkages between biodiversity and ecosystem function. I clearly showed that an increase in fungal degree-days in clearcut and not partial cuts resulted in higher decay rates in clearcuts versus partial cuts. I am sure that these degree-day measurements extend to the activity of the entire deadwood-associated community and that ultimately it is these activity levels combined with community composition that will be the best predictor of wood decay.

Finally, I return to the question: what proportion of natural diversity is required to maintain proper ecosystem functioning? I do not believe that there is an easy answer to this question. I just hope that we can gain this knowledge before we lose such a large proportion of biodiversity that we cannot return to proper ecosystem functioning.

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