THE EFFECTS OF ALTERNATIVE HARVESTING PRACTICES ON SAPROXYLIC BEETLES IN EASTERN MIXEDWOOD BOREAL FOREST OF QUEBEC

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PREFACE

This thesis contains four chapters.

Chapter 1

This chapter is a general introduction and literature review.

Chapter 2

This chapter is a manuscript in preparation for submission to *Biological Conservation.*

Webb, A., Drapeau, P., Buddle, C.M. The effect of remnant boreal forest habitats on saproxylic beetle assemblages in landscapes subjected to harvesting.

Chapter 3

This chapter is a manuscript in preparation for submission to *Forest Ecology and Management.*

Webb, A., Buddle, C.M., Drapeau, P. The effect of partial-cut harvesting on saproxylic beetle assemblages.

Chapter 4

This chapter is a general conclusion.

CONTRIBUTION OF AUTHORS

The three authors designed the first study (Chapter 2) and A. Webb planned the research outlined in Chapter 3. A. Webb collected the data, identified the specimens, performed analyses and presented the results. C.M. Buddle and P. Drapeau supervised the research, provided financial support and edited all chapters in this thesis.

ABSTRACT

I examined saproxylic beetle responses in two silvicultural systems of the eastern mixedwood boreal forest of Quebec. I first investigated habitat-use and aspen-host use of saproxylic and bark and wood-boring beetles in remnant forest patches (cut-bock separators and small patches) left after harvest, theorized to resemble natural post-fire residual trees and snags. A second study focused on effects of partial cutting, a method that may serve to imitate natural succession dynamics.

Remnant forest patches had the highest saproxylic and bark and wood-boring beetle species richness and relative abundance. Although non-significant, higher larval densities were also collected from remnant forest patches. In the second study, partial cut patches had an intermediate saproxylic beetle assemblage compared to uncut forest and clearcuts.

This research has brought new information on the effects of alternative harvesting practices on saproxylic beetles, supporting the hypothesis that biodiversity is best preserved based on forest management that is diversified and based on natural disturbance dynamics.

RÉSUMÉ

J'ai examiné la réponse des Coléoptères saproxyliques à deux systèmes de sylviculture utilisés en forêt boréale mixte d'Abitibi, Québec. En premier lieu, j'ai étudié l'utilisation de peuplements et de chicots de peuplier faux-tremble par les Coléoptères saproxyliques dans les habitats résiduels laissés après coupe à blanc (séparateurs secs et îlots de rétention). Une deuxième étude s'est concentrée sur les effets de la coupe partielle. Dans une optique d'aménagement émulant les perturbations naturelles, les séparateurs et îlots correspondent aux arbres verts laissés à la suite d'un feu de forêt, alors que les peuplements à rétention variable correspondent à different stades successionels.

Une richesse spécifique et une abondance d'insectes plus élevées ont été observés dans les habitats résiduels. Des densités larvaires plus élevées, bien que non-significatives, ont également été collectées dans ces habitats. Dans la deuxième étude, les coupes partielles ont montré des assemblages saproxyliques intermédiaires aux peuplements témoins et aux coupes à blanc.

Cette recherche apporte de nouvelles informations sur les effets des pratiques de coupes alternatives sur les Coléoptères saproxyliques, soutenant l'hypothèse que la biodiversité est mieux préservée quand la gestion de forêt est diversifiée et basée sur la dynamique de perturbation naturelle.

CHAPTER 1 : GENERAL INTRODUCTION AND LITERATURE REVIEW

Natural disturbances and dead wood in the boreal forest

The boreal forest is a circumpolar band covering one third of the world's forested ecosystems and 30% of Canada's mainland (Danks and Foottit, 1989). Insects comprise much of the biodiversity in the boreal forest, home to approximately 22 000 species and up to two thirds of Canada's insects (Danks and Foottit, 1989). The boreal forest is largely coniferous but the southern mixedwood portion has a major deciduous component dominated by trembling aspen (*Populus tremuloides* Michx.) (Rowe and Scoter, 1973; Danks and Foottit, 1989; Hogg et al., 2002).

In the south-eastern boreal forest, disturbance and succession dynamics have been extensively studied (e.g., Dansereau and Bergeron, 1993; Morin et al., 1993; Bergeron et al., 1998; Bergeron and Leduc, 1998; Bergeron, 2000; Bergeron et al., 2001; Harper et al., 2002; Lefort et al., 2003). Fire is the disturbance largely responsible for landscape patterns and forest composition in boreal coniferous stands (Bergeron et al., 2001). After stand reinitiation by fire, a first cohort of pioneer species will dominate for approximately 100 years, consisting of trembling aspen, balsam poplar (*Populus balsamifera* L.), white birch (*Betula papyrifera* Marshall) and jack pine (*Pinus banksiana* Lamb) (Harvey et al., 2002). Competition for light, water and nutrients causes the stand to self-thin, bringing in a second cohort, increasingly composed of mixedwoods (Kneeshaw and Bergeron, 1998; Sheppard et al., 2001; Harvey et al., 2002; Frey et al., 2004). However, factors most associated with aspen stand dieback are insect defoliation, drought, and freeze-thaw events (Hogg et al., 2002). The forest tent caterpillar (*Malacosoma disstria* Hübner) is the primary defoliator of trembling aspen (Ives and Wong 1988 cited in Hogg et al., 2002), increasing susceptibility to bark and wood-boring insects, pathogens and windthrow (Frey et al., 2004). After approximately 150 years, all first-cohort trees have suffered mortality and a third cohort of spruce, cedar and fir dominate (Harvey et al., 2002).

Natural disturbance is an important driving force for boreal forest ecosystem dynamics, which creates patches of dead and dying wood (Bergeron and Harvey, 1997; Harmon et al., 1986; Brassard and Chen, 2006) Dead wood is a fundamental forest resource which provides habitat for diverse organisms and plays a vital role in the regulation of nutrient and carbon cycling, erosion, drainage and geomorphic processes (Harmon et al., 1986; Speight, 1989; Samuelsson, 1994). Coarse woody debris (CWD) is a host for a large diversity of fungus, lichen, moss and plants. Dead wood is also vital to many vertebrates and invertebrates for food, cover, hibernation and temperature regulation (Harmon et al., 1986). Snags are important as foraging and nesting sites for cavity nesting birds (Harmon, 1986; Gibbs et al., 1993; Drapeau et al., 2002; 2003).

Fires create a large abundance of dead wood of high nutritional value, otherwise scarce and ephemeral, creating ideal habitat for many species dependant on dead wood (Jakubas et al., 1994; Pedlar et al., 2002). Post-fire live residual trees, snags and logs often remain while the stand re-establishes itself and contribute the structure of the stand, creating a wide ranging size-distribution of CWD and large diameter snags (Rowe and Scotter, 1973; Eberhart and Woodard, 1987; Lee et al., 1997; Brassard and Chen, 2006). At stand initiation, low competition between stems results in low CWD inputs (Brassard and Chen, 2006). Early to intermediate-aged aspen stands undergo intense competition or self-thinning, responsible for many of the small diameter snags and CWD (Lee et al., 1997; Brassard and Chen, 2006). In intermediate-late aged forest, the last of the pioneer species die and CWD reaches its maximum input during transition from an even-aged stand to an uneven aged stand (Brassard and Chen, 2006) In mature aspen stands, the CWD supply diminishes but senescence of old trees provides large diameter dead wood (Lee et al., 1997). Gap dynamics, such as wind, ice, snow, disease and insects, become more prevalent in old stands as overmature trees are more susceptible. Pedlar et al. (2002) found significantly more CWD in mixed stands than aspen stands, which had more CWD than spruce stands.

Clearcuts are the main stand-replacing event substituting fire in commercial forests, with short harvest rotations eliminating old growth stages (Siitonen, 2001). Clearcutting has been hypothesized to mimic stand reinitiation by fire and recruits first-cohort species (Bergeron et al., 2002; Harvey et al., 2002). Considerable differences in dead wood abundance, type and quality exist between clearcut and burned sites (Pedlar et al., 2002). Burned sites are primarily composed of snags in early decay stages while clearcut sites have predominantly small pieces of logging slash, while most of the wood biomass is removed (Pedlar et al., 2002; Brassard and Chen, 2006). CWD volume, snag abundance and basal area, volume of large snags and logs is significantly greater in young natural stands than clearcuts (Pedlar et al., 2002; Brassard and Chen, 2006).

Dead wood and saproxylic beetles

From early stages of mortality to complete decomposition, logs, stumps and standing dead wood of varying diameters serve as substrates for a multitude of autotrophic and heterotrophic saproxylic species (Harmon et al., 1986; Martikainen et al., 1998; Grove, 2002). Saproxylic organisms are dependant on dead or dying wood during some part of their lifecycle (Speight, 1989). Saproxylic organisms comprise a wide range of feeding groups such as bark and wood-borers, parasites and parasitoids, predators, detritivores and fungivores (Dajoz, 2000; Speight, 1989). Saproxylic organisms are crucial to ecosystem function in their breakdown of woody debris and as a food source for higher trophic groups, particularly birds (Harmon et al., 1896).

Coleoptera are a dominant order of saproxylic insects with entire families dependant on dead wood, generally in their dominant life-stage as larvae (Dajoz, 2000; Hammond, 1997; Hammond et al., 2001). The adults are short-lived and mainly play a dispersal and reproductive role (Haack and Slansky, 1987; Hanks, 1999; Saint-Germain et al., 2006). Major wood-boring taxa include Curculionidae, Buprestidae and Cerambycidae, which precondition the substrate for a succession of other species (Harmon et al., 1986; Martikainen et al., 1998;

Dajoz, 2000; Hammond et al., 2001). Wood-boring beetles are typically the first to colonize, feed and breed in recently dead or weakened trees (Harmon et al., 1986; Hammond, 1997; Hammond et al., 2001). Wood-boring beetles are mediators and vectors of humifying fungi and bacteria, and fragment dead wood by tunneling and feeding (Speight, 1989; Grove, 2002). They are attracted to dead trees through host volatiles such as ethanol, present in all decomposing wood and terpenes, present in coniferous species (Hanula, 1993; Allison et al., 2004).

Forest management and saproxylic beetles

Saproxylic insects have been intensely studied in northern Europe, in the last 10-20 years, where centuries of intense forest management has created a significant drop in species diversity (Speight, 1989; Siitonen and Martikainen, 1994; Økland et al., 1996; Kaila et al., 1997; Martikainen, 2001; Siitonen, 2001; Grove, 2002; Similä et al., 2000, Sverdrup-Thygeson and Ims, 2002; Jonsell and Weslien, 2003; Martikainen and Kaila, 2004; Lindhe et al., 2005). Short harvest rotations, clearcuts, salvage logging, fire-wood harvesting and fire-suppression have reduced the amount of decaying wood and the spatial distribution of saproxylic habitats, impoverishing the associated fauna and predators (Økland et al., 1996; Kaila et al., 1997; Grove, 2002; Sverdrup-Thygeson and Ims, 2002). Twenty to twenty-five percent of all Fennoscandian boreal forest species are dependant on dead wood, a resource which has suffered a 92-98% reduction in northern Europe (Siitonen, 2001). Four hundred and seventy four saproxylic beetles appear on the Swedish Red List (Gärdenfors, 2000 in Lindhe et al., 2005). Moreover, the aspen-dependant fauna in boreal Fennoscandia contributes disproportionately to threatened species lists (Siitonen and Martikainen, 1994; Martikainen, 2001; Sverdrup-Thyrgeson and Ims, 2002). The deciduous aspen (*P. tremula* L.) component of Europe's boreal forest has been suppressed or eliminated due to its low commercial value compared to conifers. This has disrupted continuity of substrates for aspen-feeding saproxylic organisms (Siitonen and Martikainen ,1994). In North American boreal forests, trembling aspen (*P. tremuloides*) remains very abundant and is considered the most ecologically and economically important deciduous boreal tree species (Hogg et al., 2002). Unexploited until recently, Canada's aspen stands now contribute to some of the largest pulp mills in the world (Pratt and Urquhart, 1994; Hammond et al., 2004).

The insect fauna in burned and clearcut sites have been found to differ with many species being specific to either habitat type (Ahnlund and Lindhe, 1992; Niemelä, 1997). In northern Europe, major saproxylic beetle community differences have been found between closed forest and clearcuts (Kaila et al., 1997; Sverdrup-Thygeson and Ims, 2002; Gibb et al., 2006). Clearcut areas that had remnant trees and snags contained the most threatened saproxylic beetles, in comparison with old growth stands (Kaila et al., 1997; Martikainen, 2001; Sverdrup-Thygeson and Ims, 2002). Beetles living on aspen and birch generally prefer large, dead trees in sunny open areas (Siitonen and Martikainen, 1994; Martikainen, 2001). Threatened and red-listed species have also been found predominantly associated with sun-exposed snags (Sverdrup-Thygeson and Ims, 2002; Lindhe et al., 2005). Sun exposure of dead aspen is a major community-structuring factor for aspen-feeding saproxylic beetles (Kaila et al., 1997; Martikainen, 2001; Thygeson and Ims, 2002; Lindhe et al., 2005). Jonsell et al. (1998) estimated that only 9% of Swedish red-listed saproxylic insects (feeding on all hosts) prefer shaded conditions of old forests.

Gap disturbances may also increase saproxylic beetle diversity. In a South Carolina hardwood forest, higher abundance and species richness of wood-boring beetles occurred in recent small clearcut gaps and edges than in adjacent forest due to abundance of slash debris (Ulyshen et al., 2004). However, the coarse woody debris (CWD) supply was short-lived since older gaps had significantly lower species abundance and richness than new gaps or adjacent forest (Ulyshen et al., 2004).

Further increasing habitat for saproxylic insects are forest-clearcut ecotone which may harbour an increased abundance of dead wood due to susceptibility to windthrow and wind damage in addition to mechanical damage from harvesting and microclimate change (Esseen, 1994; Peltonen, 1999; Bouget and Deulli, 2004). Peltonen (1999) recorded over 80% of dead trees within 15 m from the forest-clearcut border in southern Finland. The edge represents an ecotone where increased habitat heterogeneity influences saproxylic species diversity (Peltonen, 1999).

Remnant forest patches in clearcut areas and saproxylic beetles

Basing harvesting practices on knowledge of natural disturbance dynamics is theorized to maintain ecological function, sustainability and biodiversity (Hunter, 1993; Gauthier et al., 1996; Bergeron and Harvey, 1997; Lähde et al., 1999; Harvey et al, 2002; Bergeron et al., 2002). Alternative harvesting practices diversify forest management but their effects have yet to be adequately tested on forest species, especially those not related to timber aspects. Leaving remnant forest patches in harvested landscapes is a management strategy that may help preserve a greater range of forest processes and diversity than clearcutting alone. A large-scale study in coniferous stands in Finland found different levels of 'green tree retention' in clearcuts and uncut stands promote species richness of red-listed and threatened saproxylic beetles, although species richness was generally greater in burned sites than harvested sites.

Forest composition, age-structure, stand dynamics and characteristics of the forest mosaic should be preserved under optimal harvesting and management practices (Dansereau and Bergeron, 1993; Gauthier et al., 1996). If management fails to mimic natural disturbance patterns, interference with dead wood dynamics can result in extinction of associated species (Grove, 2002). Natural disturbances such as fire and insect outbreaks often leave a patchy remnant vegetation structure due to either variation in severity, natural fire breaks such as humid lowland forests or the low flammability of certain trees such as aspen (Lee et al., 1997, Brassard and Chen, 2006). In even-aged managed forests, small remnant patches of tree species that are not needed or are inaccessible with machinery are often left after harvest. These remnant forest patches may act as refugia for species not able to survive in clearcuts allowing population persistence in these harvested landscapes and increasing population exchanges between source forest areas and remnant forest patches (Saunders et al., 1991; Beier and Noss, 1998). However, some species may survive fragmentation by using the matrix surrounding remnant forest patches increasing in abundance and altering the composition of these patches (Halme and Niemelä, 1993). After fragmentation, the shape, size and degree of isolation of individual remnant patches and their spatial arrangement within managed landscapes influence patterns of species richness and composition across the landscape (Saunders et al., 1991; Schoereder et al., 2004; Ribas et al., 2005). A study in Germany found saproxylic beetle richness to be significantly higher in less isolated forests where the distance to next forest was less than 400m (Grohmann et al., 2004). However, small remnant forest patches may temporarily increase in species richness due to a strong influx of species from the matrix (Niemelä, 1997). In an agro-ecosystem, Halme and Niemelä (1993) found higher ground beetle (Carabidae) species richness in small (0.5-3 ha) habitat patches compared to large (10-20 ha) and medium (4-8 ha) patches. High species turnover in small patches is due to disappearance of closed canopy specialists caused by invading generalist species from the matrix (Niemelä, 1997).

Habitat corridors may alleviate negative impacts of fragmentation by linking small patches to larger areas of continuous habitat creating a "rescue effect" maintaining viable metapopulations (Hanski and Gilpin, 1991; Saunders et al., 1991). A corridor is defined as a linear habitat in a dissimilar matrix that connects two or more patches of larger habitat (Beier and Noss, 1998). Corridors are an important component of landscape connectivity if they enhance the movement of an animal between patches (Tischendorf and Fahrig, 2000). The extent to which corridors enhance connectivity depends on the nature of the matrix and corridors and the responses of the organisms of study (Beier and Noss, 1998). Since 1996, in the southern mixedwood boreal forest of Quebec, neighboring clearcuts (maximum 150 ha) must be separated by cut-block separators at least 60 m wide (NFDP, 2003; MRNFP, 2005). In harvested areas, strips of forest 20 m wide must be conserved in riparian areas, on each bank

(NFDP, 2003; MRNFP, 2005). Cut-block separators can thus potentially function as corridors, channelling beetle's movements to connected patches of forest but they could also function as retained habitats for forest-dependent beetles within the logged mosaic.

Little information exists on the use of boreal forest corridors for organisms other than birds and mammals. In Finland, moths have been shown to successfully use boreal corridors, which direct their movements and associated species, for dispersal and reproduction (Mönkkönen and Mutanen, 2003). In Australia, the greatest species richness of carabid, scarabid and tenebrionid beetles occurred in remnant mallee linear habitats, in landscapes fragmented by grazing (Driscoll and Weir, 2005). Fruit sets of hollies (*Ilex vomitoria* Ait.), pollinated by flies, butterflies, wasps and bees increased by 69% in along connected corridors compared to unconnected corridors. Holly seeds, dispersed by many birds, were twice as likely to be found in connected patches as unconnected patches (Tewksbury et al., 2002). In a release and re-capture experiment, house flies (*Musca domestica* Linnaeus*)* were captured more often in connected rather than unconnected patches (Fried et al., 2005). It was demonstrated that these corridors were intercepting dispersing house flies from the matrix but also functioning as movement conduits. Many flying insects may demonstrate edge-following behaviour (Fried et al., 2005). Corridors have also been shown to enhance microarthropod richness, abundance and biomass in fragmented moss ecosystems compared to unconnected areas (Gonzalez and Chaneton, 2002). In Tasmania, plantation forest (in this study *Eucalyptus globulus* Labill. and *Pinus radiata* D.Don.) often replaces native damp sclerophyll forest after harvest (Grove and Yaxley, 2005) and remnant native forest corridors are retained between plantations. Pitfall traps collected ground beetles in corridors, plantations and interior and edge of continuous native forest. Corridors had similar species richness as continuous native forest sites but had a different species composition, intermediate to that of plantation and native forest. Native forest edges more closely resembled corridors' assemblage composition than forest interiors. The authors suggest wider strips to allow more habitat for forest interior species (Grove and Yaxley, 2005).

To my knowledge, there have been no published studies on the use of corridors by saproxylic beetles. Martikainen (2001) suggests aspen-associated beetles in boreal regions of Finland can probably tolerate clearcuts and successfully occupy these areas if sufficient trees are retained. Although not formally tested, Martikainen (2001) speculates that most saproxylic beetles can disperse and colonize dying aspens on clearcut sites without the need of corridors of closed forest. It is suggested that a network of scattered and suitable trees or groups of trees in the beetles dispersal range are required to function as 'stepping stones' for improved colonization of dead wood in clearcut matrices and long-term population survival (Martikainen, 2001). However, the suitability of snags as habitat for a given insect species are highly ephemeral and a higher connectivity may be needed to ensure a wide enough range of substrate types over the longer time scale.

Landscape patterns affecting spatial connectivity of dead wood

Habitat fragmentation is one of the greatest threats to biodiversity characterized as habitat loss, isolation and increased edge effects (Speight,1989; Saunders et al., 1991; Niemelä, 1997). When habitat becomes fragmented into small patches, species form metapopulations with local populations frequently becoming extinct and patches are subsequently recolonized by new populations (Hanski and Gilpin, 1991). In fragmented landscapes, increasing patch isolation diminishes landscape connectivity relative to species immigration to a patch. Connectivity is defined as the degree to which the landscapes enable or inhibit species movement between habitat patches (Taylor et al., 1993; Tischendorf and Fahrig, 2000). Immigration rate depends on the ability of the species to inhabit the surrounding matrix, their dispersal and perception abilities as well as susceptibility to mortality during immigration (Tischendorf and Fahrig, 2000). Connectivity incorporates both structural connectivity, based on landscape structure, and functional connectivity, which considers behavioural responses of organisms (Tischendorf and Fahrig, 2000). The same landscape will thus demonstrate varying connectivity for different groups of organisms (Tischendorf and Fahrig, 2000).

Spatial connectivity of dead wood in space is a major limiting factor for saproxylic beetle communities, especially in northern boreal regions where climate restricts dispersal and activity of insects (Ungerer et al., 1999; Lombardero et al., 2000; Scheigg, 2000a, Grove, 2002). Habitat connectivity on a landscape scale benefits species with higher dispersal abilities (Mönkkönen and Mutanen, 2003). If the distance between dead hosts becomes too great, the colonization rate to new trees cannot compensate for the extinction rate in old dead trees (Hanski and Gilpin, 1991). Scheigg (2000a) conducted a multiscale study (50-200m) in a beech-spruce forest on the effect of log connectivity and volume on saproxylic Diptera and Coleoptera assemblages. Spatial arrangement of dead wood had a greater effect than dead wood volume on saproxylic beetle species richness, exclusively at the 150 m scale (Scheigg, 2000a). Different assemblages were collected in plots with high dead wood connectivity compared to low dead wood connectivity (Scheigg, 2000a). High habitat specificity of beetle species was found in sites with high dead wood connectivity and this was associtated to low dispersal ability (Scheigg, 2000b).

Flying ability has been described as one of the best predictors of beetle response to fragmentation (Driscoll and Weir, 2005). Many wood-boring beetle species can fly over large distances to recently disturbed patches with high dead wood availability (Kaila et al., 1997). Økland et al. (1996) demonstrated the effect of former cutting and showed that aspen volume and deciduous tree species diversity on saproxylic assemblages were exclusively detected at the 4 km scale. Significant results at the large scale are attributed to the activity range and mobility of the majority of species and better correspondence of sampling with the spatial scale of ecological differences (Økland et al., 1996).

Low dispersal ability is generally associated with non-pyrophilous specialist species dependant on stable or rare habitats such as hollow, large diameter trees and old growth forests with specific microclimatic conditions (Nilsson and Baranowski, 1997; Shieigg, 2000a; Saint-Germain, 2004). Species associated with old-growth forest may also require longer reproductive and development periods (Esseen et al., 1997). Species with lower dispersal abilities may not be able to make use of the narrow strips, which are habitats that are too different from forest interiors (Mönkkönen and Mutanen, 2003).

Partial cuts as alternatives to clearcuts

Partial cutting is an additional alternative harvesting method that diversifies forest management and may help increase yield and sustainability of timber resources compared to clearcutting alone. Partial cutting uniformly removes a percentage of stems from the stand, modifying stand composition and structure to uneven-aged second or third-cohort stand types (mid-late successional types) (Bergeron et al., 2002; Harvey et al., 2002). Theorized to mimic natural successional trajectories, partial harvest brings a deciduous-dominated stand to an increasingly mixedwood composition, eventually becoming conifer-dominated (Bergeron et al., 2002; Harvey et al., 2002). Canopy openness, penetration of sunlight, temperature, humidity, and water and air flow is influenced by the density of retained trees after partial harvest (Parker, 1995 in Schowalter et al., 2005).

In the boreal mixed-woods, there are many advantages to partial cutting over clearcuts. Partial cutting can be undertaken at shorter intervals while increasing the rotation time for the entire stand (Harvey et al., 2002). By reducing competitors, partial cutting may increase individual log value and diameter, which is especially applicable for mixedwoods composed of light tolerant and light intolerant species (Longpré et al., 1994; Lämås et al., 1996; Lähde et al., 1999; Harvey et al., 2002). Mixed, un-even aged stands may promote biodiversity, ecological stabililty (Larsen, 1995; Lähde et al., 1999) and renewal of seedbanks (Kneeshaw and Bergeron, 1996). These types of stands may also have higher resistance to wind, pests, snow, fungi and anthropogenic damage such as climate change and air pollution (see review by Lähde et al., 1999 and references therein). Potential disadvantages with partial cutting causing potential losses of lumber include stem and root damage of un-harvested trees by machinery, spread of fungus, disease and insects (Harvey et al., 2002).

There are many studies on birds involving partial cut, uncut and clearcut stands. Partial cuts have been successful in maintaining bird diversity relative to uncut forest, compared to clearcuts (Norton and Hannon, 1997; Lance and Phinney, 2001; Tittler et al., 2001; Leupin et al., 2004; Harrison et al., 2005). Species composition in partial cuts has been found to be intermediate between uncut and clearcut sites (Norton and Hannon, 1997; Lance and Phinney, 2001; Harrison et al., 2005). However, in one study, no significant differences were found between bird communities in 30% partial cut and uncut stands in British Columbia (Steventon et al., 1998). Sixty percent partial cut stands had bird species found in both clearcut and uncut stands although the composition resembled more closely uncut stands (Steventon et al., 1998). Most of these studies have dealt with live tree removal and effect on forest species.

The effects of partial cuts on arthropods, dead wood and associated fauna have been relatively less studied. In Arkansas and Oklahoma, various levels of harvesting, including partial cuts, increased species richness of beetles (saproxylic and non-saproxylic) under increasing intensity of harvest (Cook, 2002). Higher species richness of cerambycids was found in recently thinned bottomland hardwood forests compared to unthinned stands, due to increased logging slash debris (Warriner et al., 2002). Significantly higher abundance of bark beetles (Scolytinae), *Trypodendron lineatum* Olivier, and pine engravers, *Ips pini* (Say), were collected in thinned than in unthinned lodgepole pine stands (*Pinus contorta* Dougl. ex Loud.) stands in Alberta, due to an increased abundance of dead wood (Hindmarch and Reid, 2001). In lodgepole pine stands of British Columbia, an increase in abundance of bark beetles was collected in thinned, compared to unthinned stands (Safranyik et al., 2004). Carabid species richness also increased in thinned stands due to the preference of many species to open, disturbed conditions (Warriner et al., 2002). Higher ground-dwelling arthropod abundance and diversity was collected in various intensities of thinned compared to unthinned douglas fir (*Pseudotsuga menziesii* (Mirb.)) stands in Oregon (Hoonbok and Moldenke, 2005). Canopy arthropods demonstrated a non-significant short-term response to different levels of partial and clearcut harvesting in douglas fir (*Pseudotsuga menziesii* (Mirb.)) dominated forests (Schowalter et al., 2005). Thirty percent partial harvesting had no effect on microarthropod decomposer communities compared to controls, while clearcutting only slightly disturbed the community (Siira-Pietikäinen et al., 2001).

Few studies in partial cuts have focused on dead wood dynamics and associated fauna, rather than the live tree component. In the SAFE (sylviculture et aménagement forestier écosystémique) project, volume of CWD was highest in clearcuts and significant differences occurred with partial cuts (Brais et al., 2004). Clearcutting significantly reduced the volume of well-decayed CWD compared to partial cuts because decomposition rate of dead wood significantly increased after clearcut harvest (Brais et al., 2004). Due to reduced inter-tree competition in partial cut stands, a reduction in snag density and basal area can be expected compared to maturing and old growth forests (McGee et al., 1999). In this study, partial cuts had significantly lower downed log volume than old growth forests but not maturing forests (McGee et al., 1999). It is suggested that partial cutting may reduce overall CWD volume and snag density, increase decomposition rates and decrease stand and landscape heterogeneity (Brassard and Chen, 2006). Considering the effects of partial cutting on dead wood dynamics, consequences on the composition of associated fauna are to be expected.

THESIS OBJECTIVES AND RESEARCH QUESTIONS

Saproxylic Coleoptera are a diverse group dependent on dead wood, a fundamental resource in forest ecosystems (Harmon et al., 1986; Grove, 2002). Saproxylic insects have been intensely studied in northern Europe in the last 10-20 years, where a significant drop in saproxylic beetle diversity has occurred due to a long history of intense forest harvest and management (Siitonen, 2001; Grove 2002). In Northern Europe, the aspen-dependant saproxylic beetles contribute significantly to threatened species lists, particularly aspen-dependant beetles (Siitonen and Martikainen 1994, Martikainen 2001, Sverdrup-Thygeson and Ims 2002). In the Canadian boreal forest, saproxylic beetle ecology and responses to forest harvesting is poorly understood and few studies have been conducted in eastern Canada (but see Saint-Germain et al. 2004a; 2004b; 2006).

My research took place in the south-eastern boreal forest in the region of Abitibi, Quebec (near Duparquet and Clericy), where logging with short harvest rotations has extensively fragmented the landscape. The overall goal of this thesis is to investigate habitat use and aspen-host use of saproxylic insects in remnant forest patches in even-aged clearcut landscapes and in stands harvested with partial cutting. I examine saproxylic beetle responses in these two silvicultural systems because they are both used within an ecosystem management framework (Harvey et al., 2002, Bergeron and Harvey, 1997). Ecosystem management assumes that forestry practices that are based on prior knowledge of patterns and processes of boreal forest natural dynamics is a management strategy that may help preserve ecosystem processes and biodiversity (Hunter, 1993; Bergeron and Harvey, 1997; Harvey et al., 2002). Such harvesting practices provide diversified forest conditions that can maintain ecological functions, sustainability and biodiversity (Hunter, 1993; Gauthier et al., 1996; Bergeron and Harvey, 1997; Lähde et al., 1999; Harvey et al, 2002; Bergeron et al., 2002). Forest composition, age-structure, stand dynamics and key characteristics of the forest should be preserved under these harvesting and management practices (Bergeron and Danserau, 1993; Gauthier et al., 1996). One key structural feature to consider in this management strategy is deadwood dynamics. Interference with dead wood dynamics can result in extinction of associated species (Grove, 2002).

In this thesis, Chapter 2 focuses on understanding the role of forest habitat remnants (small patches and cut-block separators or corridors) on saproxylic beetle assemblages compared to clearcuts and uncut continuous forest. Chapter 3 examines whether partial cutting preserves saproxylic beetle assemblages in relation to clearcut and uncut forest. This Chapter focuses on the 1/3 and 2/3 partial cut treatments of the SAFE (Sylviculture et aménagement forestier écosystémique) project conducted in the Lake Duparquet Research and Teaching Forest.

For both chapters, analyses will be targeted towards the overall saproxylic beetle assemblage and bark and wood-boring beetles, a functional sub-group of saproxylic beetles most directly associated with dead wood.

In Chapter 2 my objective is to assess how habitat remnants in boreal forest affect saproxylic beetle assemblages in landscapes subjected to harvesting

More specifically, I address the following questions:

i) what are the effects of clearcutting and habitat remnants (small remnant patches and cut-block separators/corridors) on saproxylic and bark and wood-boring beetle diversity, abundance and species composition in aspen-dominated stands in Canada's eastern boreal forest?

Treatment patches (Small patches, corridors, large patch-edge and large patch-interior) were sampled for saproxylic beetles in three mixedwood boreal landscapes using Lindgren funnels (Lindgren, 1983) and snag dissection of aspen. The null hypothesis is there is no difference in species richness, relative abundance and species composition of saproxylic and bark and wood-boring beetles among landscape elements. An alternative prediction, based on European literature, is exposed habitats such as clearcuts and forest edges yield higher species abundance and diversity (Kaila et al. 1997, Martikainen 2001, Bouget and Deulli, 2004; Jonsell et al. 1998; Lindhe et al. 2005).

ii) What environmental variables explain the distribution of saproxylic beetles in this landscape?

A series of possible explanatory variables were measured in each treatment patch and analyzed using canonical correspondence analysis (CCA) to link environmental characteristics to the species data. The null hypothesis is these environmental variables do not explain the community structure of these beetles. Based on European studies, a prediction is open habitats and increased log and snag densities will have a positive influence on saproxylic beetle communities (e.g., Økland et al., 1996; Kaila et al., 1997, Siitonen and Martikainen, 1994; Jonsell et al. 1998; Martikainen, 2001, Bouget and Deulli, 2004; Lindhe et al., 2005).

iii) Are there differences between bark and wood-boring beetle habitat-use (Lindgren funnel) compared to aspen host-use by larvae (snag dissection) in habitat remnants and large patches of closed forest?

Lindgren funnels and snag dissection were used to sample bark and wood-boring beetle assemblages in the same treatment patches (small patches, corridors, large patch-edge and large patch-interior) of one of the three sampled sites with Lindgren funnels (site 2, near Duparquet). The null hypothesis is similar bark and wood-boring beetle assemblages should be obtained using both sampling methods in the same treatment patches. I predict that dissimilar beetle fauna will be captured with either sampling method since each target a beetles in distinct life-stage with its own unique behaviours.

In Chapter 3 my objective is to assess the effect of partial-cut harvesting on saproxylic beetle assemblages.

More specifically, I address the following questions:

i) What are the effects of partial harvesting (1/3 partial cut and 2/3 partial cut) on saproxylic and bark and wood-boring beetle diversity, abundance and species composition in aspen-dominated stands in Canada's eastern boreal forest?

Treatment patches (large patch-interior, large patch-edge, 1/3 partial cut, 2/3 partial cut, clearcut) were sampled for saproxylic beetles using Lindgren funnels in the in the SAFE (Sylviculture et aménagement forestier écosystémique) project in Lake Duparquet Research and Teaching Forest, in the Abitibi, Québec. The null hypothesis is that there is no difference between treatment patches. An alternative prediction is partial cuts should yield an intermediate beetle assemblage between large patches and clearcuts (Cook, 2002)

ii) What environmental variables explain the distribution of saproxylic beetles in the treatment patches?

A series of possible explanatory environmental variables were measured in each treatment patch. The environmental data was linked to species data by canonical correspondence analysis (CCA). The null hypothesis is that these environmental variables do not explain patterns in saproxylic beetle community structure. Similar to Chapter 2, the prediction is open habitats and higher log and snag densities will have a beneficial effect on beetle communities (Økland et al., 1996; Kaila et al., 1997, Siitonen and Martikainen, 1994; Jonsell et al., 1998; Martikainen, 2001, Bouget and Deulli, 2004; Lindhe et al., 2005).

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CONNECTING STATEMENT

In Chapter 1, I reviewed the literature concerning the relationship between saproxylic beetle communities, dead wood, forest harvest and management. Few studies have examined saproxylic beetles in managed aspen-dominated eastern mixedwood boreal forest. Chapter 2 focuses on the effect of forest habitat remnants within clearcut landscapes on saproxylic and bark and wood-boring beetles in eastern mixedwood boreal forest.

CHAPTER 2: The effect of remnant boreal forest habitats on saproxylic beetle assemblages in landscapes subjected to harvesting

ABSTRACT

Saproxylic Coleoptera are a diverse taxon that depend on dead wood, a fundamental resource in forest ecosystems. The saproxylic fauna was sampled in harvested landscapes in aspen-dominated mixedwood boreal forest in Abitibi, Québec. Remnant forest patches left after clearcutting in harvested landscapes are theorized to mimic post-fire residual trees and snags. This study's objectives are to explore: i) effects of clearcutting and habitat remnants on saproxylic beetle assemblages; ii) effects of other explanatory stand characteristics on saproxylic beetle assemblages; iii) differences between saproxylic beetle habitat-use by adult beetles (Lindgren funnels) and aspen host-use (snag dissections) by beetle larvae in these landscapes.

Adult saproxylic beetles and bark had significantly higher species richness and relative abundance in habitat remnants, compared to forest interiors. Density of bark and wood-boring larvae was higher in remnant patches, compared to forest interiors. Although abundance patterns were similar between Lindgren funnels and snag dissections, abundance and species composition were very different.

Significant indicator species were detected only in clearcuts and habitat remnants and lower trap-to-trap variance was observed in ordination in these habitats. Clearcuts were lacking many of the most abundant species in the total data set, which were preserved in habitat remnants. Generally, saproxylic beetles appear to readily use habitat remnants in clearcut landscapes supporting the hypothesis that biodiversity is best preserved when harvesting mimics natural disturbance dynamics.

INTRODUCTION

Dead wood is a fundamental component of forest ecosystems, providing habitat for diverse organisms and playing a vital role in the regulation of nutrient and carbon cycling, erosion, drainage and geomorphic processes (Harmon et al., 1986; Speight, 1989; Samuelsson et al., 1994; Grove, 2002). Saproxylic organisms are those dependant on dead or dying wood during some part of their lifecycle (Speight, 1989). They include bark and wood-borers, parasites and parasitoids, predators, detritivores and fungivores (Speight, 1989; Dajoz, 2000).

One of the most diverse orders of saproxylic insects is Coleoptera, with entire families dependant on dead wood usually in the larval stage (Speight, 1989; Dajoz, 2000; Hammond et al., 2001). Larvae are the dominant life stage for most saproxylic beetles where adults are often short-lived and play a reproductive and dispersive role (Haack and Slansky, 1987; Hanks, 1999; Saint-Germain et al., 2006). Wood-boring or xylophagous beetles are typically the first to colonize, feed and breed in recently dead or weakened trees and are attracted to them through host volatiles such as ethanol and terpenes (Speight, 1989; Harmon et al., 1986; Hanks, 1999; Hanula, 1993; Grove, 2002; Allison et al., 2004). Many derive their nutrition from wood and fungi, fragmenting dead wood by tunneling and feeding and pre-condition the substrate for a succession of other species (Speight, 1989; Harmon, 1986; Hanula, 1993; Dajoz, 2000; Grove, 2002). They are also mediators and vectors to humifying fungi and bacteria (Speight, 1989; Harmon et al., 1986; Martikainen et al., 1998; Dajoz, 2000; Grove, 2002). Little is known about the life history of most saproxylic Coleoptera, especially the larval stage, with the exception of a few economically important species (Hanula, 1993; Hammond, 1997). I considered the trophic group 'bark and wood-borers' separately in some analyses and I defined these families of beetles as feeding or breeding in bark, xylem or phloem and may also rely on fungi for nutrition (Hanula, 1993; Arnett et al., 2002).

The majority of studies on saproxylic insects have been conducted in northern Europe's boreal forest (Speight, 1989; Siitonen and Martikainen, 1994; Økland et al., 1996; Kaila et al., 1997; Martikainen, 2001; Siitonen, 2001; Similä et al., 2000; Sverdrup-Thygeson and Ims, 2002; Jonsell and Weslien, 2003; Martikainen and Kaila, 2004; Lindhe et al., 2005). Centuries of intense forest management and harvest have created a significant reduction in coarse woody debris (CWD) and species diversity of saproxylic insects (Grove, 2002). Aspen-dependant (*Populus tremula* L.) fauna in Europe is species rich and contributes disproportionately to threatened species lists (Siitonen and Martikainen, 1994; Martikainen, 2001; Sverdrup-Thygeson and Ims, 2002). In Fennoscandia, the deciduous aspen component of the boreal forest has been suppressed or eliminated due to low commercial value compared to conifers, disrupting the continuity of substrate for saproxylic organisms (Siitonen and Martikainen, 1994).

In North American boreal forests, trembling aspen (*P. tremuloides* Mchx.) remains highly abundant and is considered the most ecologically and economically important deciduous boreal tree species (Hogg et al., 2002; Hammond et al., 2004). In the Canadian boreal forest, saproxylic beetle ecology and effects of forest harvest are poorly understood (Hammond, 2004). Hammond (1997) and Hammond et al. (2001) obtained high saproxylic beetle diversity associated with trembling aspen in western Canada. Few studies on saproxylic beetles have been conducted on aspen-dependant fauna in the North American eastern boreal forest (but see Saint-Germain et al., 2004a; 2004b; 2006).

Clearcuts are now the major stand-replacing event in Quebec's boreal forest. Major saproxylic beetle community differences exist between closed canopy and clearcut stands in Northern European studies (Kaila et al., 1997; Sverdrup-Thygeson and Ims, 2002; Gibb et al., 2006). Most threatened saproxylic beetles were found in clearcut areas that had remnant sun-exposed trees and snags, in comparison with old growth stands (Kaila et al., 1997; Martikainen, 2001; Sverdrup-Thygeson and Ims, 2002; Lindhe et al., 2005).

Silvicultural systems that mimic boreal forest natural dynamics are management strategies that are hypothesized to preserve ecosystem functions and biodiversity (Hunter, 1993; Bergeron and Harvey, 1997; Bergeron et al., 2002). Natural disturbances such as fire and insect outbreaks often leave a patchy remnant forest structure (Lee et al., 1997). Post-fire live residual trees, snags and logs contribute to the structure of the re-establishing stand, creating a wide ranging size distribution of CWD and large diameter snags (Rowe and Scotter, 1973; Eberhart and Woodard, 1987; Lee et al., 1997; Brassard and Chen, 2006). Likewise, patches of remnant forest left after clearcutting may create refugia for species not able to survive in harvested areas and may enhance population exchange between source forest areas and habitat remnants (Beier and Noss, 1998; Saunders et al., 1991). Increasing levels of 'green-tree retention' in coniferous stands in Finland, was found to promote species richness of red-listed and threatened saproxylic beetles in both burned and clearcut sites, although species richness was generally greater in burned sites (Hyvärinen et al., 2006). Martikainen (2001) suggests aspen-associated beetles in Europe's boreal forest can probably tolerate clearcuts and successfully occupy these areas if sufficient remnant trees are retained.

In even-aged clearcut landscapes, cut-block separators are habitat remnants that can potentially function as corridors, directing insects to connecting large patches of uncut forest, which has been demonstrated with moths and flies (Mönkkönen and Mutanen, 2003; Fried et al. 2005). Since 1996, in the southern mixedwood boreal forest of Quebec, adjacent clearcuts (max. 150 ha) must be separated by cut-block separators (N.F.D.P., 2003; M.R.N.F.P., 2005). In Australia, Driscoll and Weir (2005) demonstrated that the greatest species richness of carabid, scarabid and tenebrionid beetles occurred in remnant mallee linear habitats in landscapes fragmented by grazed land and roads. In Tasmania, remnant native forest corridors are retained between plantations (Grove and Yaxley, 2005). Corridors had similar Carabidae species richness as continuous native forest sites, but had a different species composition, intermediate to that of plantation and native forest (Grove and Yaxley, 2005). To my knowledge, there have been no published studies on the use of corridors by saproxylic beetles.

The objectives of this research are to test the following: i) what are the effects of clearcutting and remnant habitats (small remnant patches and cut-block separators/corridors) on saproxylic and bark and wood-boring beetle communities in aspen-dominated stands in Canada's eastern boreal forest? ii) what stand characteristics explain the distribution of saproxylic and bark and wood-boring beetles in this landscape? and iii) are there differences between adult bark and wood-boring beetle assemblages (using Lindgren funnels) and host-use of aspen by larvae (sampled by snag dissection) in habitat remnants and large patches of closed forest?

MATERIALS AND METHODS

Site description

This study was conducted in the southern mixedwood boreal forest in the Abitibi region of northwestern Quebec near the towns of Duparquet (Site 1 and 2) and Clericy (Site 3) (Fig. 2.1). Sites were pre-selected using digital cover maps (SIEF, 2002). Three landscapes of mixedwood composition, with uneven-aged stands, fragmented by clearcuts of 5-10 years of age and containing landscape elements of interest were selected. Site 1 is located in the SAFE (Sylviculture et aménagement forestier écosystémique) project, where Phase 1 (bloc 1 and 3) and Phase 2 were used for sampling. In SAFE, experimental clearcuts were performed and replicated near Duparquet, where Phase 1 was harvested in 1999 and Phase 2 in 2000 (Brais et al., 2004; Brais et al., 2004b). Site 2, also near town of Duparquet and located approximately 10 km from SAFE, and Site 3, near the town of Clericy and Lac la Pause (50 km from Duparquet), are commercially harvested areas. Although located closer together, Site 1 and Site 2 are considered independent landscapes and were not located in the same clearcut area but in spatially distinct locations.

In site 1 (SAFE project) (48° 28-29' N, 79° 24-26' W), forests are dominated by trembling aspen *(P. tremuloides)* (31 % of stems > 10 cm DBH) and white birch (*Betula papyrifera* Marshall) (32%), and, in less abundance, white and black spruce (*Picea glauca* (Moench), *Picea mariana* (Mill)) (19%), balsam fir *(Abies balsamea* (L.)) (12%), balsam poplar (*Populus balsamifera* L.) (4%) and jack pine (*Pinus banksiana* Lamb) (2%). In site 2 (Duparquet) (48° 23-29' N, 79° 23-28' W), forests are composed of trembling aspen (54 %), white and black spruce (17%), white birch (12%), balsam fir (9%) and jack pine (8%). In site 3 (Clericy) (48° 25' N, 78° 33-35' W), forests were composed of white and black spruce (49%), trembling aspen (25%), balsam fir (23%), white birch (2%) and jack pine (1%).

Sampling

Lindgren funnel traps, consisting of 8 stacked funnels, were used to capture adult saproxylic beetles (Lindgren, 1983). Lindgren funnels were installed 4-7 June 2005, removed 5-8 August 2005 and emptied every 2 weeks for a total of 4 sampling dates. The collection jar contained propylene glycol diluted with 50% water as a preservative, to a depth of approximately 5 cm in the collection container. Commercial ethanol-based baits (Phero Tech Inc.) were attached to each Lindgren funnel, to increase saproxylic captures. Ethanol is a host volatile emitted from decomposing deciduous trees (Hammond et al., 2001; Allison et al. 2004).

There were three replicates of each landscape element in each of the three sites (9 total treatment replicates per landscape element). The selected landscape elements included the following: clearcuts (CPR and CPRS) of 5-10 years since harvest (clearcut area: site 1: 1.6-4.81 ha; site 2: 25-29 ha; site 3: 14-37 ha); 40-60 m wide cut-block separators that were connected to large patches; large patches of forest were greater than 80 ha; small remnant forest patches that were under 1 ha in area. Edges of large patches were sampled at approximately 20 m from the edge and interiors were sampled in the approximate center of the patch. One Lindgren funnel was placed per treatment patch for a total of 15 Lindgren funnel traps per site. Beetles were sorted from the bulk samples and preserved in 70% ethanol.

A total of 45 snags were cut down on 15 August 2005, in site 2 (Duparquet) only. The snags were taken from the same patches where the Lindgren funnels were installed. Five snags were cut from each landscape element, which include corridors, small patches and large patches, and replicated three times. Aspen snags were not present in clearcuts and this treatment was omitted from the experimental design. Large patches were sampled haphazardly following a transect at approximately 20-30 m from the edge, until 5 snags of adequate quality and diameter were selected per patch. Snags of early-mid decay (Hammond et al., 2004; Lee et al. 1997) with standardized external characteristics (no twigs, 100% bark but slightly loose, treetop windblown) and circumference ranging from 43-154 cm were selected because the bark and wood-borers are the earliest colonizers and old aspen snags were rare, especially in small patches. Snags were cut from approximately 25 cm from the ground to 100 cm in height on the bole. 75 cm boles were debarked and beetle specimens were collected. Fifty cm of the debarked logs were carefully dissected for larvae collection. The dissection consisted of cutting cross-sections of the boles with a chainsaw and using an axe to cut them into increasingly smaller pieces, removing the larvae from the galleries with forceps. Larvae were boiled in water for approximately 1 minute and then placed in 70% ethanol for identification.

Stand characteristics

A 400 m^2 quadrat was created around each Lindgren funnel. Direction of quadrats was standardized by creating one north-south and one west-south transect positioned in the middle of each side of the square. Intersecting these two transects, fallen dead logs and stumps (> 5 cm diameter) were counted and diameter measured. The formula estimating volume along these transects is taken from Harmon et al.(1986). Along the north-south transect inside the quadrat, shrubs and small understory trees that were touching the transect set at 1 m above ground were counted as either deciduous or coniferous. The average understory height was estimated and shrub density was estimated using density classes, which were estimates based on relative densities beween treatments (0=open, 1=low density, 2=medium, 3=high, 4= very high density).

Within each quadrat all live and dead standing tree species and diameter at breast height (DBH >10 cm) were characterized. Snag decay stage (early, mid, late) was estimated using external characteristics but this data is not presented due to the small sample size and high variance within and between treatments. At each

Lindgren funnel, two pictures with a digital camera with a fish-eye lens attached were taken from about 1.5 m in height. The pictures were analyzed to obtain percent canopy openness with the software Gap Light Analyzer v. 2.0 (G.L.A., 1999).

Beetle Identifications

Adult saproxylic beetles were identified to species or morphospecies using Laplante et al., 1991; Downie and Arnett, 1996; Arnett et al., 2002. Cerambycidae were identified to species using Yanega (1996) and Scolytinae were identified to species using Bright (1976). Staphylinids were not included in sapoxylic Coleoptera data because of time constraints for identification. Bark and wood-boring beetles were analyzed separately because this diverse functional group of large saproxylic beetles are most directly associated with dead wood and more taxonomic information and expertise can be obtained on species in this guild. Families that were considered part of the bark and wood-boring guild included Anobiidae, Cerambycidae, Curculionidae, Scarabidae, Lucanidae, Cephaloidae, Eucnemididae, Mordellidae, Pyrochroidae, Scarabaeidae, Scraptiidae, Melandryidae, Alleculidae and Tenebrionidae (Arnett et al., 2002).

Adult beetle specimens were either verified by S. Laplante, Y. Bousquet and/or cross-checked at the CNC (Canadian National Collection of insects, arachnids and nematodes, Ottawa, Canada). Cerambycid larva was identified to species using Craighead (1923) and M. Saint-Germain, *(pers. comm).* Bark and wood-boring larvae were identified to family using Böving and Craighead (1931). Larvae were verified by M. Saint-Germain (McGill University) and by Dr. V. Grebennikov (CNC). Adult beetle vouchers are deposited at McGill University's Lyman Entomological Museum (Ste Anne de Bellevue, Quebec, Canada) and larvae vouchers are deposited at the CNC.

ANALYSES

Saproxylic beetle habitat-use

Lindgren funnel sampling dates were pooled by sample for analyses. Using SAS (Statistical Analysis Software, 2001), one-way ANOVA or Kruskal-Wallis tests were used to assess differences between treatments (small patch, corridor, clearcut, large patch-edge and large patch-interior) on relative abundance and raw species richness (the number of species per treatment) of saproxylic and bark and wood-boring beetles. Normality and homogeneity of datasets was confirmed using a Shapiro-Wilk test and a Levene's test. Tukey's H.S.D. test (α=0.05) was used for post-hoc comparisons of means in ANOVA tests. Post-hoc comparisons for Kruskal-Wallis tests were conducted using the Mann-Whitney test for pairwise comparisons. The probabilities for each pair were corrected using a Bonferroni adjustment.

Sample-based rarefaction, using the software *EstimateS* (Colwell, 2004), was used to compare species richness between treatments based on sampling effort (Gotelli and Colwell, 2001; Buddle et al., 2005). Rarefaction shows the rate of accumulation of new species as new samples are added verifying that enough samples have been collected to make accurate species richness comparisons (Gotelli and Colwell, 2001; Buddle et al., 2005). Sample-based was chosen over individual-based rarefaction because the samples were properly replicated with comparable sampling effort per treatment and there were no disturbed traps (Buddle et al., 2005).

Indicator species analysis was performed using PC-ORD v. 4.17 (McCune and Mefford, 1999) to determine species with particular affinities for certain treatments. A probability was assigned to each indicator value using a Monte Carlo test of 1000 permutations. Indicator species were coupled with rank-abundance curves, which are based on the 20 most commonly collected saproxylic beetle species in the total data. The rank-abundance was then separated by treatment to evaluate patterns of species diversity and abundance.

Non-metric multidimensional scaling (NMS) ordination (indirect gradient analysis) was used to create ordination plots reflecting beetle compositional differences between treatments using Bray-Sorenson distance measure in PC-ORD (McCune and Mefford, 1999). NMS ordination avoids assumptions on linearity among variables and is suited for non-normal discontinuous data typical of ecological work (McCune and Grace, 2002). A starting configuration of a DCA ordination was used for the NMS ordination instead of random starting coordinates to lower stress levels and avoids local minima. Before a final ordination solution was performed by PC-ORD, a six-dimensional ordination was run to evaluate stress reduction and selection of the number of axes. A Monte Carlo test (100 runs) was conducted to evaluate the strength and significance of the axes. The stability of the solution was evaluated with the stability criterion (<0.005). The percent variance explained is calculated by multiplying 100 by r^2, the coefficient of determination between distances in the ordination space and the original space (McCune and Grace, 1999).

Saproxylic beetle responses to stand characteristics

Canonical correspondence analysis (CCA) (direct gradient analysis) was used to link possible measured explanatory variables in each treatment patch, to the species data, using the software PC-ORD (McCune and Mefford, 1999). CCA constrains a species matrix to an environmental matrix by multiple linear regression. A Monte Carlo test (99 runs) was used to assess significance of the axes with the null hypothesis being there is no relationship between the species and environmental matrix. Forty-four samples with 186 species were used in this analysis, instead of 45 samples with 188 species, because it was not possible to collect stand characteristics from one treatment patch. Apart from this discrepancy, the species matrix used for the CCA ordination was virtually identical to the matrix used in NMS ordination. The following stand characteristics were included in the environmental matrix: Deciduous tree density, coniferous tree density, deciduous snag density, coniferous snag density, % canopy openness, snag basal area, deciduous shrub density, coniferous shrub density, volume of logs, density class and deciduous tree basal area. The final ordination plot was graphed using LC scores.

The previous analysis on stand characteristics was supplemented with ANOVA or Kruskal-Wallis tests on the same stand characteristics by treatment (small patch, corridor, clearcut, large patch-edge, large patch-interior) followed by Tukey post-hoc test or a Bonferonni adjusted Mann-Whitney test.

Bark and wood-boring beetle aspen host-use

Kruskall-Wallis tests were used to determine treatment effects on bark and wood-boring larval density and Cerambycidae larval density collected from snag dissections (SAS, 2001). The proportion of snags in each treatment with bark and wood-boring and Cerambycidae larvae present was also tested with a Kruskall-Wallis test. Differences between beetle fauna caught using Lindgren funnels and snag dissections in the same treatment patches of site 2 were analyzed qualitatively.

RESULTS

A total of 6620 adult saproxylic beetles and 188 species was trapped in the 45 Lindgren funnels (Table 2.1, Appendix 2.1). The most species rich saproxylic beetle guild collected was the bark and wood-borers, and the most abundant guild was the fungivores (Table 2.1). The bark and wood-boring beetle guild had the lowest relative abundance after the aquatic saproxylic beetles.

The most commonly collected (i.e. >2% abundance) species or morphospecies caught in Lindgren funnels were: *Melanophthalma* sp. 1 (Lathridiidae) (47.14% of the total number of individuals collected), *Glishrochilus siepmanni* W.J. Brown (9.94%) (Nitidulidae), *Triplax dissimulator* (Crotch) (Erotylidae) (3.85%), *Glishrochilus sanguinolentus* (Olivier) (3.41%) (Nitidulidae) and *Cerylon* sp. 1 (Cerylonidae) (3.35%). Other commonly collected beetles were those of the closely related genera *Enicmus* and *Lathridius* spp. (Lathridiidae) (2.79%), *Mordella* sp. 1 (Mordellidae) (2.39%), and *Ampedus* sp. 1 (2.30%) (Appendix 2.1).

Saproxylic beetle habitat-use

Significantly more saproxylic beetle individuals were collected in corridors and small patches compared to the interior of large patches (Table 2.2). Significant differences also occurred between corridors, with the highest raw species richness, and interior of large patches, with the lowest species richness collected. Bark and wood-boring beetle relative abundance was non-significant for treatment effects. However, greater numbers were captured in clearcuts and corridors and the lowest relative abundance occurred in interior of large patches. Species richness was significant across treatments for bark and wood-borers with small patches having the highest number of species collected and interior of large patches collecting the fewest species. Site effects were non-significant in ANOVA tests for saproxylic beetle relative abundance (square root transformed data, $p=0.19$; $F_{2,42}=1.74$; means +/-S.E.: site $1=11.27 \pm 0.56$; site $2=12.9 \pm 0.71$; site $3=11.20 \pm 0.88$). For bark and wood-boring beetle relative abundance, site effects were marginally significant (square root transformed data, $p=0.04$; $F_{2,42}=3.48$; Means +/-S.E.: site $1=4.11 \pm 0.33$; site $2=4.11 \pm 0.33$; site $3=3.22 \pm 0.30$); however, the Tukey H.S.D. test did not detect significant differences between sites. Rarefaction curves showing the effect of site on species accumulation rate showed no significant effects (data not shown). An NMS ordination demonstrated no clear patterns of species composition for sites (data not shown). Due to the lack of site effects on beetle abundance, species richness and composition, analyses will focused on treatment effects.

Because clearcuts differed in size, simple linear regressions between clearcut size and relative abundance of saproxylic and bark and wood-boring beetles were attempted, revealing no significant differences (data not shown). Similarly, no significant results were obtained for simple linear regressions between clearcut size and saproxylic and bark and wood-boring beetle species richness.

The rarefaction curves (Fig. 2.2a) confirm the results found for saproxylic beetle raw species richness. At sample effort of 9 traps per treatment, more saproxylic beetle species were caught in corridors and small patches than interior of large patches (Fig 2.2a). The rarefaction curve for bark and wood-boring beetles (Fig. 2.2b) also confirms patterns observed with raw species richness, where small patches and corridors have higher species richness than interior of large patches.

A matrix containing untransformed, total saproxylic species data was analyzed by NMS ordination (Fig. 2.3). Axis 1 explained slightly more variation than axis 2, and each axis was significantly different than would have been expected by chance. No clear patterns result from this ordination, although habitat remnants, corridors and small patches, appear to be loosely grouped away from clearcuts with some overlap. The interior of large patches, are somewhat distinct in terms of species composition and have higher trap-to-trap variance than other treatments. Bark and wood-boring beetle data was analyzed separately in a NMS ordination because of potentially different distribution patterns than saproxylic beetles (Fig 2.4). The resulting 3-dimensional ordination shows axis 1 and 2 explaining the most variation, and all axes were significantly different than could have been obtained by chance. Again, there is little structure to the bark and wood-borer data in the NMS ordination, however, the corridors have a tightly grouped beetle community with low trap-to-trap variance while large patches are highly variable.

Rank-abundance curves are presented to analyze patterns of saproxylic species diversity, focusing on the 20 most commonly collected species (ranked according to total abundance, experiment-wide) (Fig. 2.5). Some of the top ranking species present, such as the family *Rhizophagus* sp. 1, *Xyleborus sayi* (Hopkins), Corylophidae sp. 1 and *Pseudanostirus propola* (Leconte) were never captured or occurred as singletons in clearcuts. *Ampedus pullus* Germar was never captured and only a singleton of *Xyleborus sayi* was collected at edges of large patches (Hopkins). *Ampedus apicatus* (Say) was never captured in interiors of large patches, where only a singleton of *A. pullus* Germar was trapped. Within the top 20 most commonly collected species, three significant indicator species occurred in clearcuts and two significant indicator species were found in small patches and corridors (Fig. 2.5, Table 2.3). Large patches had no significant indicator species. In the total data, significant indicator species appeared predominantly in clearcuts, in less abundance in small patches and corridors and never in large patches (Table 2.3).

Saproxylic beetle response to stand characteristics

The CCA ordination only explained 12.1% of the total variance in the community data and only axis 1 was found to be significantly different than could have been obtained by chance (Monte Carlo test, 99 runs). Log-transformations, presence/absence and exclusion of rare species were also attempted with no new patterns revealed or higher variance explained. Variables with intraset correlations of greater than 0.5 or smaller than –0.5 were graphed (Fig. 2.6, Table 2.4). Coniferous tree and shrub density appear important in structuring beetle assemblages in large patches, small patches and corridors. Deciduous shrub density, shrub density class and % canopy openness vectors are associated with beetle communities in clearcuts while coniferous trees are negatively linked with beetle communities in clearcut areas. ANOVA results on stand characteristics by treatment explain these patterns further (Table 2.5); as expected, clearcuts have significantly more open canopy and lowest deciduous tree density, compared to other treatments. Small patches have the highest coniferous tree density and are significantly different from clearcuts. Small patches and corridors have the highest snag density and snag basal area and are significantly different from clearcuts. Interior of large patches have the least snags after clearcuts; however, interior of large patches have the highest coniferous snag density, significantly different from clearcuts. In CCA, coniferous snag density had an intraset correlation that was close to the 0.5 cut-off for axis 1 but may still be ecologically important in explaining species variation.

Bark and wood-boring beetles aspen host-use

A total of 488 bark and wood-boring larvae, from families Cerambycidae (45.1 % of total density), Melandryidae (42 %), Tenebrionidae (7.4%) and Buprestidae (5.4%), was dissected from aspen snags. Two hundred and forty-six

Cerambycidae larvae were dissected from snags and identified to species. The Cerambycidae species with the highest density was *Anthophylax attenuatus* (Haldeman) (48.5 % of Cerambycidae density) followed by *Bellamira scalaris* (Say) (19.9%), *Trigonarthus minnesotana* (Casey) (4.1%) and *Trachysida mutabilis* (Newman) (1.3 %). Density is presented in Table 2.6 for Kruskal-Wallis tests to control for variation in diameter of the snags. Due to high variance in the data, no significant effects were found for bark and wood-boring larvae, Cerambycidae larvae and Melandryidae larvae although corridors have considerably higher larval densities than large patches for these families (Table 2.6). Significant results were found for Buprestidae larvae, which had equal densities in corridors and small patches but were absent from large patches. Tenebrionidae larval density was marginally non-significant with small patches having the highest larval density and large patches the lowest larval density. The Kruskall-Wallis test on the proportion of snags with bark and wood-boring larvae present and Cerambycidae larvae present is also marginally non-significant but has high variance. Bark and wood-boring larvae and Cerambycidae larvae, small patches and corridors have increased larval presence per snag, compared to large patches.

The density of larvae of bark and wood-boring families from snag dissections are compared with relative abundance of beetles captured in Lindgren funnels from the same families and in the same treatment patches (Table 2.7). Cerambycidae is the most abundant bark and wood-boring family for both sampling methods. Melandryidae was more common in snag dissections than Lindgren funnel captures. Tenebrionidae was never captured in Lindgren funnels of site 2 but was common in snag dissections.

Table 2.7 compares aspen-feeding Cerambycidae fauna using Lindgren funnel relative abundance and snag dissection larval density from the same treatment patches. *Anthophylax attenuatus* (Haldeman) was the most abundant Cerambycidae dissected from snags but there were only 3 captures in Lindgren funnels. *Clytus ruricola* (Olivier), the most abundant Cerambycidae caught in Lindgren funnels was never found in snag dissections. Forty-five *Bellamira* *scalaris* (Say) larvae were dissected from snags while only one was captured in Lindgren funnels. *Trachyisida mutabilis* (Newman) and *Trigonarthris minnesotana* (Casey) were never caught in Lindgren funnels. Two additional species, *P. supernotatus* (Say), *A. modestus* Gyllenhal, were caught once each in Lindgren funnels but were never found in snags.

DISCUSSION

Effects of habitat remnants on saproxylic beetles

Habitat remnants, such as corridors and small patches, may have beneficial effects on saptroxylic biodiversity within clearcuts by resembling the patchy remnant vegetation structure of natural post-fire residual trees and snags (Work et al., 2003; Gandhi et al., 2001). The highest species richness of saproxylic and bark and wood-boring beetles was collected in habitat remnants. Higher relative abundance of saproxylic beetles and larval densities were collected from habitat remnants, although data from snag dissection were too variable to exhibit significant results. The greatest differences between treatments occurred between habitat remnants and interior of large patches, which had the lowest relative abundance and species richness of saproxylic and bark and wood-boring beetles.

Small patches and corridors had the highest snag density and basal area, increasing habitat for many saproxylic beetles. Increased edge around these remnant habitats can increase abiotic influences like wind and temperature as well as mechanical damage from harvesting and microclimate change (Esseen, 1994; Peltonen, 1999; Bouget and Deulli, 2004). Peltonen (1999) recorded that over 80% of dead trees were within 15 m from the forest-clearcut border in southern Finland.

Forest interiors had the lowest snag density, deciduous snag density and snag basal areas. This partially explains the low species richness and relative abundance in interior patches. Fewer saproxylic beetles may be actively dispersing in search of potential hosts in interior patches, compared to other treatments. Forest interiors had the highest coniferous snag densities and species dependant on dead wood from late successional species may be more negatively affected by forest harvest.

When comparing edge habitat in relation to patch size, edges of large patches collected consistently lower relative abundances and fewer species of beetles than small remnant forest patches. Insect density in relation to patch size is linked to insect immigration behaviour (Bowman et al., 2002). For aerial and ground-moving insects movement, a negative relationship between patch size and population density would be expected (Bowman et al., 2002). Landscapes that are "more fragmented" or have a higher number of smaller patches should collect more stranded individuals, producing higher densities than less fragmented habitats containing the same surface area of habitat (Bowman et al., 2002). Fragmented landscapes may temporarily increase biodiversity after harvest in small remnant patches due to crowding from an influx of species from the clearcut, while interior forest species disappear (Debinski and Holt 2000, Halme and Niemelä 1993, Niemelä 1997; Grez et al. 2004).

When comparing connectivity of remnant habitats, similar species richness and relative abundance was collected in unconnected small patches as the larger, connected corridors. Corridors may be intercepting but not directing beetles to large patches. This agrees with Martikainen's (2001) suggestion that dead aspens in a network of small patches of trees and snags can be colonized by most saproxylic beetles without the need of corridors. However, over a longer periods, a higher connectivity may be needed to ensure a wide enough range of substrate types for the diversity of saproxylic beetles.

Effects of clearcuts on saproxylic beetles

Clearcut treatments had intermediate relative abundance (for saproxylic beetles) and species richness (both saproxylic and bark and wood-boring beetles), compared to habitat remnants and forest interiors, but did not differ significantly from these treatments. The ordination results demonstrate a distinctive separation between the species composition of clearcut and interor of large patches. Similarly, for saproxylic beetles in Europe's boreal forest differences in species composition were found between clearcut and uncut forest (Kaila et al., 1997, Sverdrup-Thygeson and Ims, 2002). However, no major differences were detected for standardized species richness (Kaila et al., 1997, Sverdrup-Thygeson and Ims, 2002).

The highest relative abundance of bark and wood-borers was found in clearcuts but was not significantly different from other treatments. Martikainen (2001) found more aspen-specialist species and individuals in clearcut stands. Aspen-dependant beetles are adapted to natural disturbance and prefer large, dead trees in sunny open areas (Kaila et al. 1997; Martikainen, 2001; Sverdrup-Thygeson and Ims 2002; Lindhe et al. 2005). In the CCA, % canopy openness and deciduous shrubs were community structuring stand characteristics in clearcuts. In ANOVA, % canopy openness was significantly higher in clearcuts than all other treatments. Jonsell et al. (1998) estimated that 24% of species prefer sunny open areas, only 9% of Swedish red-listed saproxylic insects prefer shaded conditions of old forests, 35% are indifferent and 23% are have unknown preferences to light conditions. In cut high-stumps of spruce, birch, aspen and oak, 2/3 of all saproxylic beetles caught using emergence traps for 7 years preferred semi or fully sun-exposed substrates, where most red-listed species were found (Lindhe et al., 2005).

A hypothesis explaining high captures of some in clearcuts is the hypoythesis that some saproxylic beetles use visual cues on a landscape scale to search for a silhouette of a snag and individual tree hosts by selection through trial and error landing (Chenier and Philogene, 1989; Saint-Germain et al., 2006). In a clearcut or edge habitat, the silhouette of a snag or Lindgren funnel may be more visible while in flight than in forest interiors. The probability of capture may be higher in a clearcut, where there are less potential hosts to land on. Higher temperatures in clearcuts may have also increased the activity of insects (Kaila et al., 1997).

Effects of habitat remnants on species composition

In ordinations, large patches had high trap-to-trap variance in species composition for both saproxylic and bark and wood-boring beetles. Clearcuts and habitat remnants had a more distinct community structure and exhibited much less variance, especially for wood and bark-borers. To support this finding, significant indicator species were found predominantly in clearcuts and also in habitat remnants but never in large patches. This suggests more habitat specialists may be found in forest remnants and clearcuts than in large patches. However, remnant habitats may support a wider range of species then clearcuts. Many of the most abundant species of the total data were never collected in clearcuts, however habitat remnants collected all 20 of the most abundant species.

Little is known about the life history of saproxylic beetles, although the few economically important species are an exception. Some species in the family Leiodidae were indicators of clearcuts and are known to have rapid dispersal capabilities and are abundant in open areas and disturbed sites (Baranowski, 1993). *Triplax dissimulator* (Erotylidae) was an indicator of small patches yet was very rare in clearcuts. Some species of the genera *Triplax* are endangered or threatened in European countries (Franc, 1997). Mycetophilous beetles, which include *Triplax,* are considered indicators of well-preserved ecosystems in Europe (Franc, 1997). In North America, genus *Triplax* is generally distributed and larvae feed on soft bracket fungi, primarily of the genus *Inonotus* and *Pleurotus* (Arnett et al., 2002). *Cyphon* species have aquatic saproxylic larvae, which were indicators for corridors, which are often positioned over small streams.

Saproxylic beetle response to stand characteristics

There were weak species-environment relationships in the CCA ordination, although species composition in deciduous and coniferous sites were dissimilar in relation to canopy openness. One explanation, regarding the lack of strong relationships between stand characteristics and adult beetle captures, is the composition of host trees may not affect adults dispersing at local scales in this managed system. An alternative explanation is that Lindren funnels may not be the appropriate sampling device to measure local responses of saproxylic insects to dead wood availability. A large larvae dataset from snag dissection, identified at least to genera, may have stronger relationships to stand characteristics in CCA analysis.

The lack of strong relationships in the CCA results are partially supported in Økland et al.'s study (1996), which found stronger relationships between species data and stand characteristics at the landscape scale than the stand scale. Availability of habitat for survival of saproxylic species appears important at 1-10 km^2 scales in Sweden (Gibb et al., 2006). This is speculated to be due to better correspondence with activity ranges of saproxylic beetles, less influence of local heterogeneity and a better relationship between sampling scale and scale of ecological differences on the landscape (Økland et al., 1996). Furthermore, beetles respond to their environment at highly variable scales depending on the species. Holland et al. (2005) found that scale of the response of 31 different Cerambycidae species to stand characteristics varied greatly. For example, *Stictoleptura canadensis* (Olivier) responds at 1600 m scale and *Clytus ruricola* responds at 100 m scale. Larger beetles typically have responses to habitat at larger scales, and body length differed by many orders of magnitude for my beetle samples.

Saproxylic beetle habitat-use versus aspen host-use

Snag dissections and Lindgren funnels collected very different bark and wood-boring families and Cerambycidae, in terms of species and abundance. There are many reasons why there are such wide differences between the fauna collected with each technique. First, using flight traps, beetles actively dispersing are captured in habitats not necessarily associated to host-use. Second, the probability of collecting certain species is increased in snag dissections as beetles may spend a few years in the larval stage. The same species may only fly as an adult for a few weeks of the summer, making a Lindgren funnel capture less likely. Therefore, if an adult beetle is rarely captured in a flight trap, it does not necessarily mean it is rare in that habitat as the larvae may be living in high numbers in nearby snags. Third, a portion of the larval fauna may colonize an area higher on the bole than I sampled in snag dissections (i.e. 25 – 100 cm above ground). For example, *C. ruricola* was more often collected in the canopy than understory flight-intercept traps (Vance et al., 2003). *Anthophylax attenuatus* was exclusively captured in the understory in Vance et al. (2003) and was abundant in the lower bole samples dissected in my study.

Conclusions

To prevent the declines in saproxylic fauna, as experienced in Europe's boreal forest, it is necessary to know what species exist and their range of habitat requirements. Leaving habitat remnants after clearcutting is a strategy diversifying even-aged harvest that may help preserve biodiversity. The highest saproxylic beetle species richness and abundance was collected in habitat remnants, which also had highest snag densities. This suggests that habitat remnants are readily used by saproxylic insects in harvested landscapes. Based on ordination results and rank-abundance plots, forest remnants appear to have more habitat specialists than large patches but also preserve a wider range of species than clearcuts. The use of habitat remnants by saproxylic beetles in clearcut landscapes supports the hypothesis that biodiversity is best preserved when harvesting more closely mimics natural disturbance.

Retaining remnant trees, snags and logs within clearcuts may assist in supplementing the regenerating stand with a wide range of dead wood in terms of diameter, decay class and later successional tree species (Rowe and Scotter, 1973; Eberhart and Woodard, 1987; Lee et al., 1997; Brassard and Chen, 2006). Suitable dead wood habitat for a given insect species is highly ephemeral and adequate spatial and temporal connectivity is needed in harvested landscapes. A more natural stand structure during regeneration of the clearcut may be ensured using remnant forest patches as post-fire residual analogues. It is recommended to retain large patches of forest in addition to habitat remnants within harvested landscapes.

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Fig. 2.1: Location of sampling sites and closest towns in Abitibi-Témiscamingue, Québec.

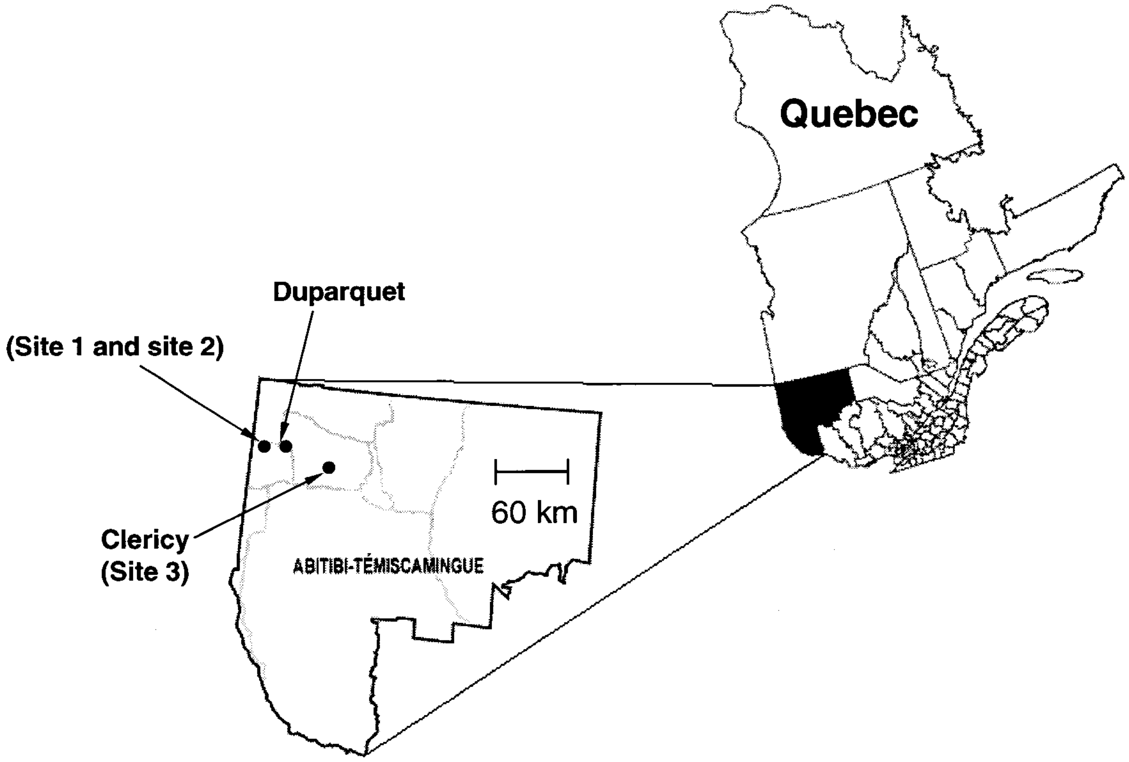

Table 2.1: Saproxylic beetle relative abundance and raw species richness by larval guild from 45 Lindgren funnels collected from treatment patches (small patch, corridor, clearcut, large patch-edge, large patch-interior) of mixedwood boreal forest

Guild	**Relative abundance**	**Species richness**
Bark and wood-boring	710	82
Fungivore	5069	54
Predators of saproxylics	812	48
Aquatic saproxylic	29	4
Total	**6620**	**188**

Table 2.2: Results from one-way ANOVA and Kruskall-Wallis tests for the effects of treatment patches (small patch, corridor, clearcut, large patch-edge, large patch-interior) on saproxylic beetle and bark and wood-boring beetle relative abundance and raw species richness. Data presented as means (n=45) (± S.E.). Post-hoc comparisons for ANOVA are represented by different letters using the Tukey post-hoc test ($\alpha<0.05$). For Kruskal-Wallis tests, post-hoc tests are Bonferroni adjusted pairwise comparisons using the Mann-Whitney test

	Treatment patch						
	Small patch	**Corridor**	**Clearcut**	**Lp-edge**	**Lp-interior**	**$F_{4,40}$ or $Chi^2_{4,40}$**	**P value**
Mean saproxylic relative abundance †	13.08 ± 0.82a	13.45 ± 0.85a	12.24 ± 0.87ab	10.95 ± 0.77ab	9.24 ± 0.92b	4.11	**0.01**
Mean saproxylic species richness*	29.67 ± 2.38ab	33.11 ± 1.06a	28.89 ± 3.42ab	25.11 ± 2.69ab	20.78 ± 1.71b	12.28	**0.02**
Mean bark and wood borer relative abundance*	16.22 + 1.91	19.44 ± 2.29	20.56 ± 5.57	13.00 ± 1.55	9.67 ± 1.85	8.47	0.08
Mean bark and wood borer species richness*	10.89 ± 1.05a	8.67 ± 0.97ab	8.22 ± 1.40ab	6.89 ± 0.92ab	5.11 ± 0.54b	14.59	**0.01**

*Kruskall-Wallis test
†Square-root transformed data

Fig. 2.2: Sample-based rarefaction estimates (+/- 1 S.D.) for number of saproxylic beetle species (188 species) (A) and bark and wood-boring species (53 species) (B) in treatment patches (small patch, corridor, clearcut, large patch-edge, large patch-interior) using 9 samples per treatment

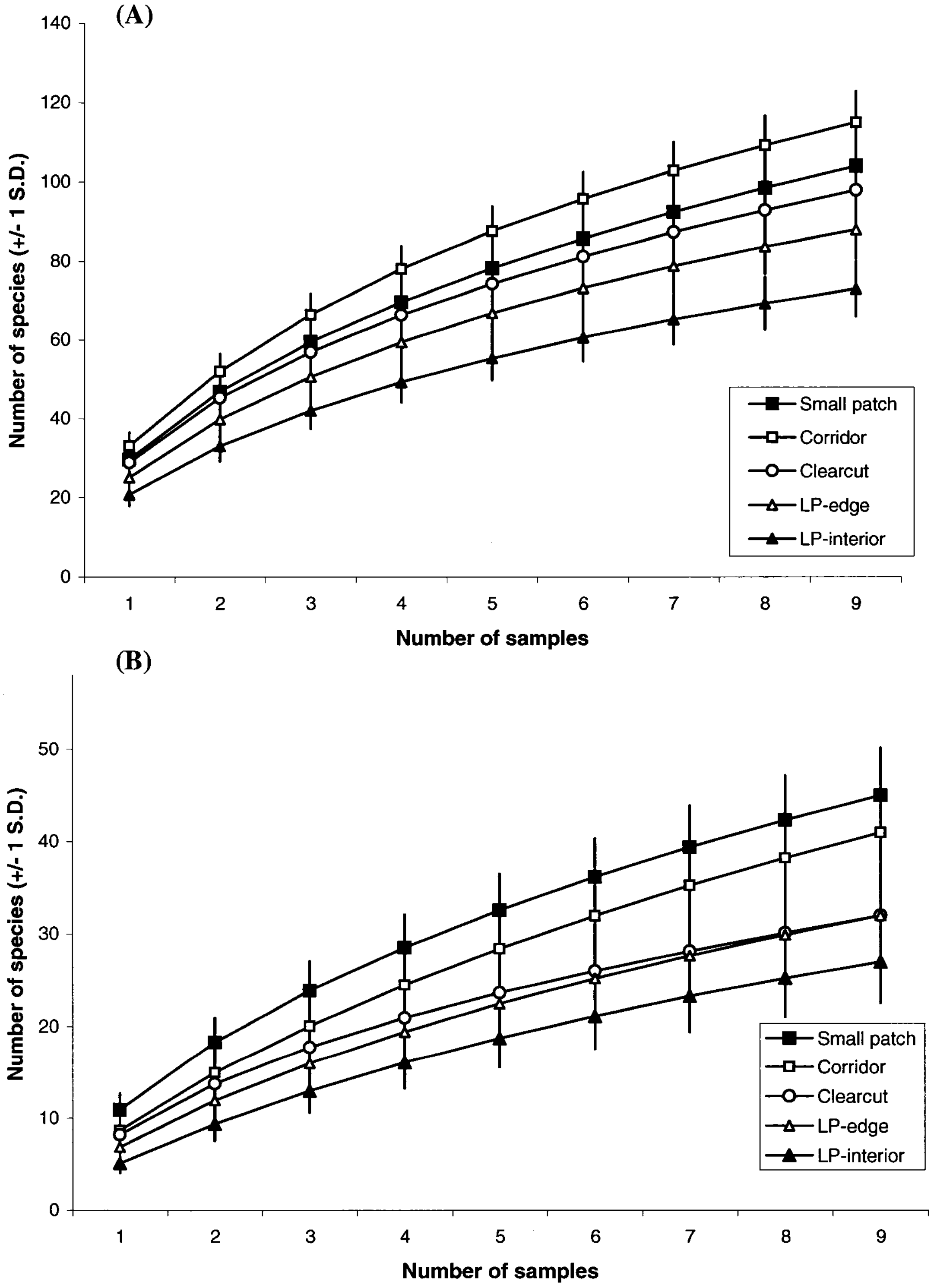

Fig. 2.3: Nonmetric multidimensional scaling (NMS) ordination (axis 1 and 2) plot of 188 saproxylic beetle species from 45 traps in treatment patches (small patch, corridor, clearcut, large patch-edge, large patch-interior). Final stress=13.7, axis 1: p=0.03, axis 2: p=0.001.

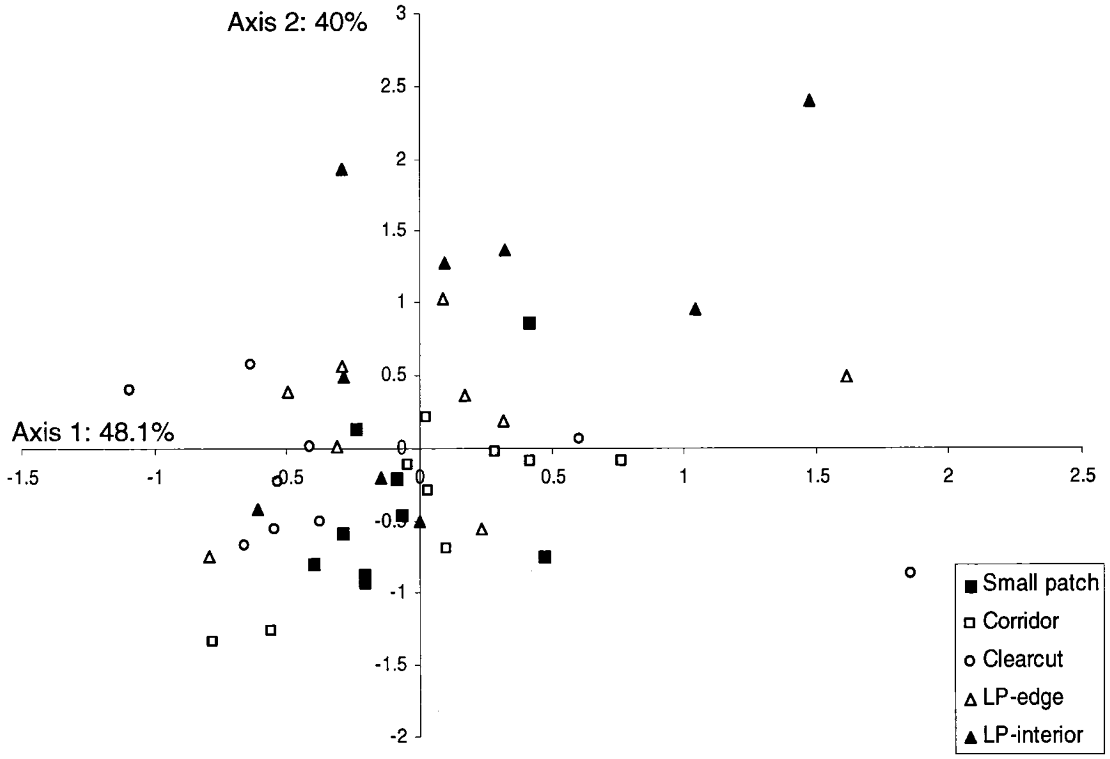

Fig. 2.4: Nonmetric multidimensional scaling (NMS) ordination (axis 1, 2 and 3) plot of 82 bark and wood-boring species from 45 traps in treatment patches (small patch, corridor, clearcut, large patch-edge, large patch-interior). Final stress=18.07, axis 1: p= 0.01, axis 2: p=0.02, axis 3: p=0.01.

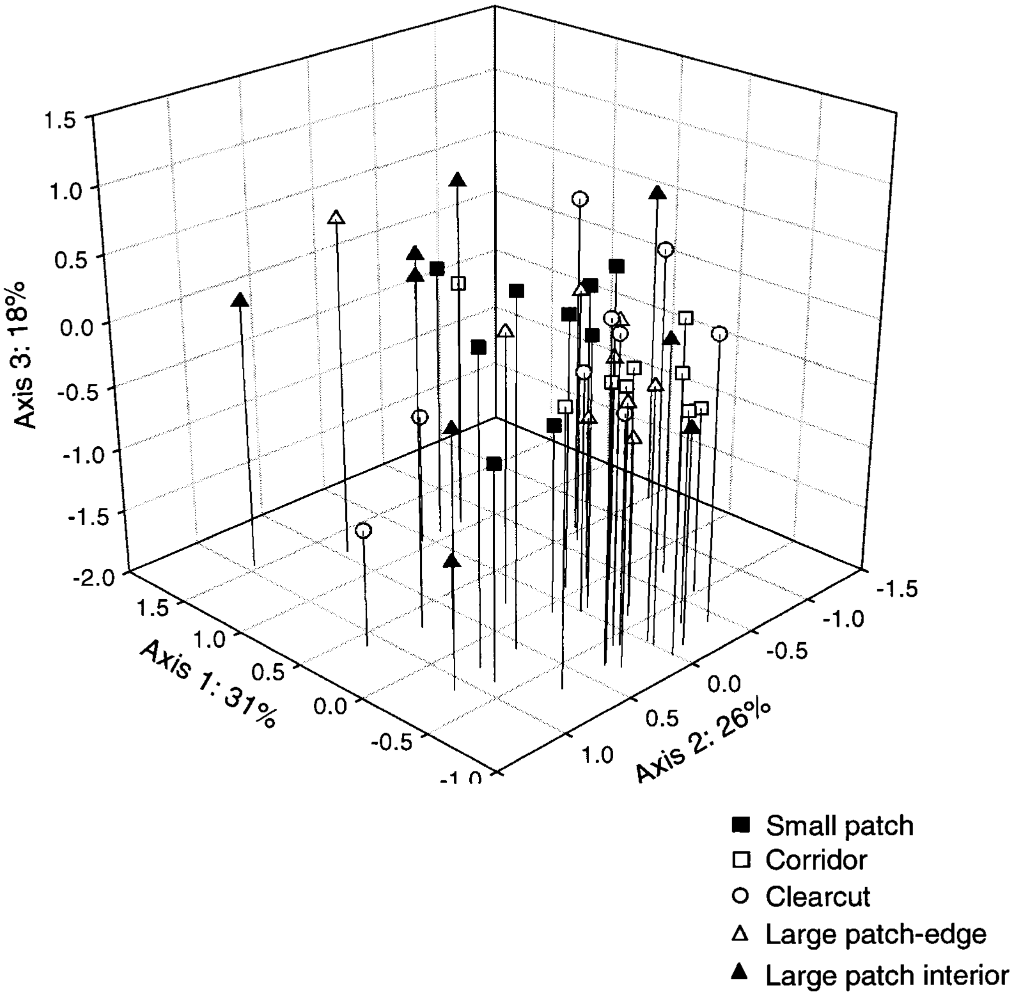

Fig 2.5: Rank-abundance curves: The top 20 most abundant species from total saproxylic beetle data are represented by bars and separated by treatment. Black bars represent significant ($p<0.05$) indicator species. Species codes with full species names are found in Appendix 2.1

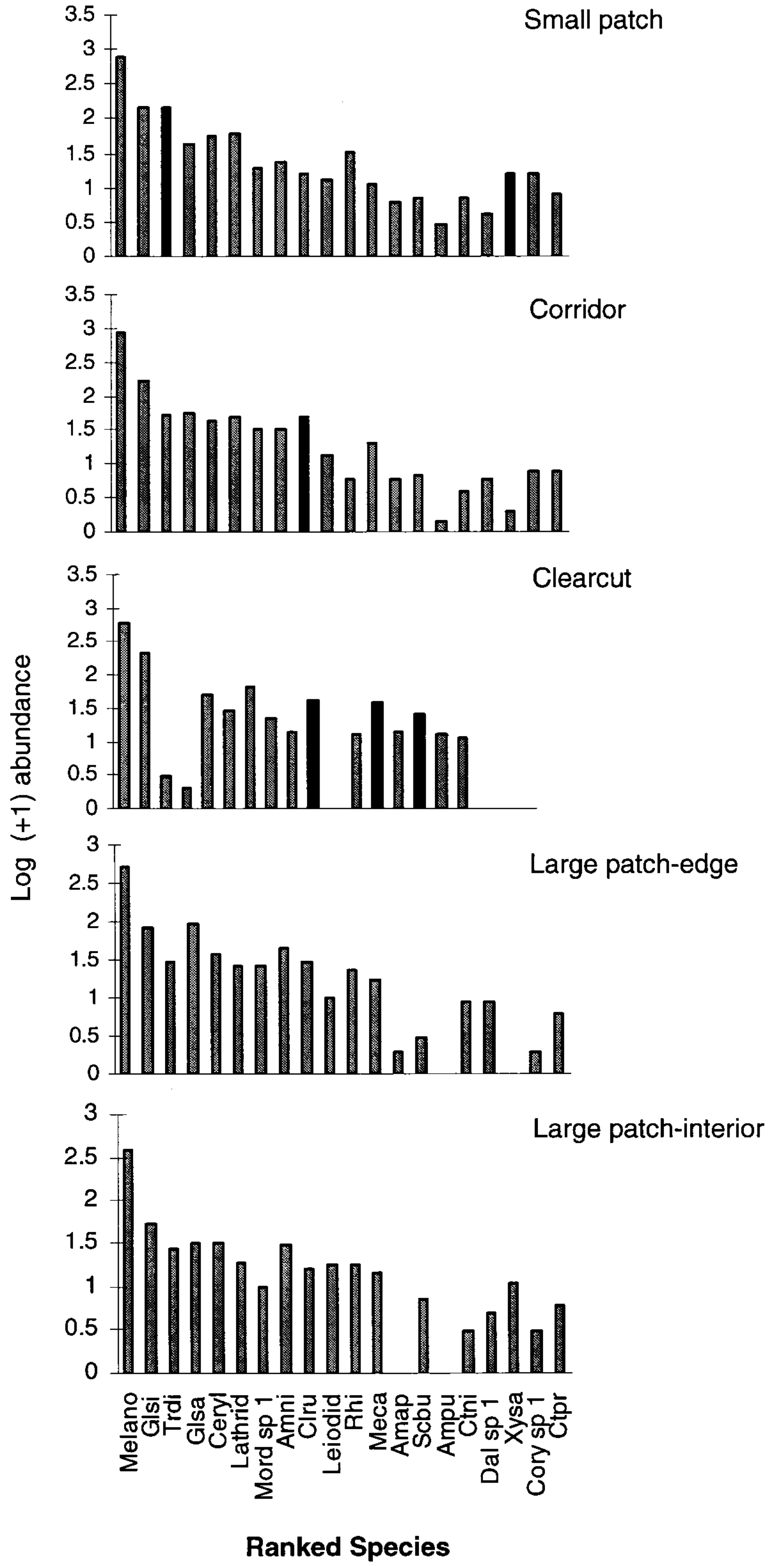

Table 2.3: Indicator species analysis: Significant indicator values ($\alpha<0.05$) for saproxylic beetles by treatment (n=45, 188 species) using MONTE CARLO test of significance of observed maximum indicator value for species using 1000 permutations. Treatment patches where species attain maximum relative abundance, mean relative abundance and standard deviations are also represented.

Family	**Genus**	**Species**	**Author**	**Species code**	**Max treatment**	**Mean**	**Std dev**	**Indicator value (IV)**
Erotylidae	*Triplax*	*dissimulator*	(Crotch)	Trdi	Small patch	27.4	7.43	50.2*
Melandryidae	*Melandrya*	*striata*	Say	Mest	Small patch	16.4	6.46	40*
Scolytidae	*Xyleborus*	*sayi*	(Hopkins)	Xysa	Small patch	18.3	8.35	35.6*
Cerambycidae	*Clytus*	*ruricola*	(Olivier)	Clru	Corridor	24.2	5.3	34.7*
Helodidae	*Cyphon*	sp. 1		Cyph Sp. 1	Corridor	15.6	7.1	37*
Cerambycidae	*Trachyisida*	*mutabilis*	(Newman)	Trmu	Clearcut	9.6	7.03	33.3*
Elateridae	*Ampedus*	*pullus*	Germar	Ampu	Clearcut	18.8	7.94	54.7**
Elateridae	*Pseudanostirus*	*hieroglyphicus*	(Say)	Cthi	Clearcut	14.4	6.46	25.3*
Lampyridae	*Lucidota*	*atra*	(Fabricius)	Luco	Clearcut	16.6	6.42	40**
Lampyridae	*Pyractomena*	*borealis*	(Randall)	Pybo	Clearcut	15.7	6.42	44.4**
Leiodidae	spp.			Leiodid	Clearcut	24.4	5.59	37.8*

* $p<0.05$, ** $p<0.01$

Fig 2.6 Canonical correspondence analysis of 11 measured environmental variables on 186 saproxylic beetle species from 44 samples. Environmental variables with correlations > 0.5 or < –0.5 are graphed

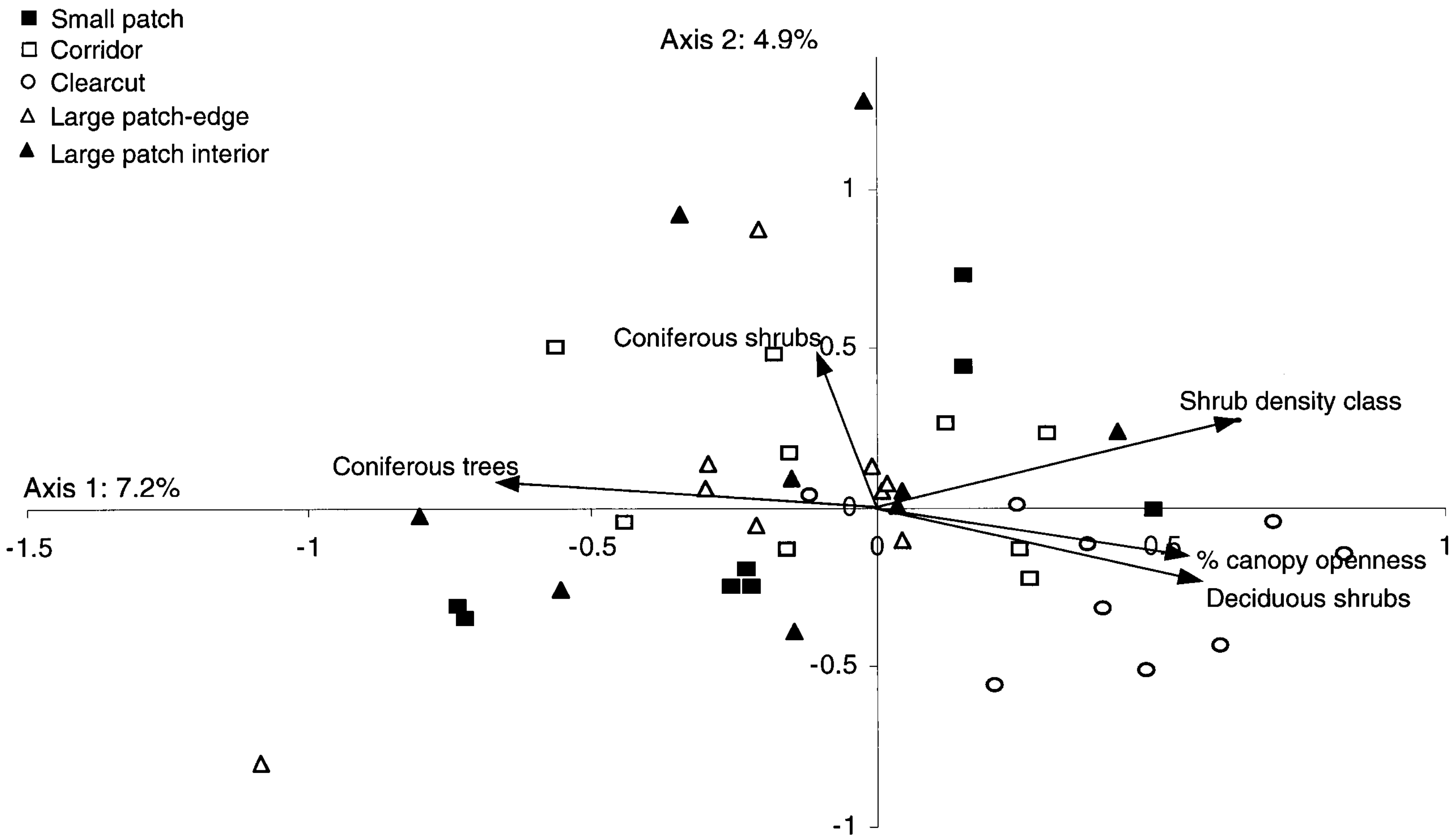

Table 2.4: Results and correlations from a CCA ordination of saproxylic beetles from 44 samples of untransformed data (correlations > 0.5 or <-0.5 in bold).

	Axis	
	1	2
Eigenvalues	0.17	0.12
Species-env. relationship	0.88	0.80
Correlations		
Dec. tree density	-0.12	0.08
Con. tree density	**-0.77**	0.11
Dec. snag density	0.06	0.15
Con. snag density	-0.45	0.25
% Canopy openness	**0.64**	-0.22
Snag basal area	-0.05	0.14
Dec. Shrub density	**0.69**	-0.32
Con. Shrub density	-0.19	**0.65**
Volume of logs	0.29	0.23
Density class	**0.77**	0.39
Dec. tree basal area	-0.02	-0.04

Table 2.5: Results from one-way ANOVA and Kruskall-Wallis testing for the effects of treatment patches (small patch, corridor, clearcut, large patch-edge, large patch-interior) on stand characteristics. Data presented as means ± S.E. Post-hoc comparisons for ANOVA are represented by different letters using the Tukey post-hoc test ($\alpha<0.05$). For Kruskal-Wallis tests, post-hoc tests are Bonferroni corrected pairwise comparisons using the Mann-Whitney test.

Stand Characteristic				**Treatment patch**				
ANOVA	**Small patch**	**Corridor**	**Clearcut**	**Lp-edge**	**Lp-interior**	**F, D.F.**	**F value**	**P value**
Deciduous tree density	14.87 ± 3.14a	14.56 ± 3.83a	0.11 ± 0.11b	14.33 ± 3.03a	13.22 ± 2.54a	$F_{4, 15.49}$	18.73	**<0.0001***
Coniferous tree density	16.75 ± 4.19a	10.33 ± 2.11ab	2.22 ± 1.39b	10.11 ± 2.93ab	10.78 ± 2.86ab	$F_{4, 18.54}$	5.07	**0.006***
Snag density	10.63 ± 1.52a	10.67 ± 2.375a	3.33 ± 0.726b	9.11 ± 2.22ab	6.67 ± 1.08ab	$F_{4, 18.44}$	6.45	**0.002***
Snag basal area†	1.75 ± 0.13a	1.74 ± 0.17a	0.75 ± 0.18b	1.57 ± 0.27a	1.37 ± 0.17ab	$F_{4, 39}$	4.62	**0.004**
Deciduous snag basal area†	1.45 ± 0.26	1.41 ± 0.23	0.70 ± 0.17	1.40 ± 0.28	0.86 ± 0.24	$F_{4, 19.18}$	2.56	0.07*
Deciduous shrub density	15.22 ± 3.12	16.67 ± 4.79	26.44 ± 5.33	15.44 ± 3.44	18.44 ± 5.75	$F_{4, 19.71}$	0.85	0.51*
Log volume††	0.16 ± 0.02	0.18 ± 0.02	0.19 ± 0.02	0.13 ± 0.02	0.13 ± 0.01	$F_{4, 19.14}$	2.64	0.07*
% canopy openness	25.98 ± 3.37a	24.55 ± 1.30a	51.72 ± 4.15b	20.53 ± 1.67a	17.14 ± 0.83a	$F_{4,18.40}$	19.24	**<0.0001***
Kruskal-Wallis	**Small patch**	**Corridor**	**Clearcut**	**Lp-edge**	**Lp-interior**	**Chi^2 D.F.**	**Chi^2 value**	**P value**
Coniferous snag density	1.75 ± 0.84ab	2.22 ± 0.62ab	0.44 ± 0.44a	1.22 ± 0.55ab	3 ± 0.75b	$F_{4,39}$	10.27	**0.04**
Coniferous shrub density	4.56 ± 2.08	2.67 ± 1.17	3.78 ± 1.12	5.00 ± 2.24	6.00 ± 3.01	$F_{4,40}$	0.52	0.97
Density class	2.06 ± 3.5	2.50 ± 2.04	3.22 ± 0.31	2.28 ± 0.324	2.28 ± 0.383	$F_{4,40}$	7.95	0.09
Deciduous snag density	8.75 ± 2.05	8.33 ± 2.60	2.78 ± 0.494	7.56 ± 2.02	3.56 ± 1.13	$F_{4,39}$	8.53	0.07

† Log transformed, †† Square-root transformed

*Welch's F statistic and p=value used to correct for inequality of variance

Table 2.6: Results from Kruskall-Wallis tests for the effects of treatment patches (small patch, corridor, large patch) on aspen-feeding beetle larval density and larval density by family, for snag dissections. Results from Kruskall-Wallis tests for effects of treatment patches on the proportion of snags with aspen-feeding beetle larvae and Cerambycidae larvae present. Data presented as means (n=45) ± S.E. Post-hoc tests performed with pairwise comparisons using a Bonferroni adjusted Mann-Whitney test

	Treatment patch				
	Small patch	**Corridor**	**Large patch**	**Chi$^2_{2,42}$**	**P value**
Mean aspen-feeding beetle larval density	0.52 ± 0.17	1.18 ± 0.60	0.31 ± 0.15	4.42	0.11
Mean Cerambycidae larval density	0.25 ± 0.14	0.45 ± 0.26	0.20 ± 0.14	4.22	0.12
Mean Buprestidae larval density	0.054 ± 0.03	0.054 ± 0.02	0	7.08	**0.03***
Mean Melandryidae larval density	0.13 ± 0.05	0.63 ± 0.52	0.088 ± 0.05	1.76	0.41
Mean Tenebrionidae larval density	0.094 ± 0.03	0.040 ± 0.01	0.016 ± 0.01	5.91	0.05
Proportion of snags with aspen-feeding beetle larvae present	0.17 ± 0.02	0.15 ± 0.02	0.09 ± 0.03	5.68	0.06
Proportion of snags with Cerambycidae larvae present	0.11± 0.03	0.09± 0.03	0.03± 0.02	5.73	0.06

* Post-hoc test does not detect significant differences with Bonferroni adjustment

Table 2.7: Comparison of bark and wood-borer families (Duparquet) (A), and total aspen-feeding Cerambycidae (B) captured in Lindgren funnels (n=15) or density (/dm^3) dissected from snags (n=15) in same treatment patches of site 2 (Duparquet)

(A)	**Lindgren funnels (Adult relative abundance)**					**Snag dissections (Larval density/dm^3)**			
	Small patch	Corridor	Large patch-edge	Large patch-interior	**Total**	Small patch	Corridor	Large patch	**Total**
Cerambycidae	12	32	22	15	**81**	3.8	6.8	3.0	**13.6**
Buprestidae	0	1	0	0	**1**	0.8	0.8	0.0	**1.6**
Melandryidae	13	4	7	6	**30**	1.9	9.4	1.3	**12.6**
Tenebrionidae	0	0	0	0	**0**	1.4	0.6	0.2	**2.2**

(B)		**Lindgren funnels (Adult relative abundance)**					**Snag dissections (Larval density/dm^3)**			
		Small patch	Corridor	Large patch-edge	Large patch-interior	**Total**	Small patch	Corridor	Large patch	**Total**
A. attenuatus	(Haldeman)	1	0	2	0	**3**	0.4	5.3	0.9	**6.6**
B. scalaris	(Say)	1	0	0	0	**1**	2.1	0.6	0.0	**2.7**
T. mutabilis	(Newman)	0	0	0	0	**0**	0.1	0.1	0.0	**0.2**
T. minnesotana	(Casey)	0	0	0	0	**0**	0.3	0.2	0.0	**0.6**
C. ruricola	(Olivier)	8	32	17	15	**57**	0.0	0.0	0.0	**0.0**
P. supernotatus	(Say)	0	0	1	0	**1**	0.0	0.0	0.0	**0.0**
A. modestus	Gyllenhal	0	0	1	0	**1**	0.0	0.0	0.0	**0.0**

Appendix 2.1: Saproxylic beetles captured in 45 Lindgren funnels in treatment patches (small patch, corridor, clearcut, large patch-edge, large patch-interior) in Abitibi, Quebec.

Family	**Genus**	**Species**	**Author**	**Code**	**Small patch**	**Corridors**	**Clearcuts**	**LP-edge**	**LP-interior**	**Total**
Alleculidae	*Androchirus*	*erythropus*	(Kirby)	Aner	0	0	0	0	1	1
Alleculidae	*Hymenorus*	*niger*	(Melsheimer)	Hyni	0	1	2	0	1	4
Alleculidae	*Isomira*	*quadristriata*	(Couper)	Isqu	4	3	7	7	5	26
Alleculidae	*Mycetochara*	*bicolor*	(Couper)	Mybi	2	0	0	0	1	3
Alleculidae	*Mycetochara*	*foveata*	(LeConte)	Myfo	0	1	0	0	0	1
Alleculidae	*Mycetochara*	*fraterna*	(Say)	Myfr	1	1	0	1	0	3
Alleculidae	*Platydema*	*americanum*	Laporte de Castelneau & Brullé	Plam	0	1	0	0	0	1
Alleculidae	*Pseudocistela*	*brevis*	(Say)	Psbr	0	1	0	0	0	1
Anobiidae	*Priobium*	*sericeum*	(Say)	Prse	2	1	6	1	0	10
Anobiidae	*Ptilinus*	*ruficornis*	Say	Ptru	2	0	0	0	0	2
Anthribiidae	*Euparius*	*marmoneus*	(Olivier)	Euma	0	0	2	0	0	2
Apionidae	sp. 1			Apio sp. 1	2	0	1	1	1	5
Buprestidae	*Agrilus*	*anxius*	Gory	Agan	2	1	0	0	0	3
Buprestidae	*Buprestis*	*maculativentris*	Say	Buma	0	1	0	0	0	1
Buprestidae	*Dicerca*	*divaricata*	(Say)	Didi	0	0	1	0	0	1
Buprestidae	*Dicerca*	*tenebrica*	(Kirby)	Dite	2	2	3	0	0	7
Cephaloidae	*Cephaloon*	*ungulare*	LeConte	Ceun	0	0	0	0	0	0
Cerambycidae	*Acmaeops*	*proteus*	(Kirby)	Acpr	1	0	0	0	0	1
Cerambycidae	*Aegomorphus*	*modestus*	(Gyllenhal)	Aemo	0	0	1	1	0	2
Cerambycidae	*Anthophylax*	*attenuatus*	(Haldeman)	Anat	1	0	2	3	0	6
Cerambycidae	*Bellamira*	*scalaris*	(Say)	Besc	1	0	0	0	0	1
Cerambycidae	*Clytus*	*ruricola*	(Olivier)	Clru	16	48	14	29	16	123
Cerambycidae	*Monochamus*	*scutellatus*	(Say)	Mosc	1	2	0	0	0	3

Family	Genus	Species	Author	Code	Small patch	Corridors	Clearcuts	LP-edge	LP-interior	Total
Cerambycidae	*Neoclytus*	*leucozonus*	(Laporte de Castelneau & Gory)	Nele	1	0	1	0	0	2
Cerambycidae	*Phymatodes*	*dimidiatus*	(Kirby)	Phdi	0	0	0	1	0	1
Cerambycidae	*Pogonocherus*	*penicillatus*	LeConte	Pope	1	0	0	0	0	1
Cerambycidae	*Psenocerus*	*supernotatus*	(Say)	Pssu	0	0	0	1	0	1
Cerambycidae	*Pygoleptura*	*nigrella*	(Say)	Pyni	1	0	0	0	0	1
Cerambycidae	*Stictoleptura*	*canadensis*	(Olivier)	Stca	3	2	3	2	0	10
Cerambycidae	*Trachyisida*	*mutabilis*	(Newman)	Trmu	0	0	3	0	0	3
Cerambycidae	*Trigonarthris*	*minnesotana*	(Casey)	Trmi	0	1	0	0	0	1
Cerambycidae	*Xylotrechus*	*undulatus*	(Say)	Xyun	1	1	0	0	0	2
Cerylonidae	*Cerylon*	sp. 1		Ceryl	58	43	51	38	32	222
Ciidae	sp. 1			Cii Sp 1	1	1	1	0	0	3
Ciidae	sp. 2			Cii Sp 2	0	0	0	1	0	1
Ciidae	sp. 3			Cii Sp 3	0	1	0	0	0	1
Ciidae	sp. 4			Cii Sp 4	0	0	1	0	0	1
Ciidae	sp. 5			Cii Sp 5	1	0	0	0	0	1
Cleridae	*Chariessa*	*pilosa*	(Forster)	Chpi	0	1	1	0	0	2
Cleridae	*Cymatodera*	*bicolor*	(Say)	Cybi	0	0	1	0	0	1
Cleridae	*Madioniella*	*dislocatus*	(Say)	Madi	1	3	3	3	0	10
Cleridae	*Thanasimus*	*undatulus*	(Say)	Thun	1	2	0	0	0	3
Cleridae	*Zenodosus*	*sanguineus*	(Say)	Zesa	6	4	0	6	9	25
Colydiidae	*Lasconotus*	*borealis*	Horn	Labo	0	0	0	1	0	1
Colydiidae	*Synchita*	*fuliginosa*	Melsheimer	Syfu	0	0	0	0	1	1
Corylophidae	sp. 1			Cory sp 1	16	8	0	2	3	29
Corylophidae	*Molamba*	*fasciata*	(Say)	Mofa	1	2	0	2	1	6
Cryptophagidae	*Atomaria*	sp. 1		Atom sp	3	9	4	9	3	28
Cryptophagidae	*Cryptophagus*	sp. 1		Crypt Sp 1	0	1	1	0	3	5

Family	Genus	Species	Author	Code	Small patch	Corridors	Clearcuts	LP-edge	LP-interior	Total
Cryptophagidae	*Cryptophagus*	sp. 2		Crypt Sp 2	0	1	0	2	0	3
Cryptophagidae	*Cryptophagus*	sp. 3		Crypt Sp 3	0	0	0	0	2	2
Cryptophagidae	*Cryptophagus*	sp. 4		Crypt Sp 4	1	1	0	1	0	3
Cucujidae	*Cucujus*	*clavipes*	Fabricius	Cucl	1	1	0	0	0	2
Cucujidae	*Pediacus*	*fuscus*	Erichson	Pefu	0	1	0	0	0	1
Curculionidae	sp. 3			Cur sp 10	1	0	2	3	0	6
Curculionidae	*Cossonus*	sp. 4		Cur sp 11	0	0	1	1	1	3
Curculionidae	*Cossonus*	sp. 5		Cur sp 12	0	0	2	0	0	2
Curculionidae	*Rhyncolini*	sp. 6		Cur sp 3	1	0	0	0	0	1
Curculionidae	*Hylobius*	*pinicola*	(Couper)	Cur Sp 4	0	1	0	0	0	1
Curculionidae	*Pissodes*	*fiskei*	(Hopkins)	Cur sp 5	0	1	0	0	0	1
Curculionidae	sp. 9			Cur sp 6	1	0	0	0	0	1
Curculionidae	sp. 10			Cur sp 7	1	0	0	0	0	1
Curculionidae	sp. 11			Cur sp 8	0	0	0	0	1	1
Curculionidae	sp. 12			Cur sp 9	0	0	0	0	1	1
Curculionidae	*Dendroctonus*	*rufipennis*	(Kirby)	De sp 1	0	0	0	0	1	1
Curculionidae	*Dryocoetes*	*affaber*	(Mannerheim)	Draf	0	3	0	0	1	4
Curculionidae	*Dryocoetes*	*autographus*	(Ratzeburg)	Drau	3	5	0	7	8	23
Curculionidae	*Hypothenemus*	*dissimilis*	(Zimmermann)	Hydi	0	4	1	1	1	7
Curculionidae	*Ips*	*latidens*	(LeConte)	Ipla	0	0	1	0	0	1
Curculionidae	*Polygraphus*	*rufipennis*	(Kirby)	Poru	1	12	0	2	2	17
Curculionidae	sp. 1			Sco sp 1	0	1	0	0	0	1
Curculionidae	*Typodendron*	*betulae*	Swaine	Tybe	1	0	0	2	2	5
Curculionidae	*Typodendron*	*lineatum*	(Olivier)	Tyli	1	1	0	1	0	3
Curculionidae	sp. 3			Tini-sco 3	1	0	0	0	0	1
Curculionidae	sp. 4			Tini-sco 4	0	0	0	1	0	1
Curculionidae	*Crypturgus*	*pusillus*	(Gyllenhal)	Crpu	0	0	0	0	1	1
Curculionidae	*Xyleborus*	*sayi*	(Hopkins)	Xysa	16	2	0	1	11	30
Curculionidae	*Xylosterinus*	*politus*	(Say)	Xypo	0	1	0	0	1	2

Family	Genus	Species	Author	Code	Small patch	Corridors	Clearcuts	LP-edge	LP-interior	Total
Elateridae	*Agriotella*	*begiminata*	(Randall)	Agbi	0	0	1	0	0	1
Elateridae	*Agriotella*	*debilis*	LeConte	Agde	5	9	2	1	2	19
Elateridae	*Agriotes*	*fucosus*	(LeConte)	Agfu	1	3	2	4	2	12
Elateridae	*Ampedus*	*apicatus*	(Say)	Amap	6	6	39	2	0	53
Elateridae	*Ampedus*	*evansi*	W.J. Brown	Amev	1	0	0	0	0	1
Elateridae	*Ampedus*	*fusculus*	(LeConte)	Amfu	0	0	0	1	1	2
Elateridae	*Ampedus*	*luctuousus*	(LeConte)	Am sp 1	4	3	4	1	0	12
Elateridae	*Ampedus*	*laurentinus*	(W.J. Brown)	Amla	0	0	1	0	0	1
Elateridae	*Ampedus* sp. 1	*(nigrinus or deletus)*	(Herbst)(LeConte)	Amni	23	32	22	45	30	152
Elateridae	*Ampedus*	*pullus*	Germar	Ampu	3	7	26	0	1	37
Elateridae	*Athous*	*productus*	(Randall)	Atpr	1	0	1	1	0	3
Elateridae	*Athous*	*rufifrons*	(Randall)	Atru	3	3	0	5	2	13
Elateridae	*Ctenicera*	*insidiosa*	(LeConte)	Ctin	0	0	1	0	0	1
Elateridae	*Ctenicera*	*resplendens*	(Randall)	Ctre	0	0	3	2	0	5
Elateridae	*Dalopius*	*cognatus*	W.J. Brown	Dal sp 1	4	6	11	9	5	35
Elateridae	*Danosoma*	*brevicorne*	(LeConte)	Dabr	1	1	5	0	0	7
Elateridae	*Denticollis*	*denticornis*	(Kirby)	Dede	8	4	4	0	6	22
Elateridae	*Eanus*	*estriatus*	(LeConte)	Eaes	0	1	0	1	0	2
Elateridae	*Eanus*	sp. 1		Ean sp 1	0	1	0	0	0	1
Elateridae	*Limonius*	*aegar*	LeConte	Liae	0	1	0	0	0	1
Elateridae	*Liotrichus*	*falsifica*	(LeConte)	Lifa	1	0	0	0	0	1
Elateridae	*Liotrichus*	*spinosa*	(LeConte)	Ctsp	2	1	1	4	0	8
Elateridae	*Melanotus*	*castanipes*	(Paykull)	Meca	11	20	13	17	14	75
Elateridae	*Pseudanostirus*	*hieroglyphicus*	(Say)	Cthi	1	5	5	0	0	11
Elateridae	*Pseudanostirus*	*propolus*	(LeConte)	Ctpr	8	8	1	6	6	29
Elateridae	*Pseudanostirus*	*triundulatus*	(Randall)	Cttr	7	8	7	3	2	27
Elateridae	*Selatosomus*	*appropinquans*	(Randall)	Ctap	0	2	2	1	0	5

Family	Genus	Species	Author	Code	Small patch	Corridors	Clearcuts	LP-edge	LP-interior	Total
Elateridae	*Selatosomus*	*aratus*	(LeConte)	Sear	0	1	2	0	0	3
Elateridae	*Selatosomus*	*nitidula*	(LeConte)	Ctni	7	4	13	9	3	36
Elateridae	sp. 1			Elat sp 1	0	0	1	0	0	1
Elateridae	sp. 2			Elat sp 2	0	1	0	0	0	1
Endomychidae	*Endomychus*	*biguttatus*	Say	Enbi	0	5	11	7	5	28
Endomychidae	*Lycoperdina*	*ferruginea*	(LeConte)	Lyfe	0	0	1	0	0	1
Endomychidae	*Mycetina*	*perpulcha*	(Newman)	Mype	0	0	4	1	0	5
Endomychidae	*Phymaphora*	*pulchella*	Newman	Phpu	5	7	1	5	8	26
Erotylidae	*Triplax*	*dissimulator*	((Crotch))	Trdi	144	51	3	30	27	255
Erotylidae	*Triplax*	*frosti*	Casey	Trfr	1	1	0	1	0	3
Erotylidae	*Triplax*	*thoracica*	Say	Trth	3	1	1	4	0	9
Erotylidae	*Tritoma*	*pulchra*	(Say)	Trpu	0	1	0	0	0	1
Eucinetidae	*Eucinetus*	sp. 1	LeConte	Euci sp 1	0	1	2	0	0	3
Eucinetidae	*Eucinetus*	*terminalis*	LeConte	Eute	1	5	2	2	2	12
Eucnemididae	*Deltometopus*	*amoenicornis*	(Say)	Deam	0	0	3	0	0	3
Eucnemididae	*Dromaeolus*	*harringtoni*	Horn	Drha	2	6	4	1	2	15
Eucnemididae	*Hylis*	*terminalis*	(LeConte)	Hyte	1	0	0	0	0	1
Eucnemididae	*Isorhipis*	*obliqua*	(Say)	Isob	1	0	0	0	0	1
Eucnemididae	*Microrhagus*	sp. 1		Micr sp 1	2	1	1	0	0	4
Eucnemididae	*Nematodes*	*penetrans*	(LeConte)	Nepe	2	1	0	1	0	4
Helodidae	*Nycteus*	*oviformis*	(LeConte)	Nyov	0	1	1	0	1	3
Helodidae	*Cyphon*	sp. 1		Cyph sp 1	2	10	2	0	1	15
Helodidae	*Cyphon*	sp. 2		Cyph sp 2	4	4	1	0	0	9
Helodidae	*Cyphon*	sp. 3		Cyph sp 3	0	0	2	0	0	2
Laemophloeidae	*Laemophloeus*	sp. 1	(Say)	Laem	1	1	3	10	13	28
Lampyridae	*Lucidota*	*corrusca*	(Linné)	Luco	0	6	15	2	2	25
Lampyridae	*Photuris*	*pensylvanica*	(DeGreer)	Phpe	0	1	1	0	0	2
Lampyridae	*Pyractomena*	*borealis*	(Randall)	Pybo	2	2	10	1	0	15

Family	Genus	Species	Author	Code	Small patch	Corridors	Clearcuts	LP-edge	LP-interior	Total
Lathridiidae	*Enicmus or Lathridius.*	Spp.		Lathrid	61	49	29	27	19	185
Lathridiidae	*Melanophthalma*	sp. 1		Melano	752	867	614	499	389	3121
Leiodidae	spp.			Leiodid	13	13	40	10	18	94
Lucanidae	*Platycerus*	*depressus*	LeConte	Plde	1	0	0	0	0	1
Lycidae	*Caenia*	*dimidiata*	(Fabricius)	Cadi	0	1	0	0	0	1
Lycidae	*Dictyopterus*	*aurora*	(Herbst)	Diau	0	2	1	2	0	5
Lycidae	*Leptoceletes*	*basalis*	LeConte	Ceba	0	1	1	1	0	3
Lycidae	*Plateros*	sp. 1		Plat Sp 1	0	0	3	0	0	3
Melandryidae	*Dircaea*	*liturata*	(LeConte)	Dili	0	0	3	1	0	4
Melandryidae	*Enchodes*	*sericea*	(Haldeman)	Ecse	2	1	0	3	1	7
Melandryidae	*Melandrya*	*striata*	Say	Mest	12	1	5	1	1	20
Melandryidae	*Melandrya or Emmesa*	*connectens*	Newman	Meco	9	2	8	5	4	28
Melandryidae	*Orchesia*	*castanea*	(Melsheimer)	Orca	5	2	5	0	1	13
Melandryidae	*Orchesia*	*ovata*	Laliberté	Orov	1	0	0	0	0	1
Melandryidae	*Scotochroa*	*buprestoides*	(Kirby)	Scbu	7	7	14	3	7	38
Melandryidae	*Serropalpus*	*substriatus*	Haldeman	Sesu	0	1	0	1	2	4
Melandryidae	*Xylita*	*livida*	(C.R. Sahlberg)	Xyli	1	0	0	0	0	1
Mordellidae	*Mordella*	sp. 1		Mord sp 1	19	36	67	26	10	158
Mordellidae	*Tomoxia*	*lineella*	LeConte	Toli	0	0	0	1	0	1
Mycetophagidae	*Mycetophagus*	sp. 3		Myc sp 3	0	0	1	0	0	1
Mycetophagidae	*Mycetophagus*	sp. 1		Myc sp 1	2	0	0	0	0	2
Mycetophagidae	*Mycetophagus*	*flexuosus*	Say	Myc sp 2	0	0	1	0	0	1
Nitidulidae	*Epuraea*	*flavomaculata*	Mäklin	Epfl	18	3	0	3	0	24
Nitidulidae	*Epuraea*	*planulata*	Erichson	Eppl	6	8	2	4	4	24
Nitidulidae	*Epuraea*	*rufa*	(Say)	Epru	3	0	0	0	0	3
Nitidulidae	*Epuraea*	sp. 1		Epu sp 1	2	0	0	0	2	4
Nitidulidae	*Epuraea*	sp. 2		Epu sp 2	1	1	0	2	2	6
Nitidulidae	*Epuraea*	sp. 3		Epu sp 3	0	0	0	4	1	5

Family	Genus	Species	Author	Code	Small patch	Corridors	Clearcuts	LP-edge	LP-interior	Total
Nitidulidae	*Epuraea*	sp. 4		Epu sp 4	0	0	0	2	1	3
Nitidulidae	*Glishrochilus*	*moratus*	(W.J. Brown)	Glmo	1	0	0	0	0	1
Nitidulidae	*Glishrochilus*	*sanguinolentus*	(Olivier)	Glsa	44	55	2	93	32	226
Nitidulidae	*Glishrochilus*	*siepmanni*	W.J. Brown	Glsi	141	164	214	84	55	658
Nitidulidae	*Glishrochilus*	*vittatus*	(Say)	Glvi	0	0	0	0	1	1
Pyrochroidae	*Dendroides*	*concolor*	(Newman)	Deco	1	4	4	0	2	11
Pyrochroidae	*Schizotus*	*cervicalis*	Newman	Scce	0	0	1	0	0	1
Rhizophagidae	*Rhizophagus*	sp. 1		Rhi	32	6	1	23	18	80
Salpingidae	*Rhinosimus*	*viridiaeneus*	Randall	Rhvi	3	9	1	2	1	16
Scarabaeidae	*Caelius*	*rufescens*	Horn	Caru	0	1	0	0	0	1
Scarabaeidae	*Osmoderma*	*scabra*	Beauvois	Ossc	1	0	0	0	0	1
Scarabaeidae	*Trichiotinus*	*assimilis*	(Kirby)	Scar sp 1	0	0	1	0	0	1
Scraptiidae	*Anaspis*	*nigrina*	Csiki	Anni	0	1	0	0	0	1
Scraptiidae	*Anaspis*	*rufa*	Say	Anru	4	7	0	2	0	13
Scraptiidae	*Canifa*	sp. 1		Can sp 1	3	5	10	4	0	22
Scraptiidae	*Canifa*	sp. 2		Can sp 2	7	2	4	2	2	17
Silvanidae	*Dendrophagus*	cygnaei	Mannerheim	Decy	2	4	0	1	5	12
Silvanidae	sp. 1			Sil sp 1	0	1	0	0	0	1
Sphindidae	*Odontosphindus*	*denticollis*	LeConte	Odde	1	3	1	0	2	7
Sphindidae	*Sphindus*	*trinifer*	Casey	Sptr	0	3	5	3	1	12
Tenebrionidae	*Neatus*	*tenebrioides*	(Beauvois)	Nete	0	0	1	0	0	1
Tenebrionidae	sp. 1			Ten sp 1	0	1	0	0	0	1
Tenebrionidae	*Upis*	*ceramboides*	(Linné)	Upce	0	0	8	0	0	8
Tetratomidae	*Penthe*	*obliquata*	(Fabricius)	Peob	0	0	2	0	0	2
Tetratomidae	*Penthe*	*pimelia*	(Fabricius)	Pepi	0	3	0	1	0	4
Tetratomidae	*Tetratoma*	sp. 1		Tetra sp 1	0	1	0	0	0	1
Tetratomidae	*Tetratoma*	*tesselata*	(Melsheimer)	Tete	1	3	2	1	0	7
Trogossitidae	*Thymalus*	*marginicollis*	Chevrolat	Thyma	3	2	0	2	4	11

CONNECTING STATEMENT

Chapter 2 has shown that habitat remnants such as small patches and corridors may help preserve biodiversity in harvested landscapes by mimicking post-fire residuals. Chapter 3 focuses on the effect of partial cutting, believed to imitate natural gap dynamics, on saproxylic beetle assemblages. Alternative management strategies to clearcutting further diversify forest management and few studies have tested their effects on saproxylic biodiversity.

CHAPER 3: The effect of partial-cut harvesting on saproxylic beetle assemblages

ABSTRACT

This study explores the effects of partial harvesting on saproxylic beetles, a diverse group dependant on dead or dying wood. In 1/3 and 2/3 partial cut patches, saproxylic beetle relative abundance, raw species richness and species composition was found to be intermediate to that of clearcut and uncut forest. However, bark and wood-boring beetle species accumulated at the fastest rate in partial cuts and uncut forest but at the lowest rate in clearcuts, which had the fewest snags. Partial cuts had higher densities and basal areas of deciduous and coniferous snags than other treatments. Beetle species that were most abundant in the total data were captured more often in partial cuts than other treatments. Diversification of forest management with partial cutting may conserve a broad range of species by keeping characteristics of uncut forest undergoing gap disturbances.

INTRODUCTION

Natural disturbance and succession dynamics have been studied extensively in the south-eastern boreal forest of Abitibi, Quebec (Dansereau and Bergeron, 1993; Morin et al., 1993; Paré and Bergeron, 1996; Bergeron et al., 1998; Bergeron and Leduc, 1998; Bergeron, 2000; Bergeron et al., 200; Harper et al., 2002; Kneeshaw and Bergeron, 1996; 1998; Lefort et al., 2003). Management models for harvesting practices that better mimic natural disturbance and succession dynamics have been developed as an approach to maintaining ecological sustainability and biodiversity (Hunter, 1993; Gauthier et al., 1996; Bergeron and Harvey, 1997; Lähde et al., 1999; Harvey et al., 2002; Bergeron et al., 2002). Harvesting and management practices should aim to maintain natural forest composition, age-structure, stand dynamics and characteristics of the forest mosaic (Harvey et al., 2002; Bergeron and Harvey, 1997; Gauthier et al., 1996).

Partial cutting is an uneven-aged harvesting method, which uniformly removes a percentage of stems from the stand. This modifies the composition and structure of the stand towards older forest cover types (mid-late successional types) (Bergeron et al., 2002; Harvey et al., 2002). Partial harvest is theorized to mimic natural succession and disturbance (i.e. gap dynamics) patterns, which bring a deciduous-dominated stand to an increasingly mixedwood composition and later into a conifer-dominated stand (Bergeron and Harvey, 1997; Bergeron et al., 2002; Harvey et al., 2002). Density of retained trees after partial harvest affects canopy openness, penetration of sunlight, temperature, humidity, water and air flow (Parker, 1995 in Schowalter et al., 2005). Partial cutting reduces the contrast between harvested and unharvested areas, which may increase associated faunal diversity.

There is concern about the effects of forest management on biodiversity and more studies are needed to test the efficacy of alternative silvicultural practices on flora and fauna. The effects of partial cuts on arthropods have been relatively less studied compared to small mammals and birds (e.g. Norton and Hannon, 1997; Lance and Phinney, 2001; Tittler et al., 2001; Harrison et al., 2005). Hoonbok and Moldenke (2005) found higher ground-dwelling arthropod abundance and diversity in various intensities of thinned stands compared to unthinned treatments in young douglas fir (*Pseudotsuga menziesii* (Mirb.)) stands in Oregon. Species richness of carabids increased in thinned bottomland hardwood stands due to the preference of many species to open, disturbed conditions (Warriner et al., 2002). Canopy arthropods showed little short-term response to different levels of partial and clearcut harvesting in douglas fir dominated forests (Schowalter et al., 2005). Partial harvesting (30%) had no effect on decomposing soil invertebrates (Collembolans and enchytraeids) compared to controls, while clearcutting only slightly disturbed the community (Siira-Pietikäinen et al., 2001).

In mixed pine-hardwood stands in Arkansas and Oklahoma, an intermediate diversity of beetles was collected in partial cuts, compared to uncut and clearcut forest, with a higher number of species collected under increasingly intense forest harvest (Cook, 2002). Species richness of cerambycids was higher in recently thinned hardwood forests than unthinned stands, due to the presence of increased logging slash debris (Warriner et al., 2002). In lodgepole pine stands (*Pinus contorta* Dougl. ex Loud.) in Alberta, abundance of bark beetles (Scolytinae), *Trypodendron lineatum* Olivier, and pine engravers, *Ips pini* (Say), collected in baited funnel traps and window traps, were significantly higher in thinned stands than in unthinned stands for all 3 years after thinning due to an increased abundance of dead wood (Hindmarch and Reid, 2001). In lodgepole pine stands of British Columbia, an increase in abundance of bark beetles was collected in thinned stands 2 years after treatment, compared to unthinned stands (Safranyik et al., 2004).

Few published studies have assessed the role of partial harvesting in conservation of boreal forest saproxylic beetle communities. Saproxylic refers to organisms that are dependant on dead or dying wood during some part of their lifecycle (Speight, 1989). These organisms include bark and wood-borers, parasites and parasitoids, predators, detritivores and fungivores (Speight, 1989; Dajoz, 2000). Saproxylic insects have been shown to be sensitive to management practices (Berg et al., 1994, Siitonen and Martikainen, 1994; Martikainen et al., 2000; Siitonen, 2001; Grove, 2002a; Grove, 2002b; Maeto et al., 2002) and major saproxylic beetle community differences have been found between closed forest and clearcut stands (Kaila et al., 1997; Grove, 2002b; Sverdrup-Thygeson and Ims, 2002). Saproxylic organisms are crucial to ecosystem function as decomposers of woody debris and as a food source for higher trophic groups, particularly birds (Harmon et al., 1896; Speight, 1989; Grove, 2000a).

The majority of studies in partial cuts have focused on the effect of canopy removal and the live tree component rather than on the dead wood dynamics and associated fauna of partial cuts. In the SAFE (sylviculture et aménagement forestier écosystémique) project where our research takes place, there were large increases in fresh coarse woody debris (CWD) in clearcuts and significant differences occurred with partial cuts (Brais et al., 2004b). However, clearcut harvest significantly reduced the volume of well-decayed CWD compared to partial cuts. Decomposition rate of dead wood significantly increased after clearcut harvest compared to partial cuts (Brais et al., 2004b). In hardwood forests of the Adirondack mountains, large diameter snag densities and basal areas were significantly lower in partial cut stands compared to maturing and old growth forests because of reduced inter-tree competition in partial cut stands (McGee et al., 1999). Partial cuts had significantly lower downed log volume than old growth forests but not maturing forests (McGee et al., 1999). These studies demonstrate that partial cutting has effects on dead wood quality and abundance and associated fauna may be affected.

This study will compare partial cuts to uncut forest and clearcut areas to assess the relative effects of different levels of canopy removal on saproxylic beetle communities. The goal of this study is to assess the effects of partial harvest in terms of: i) relative abundance and species richness of saproxylic and bark and wood-boring beetles; ii) saproxylic beetle species composition; and iii) local stand characteristics best explaining species composition with emphasis on standing dead wood availability. I predict that the intensity of harvest will increasingly alter beetle species composition compared to uncut patches. I also predict that clearcuts and interiors of uncut patches will have the most dissimilar species composition and partial cuts will be intermediate. Insect relative abundance should increase with intensity of harvest, however species richness should be highest in partial cuts because clearcuts may not support forest interior species.

METHODS

Study area

This study was conducted in the mixedwood boreal forest in the Abitibi region of northwest Quebec, in the SAFE (Sylviculture et aménagement forestier écosystémique) project (48° 28-29', 79° 24-26'). In SAFE, experimental clearcuts were performed and replicated near the Lake Duparquet teaching forest. Detailed maps can be found in Brais et al. (2004a). Phase1 (bloc 1, 2 and 3) and Phase 2 (bloc 2) were sampled in three replicates of each treatment patch: clearcut, 1/3 partial cut, 2/3 partial cut and uncut. Phase 1 dates back to a 1923 fire and Phase 2 dates back to a 1760 fire but has also been affected by the last spruce budworm outbreak in 1970-1987, increasing the deciduous component of the forest (Brais et al., 2004a). Phase 1 is aspen-dominated and was harvested in 1999; Phase 2 is also aspen-dominated but has more mixedwood and was harvested in 2000 (Brais et al., 2004a; Brais et al., 2004b). Clearcuts were CPRS (Cut with protection of regeneration of soils) and were between 1.6 and 4.8 ha and partial cuts were between 1.9 and 3.4 ha. In 1/3 cut treatments, 27 % of lower quality stems were removed leaving conifers and healthy aspen trees (Brais, 2004a). In the 2/3 cut stand, 58 % of the good quality aspen stems were harvested leaving conifers and lower quality aspen. Controls were large continuous uncut patches of forest (Brais et al., 2004a).

Using sampling quadrats (400 m^2) to measure tree density, it was determined that our sampling sites were dominated by trembling aspen (*Populus tremuloides* Mchx.) (60% of stems > 10 cm DBH), white birch (*Betula papyrifera* Marshall) (33%) and in less abundance, white and black spruce (*Picea glauca* (Moench), *P. mariana* (Mill)) (24%), balsam fir (*Abies balsamea* (L.)) (15%), balsam poplar (*Populus balsamifera* (L.)) (4%) and jack pine (*Pinus banksiana* Lamb) (5%).

Beetle Sampling

One Lindgren funnel, consisting of eight stacked funnels, (Lindgren, 1983) and one trunk-window trap was placed approximately in the center of each treatment patch to collect adult saproxylic beetles, except in large patches where one trap was placed on the edge (approx. 20 m from the edge) and one in the interior (approx. in the center of the patch). Since both sampling devices target dispersing adults, trunk traps were used to supplement the Lindgren funnel data. All samples were taken from Phase 1 except one large patch and one clearcut from Phase 2 because of practical constraints related to size of clear-cuts and accessibility. However, these were directly comparable to Phase 1 in tree composition and patch size. Traps were installed on 4 June 2005, removed 8 August 2005, and emptied every two weeks for a total of four sampling dates. Trunk-window traps and Lindgren funnels were collected on the same sampling dates. The trunk-window traps were constructed out of a rectangular piece of plexiglass (14 x 23 cm), attached to an inverted transparent plastic soda bottle, forming a funnel. A plastic container (6.5 x 7.5 cm) was attached to the neck of the soda bottle and was half-filled with 50% propylene glycol and 50% water, functioning as a collection jar. The Lindgren funnel collection jar was filled to a depth of 5 cm with the same solution. The trunk-window traps were installed on trembling aspen or white birch snags (early-mid decay class) approximately 15-30 m away from the Lindgren funnel. Commercial ethanol-based bait was purchased through Pherotech Inc., to increase saproxylic captures. The baits were attached to Lindgren funnels and replaced when empty throughout the sampling period. Beetles were sorted from the bulk samples and preserved in 70% ethanol.

Stand characteristics

A 400 m^2 quadrat was formed around each Lindgren with one north-south and one east-west transect positioned in the middle of each side of the square quadrat. Fallen dead logs and stumps (> 5 cm diameter) intersecting the transects were counted and the diameters measured. The formula estimating volume along these transects was retrieved from Harmon et al. (1986). Live and dead standing tree species (DBH >10 cm) were counted in each quadrat and diameter at breast height was measured. Snag decay stage (early, mid, late) was assessed using external characteristics but this data is not presented due to the small sample size and high variance. Along the north-south transect, shrubs and small understory trees touching the transect, which was set at 1 m above ground, were counted as either deciduous or coniferous. The average understory height was estimated and shrub density was categorized using density classes, which were based on relative shrub densities in SAFE (0=open, 1=low density, 2=medium, 3=high, 4=very high density). At each Lindgren funnel, two pictures with a digital camera with a fish-eye lens attached was taken from about 1.5 m in height. The pictures were analyzed to obtain percent canopy openness with the software Gap Light Analyzer (G.L.A., 1999).

Beetle Identification

Adult saproxylic beetles were identified to species or morphospecies using Arnett et al. (2002), Downie and Arnett (1996), and Laplante et al. (1991). Cerambycidae were identified to species using Yanega (1996) and Scolytinae were identified using Bright (1976). Staphylinids were not identified and included in this study due to time constraints. Adult beetle specimens were either verified by S. Laplante, Y. Bousquet or cross-checked at the Canadian National Collection of insects, arachnids and nematodes (Ottawa, Canada).

Bark and wood-boring beetles were analyzed separately from total saproxylic beetles because this diverse functional group are most directly associated with dead wood and more taxonomic resources and expertise can be obtained for species in this guild. Families that were considered bark and wood-borers, although some feed on bark or fungi-infected wood, include Anobiidae, Alleculidae, Buprestidae, Cephaloidae, Cerambycidae, Curculionidae, Eucnemididae, Melandryidae, Mordellidae, Pyrochroidae, Scarabaeidae, Scraptiidae, and Tenebrionidae.

ANALYSES

Sampling dates for Lindgren funnels and trunk-traps were pooled together by treatment for all analyses. Using SAS (Statistical Analysis Software v. 8.02, 2001), one-way ANOVA was used to assess differences between treatments (1/3 cut, 2/3 cut, clearcut, large patch-edge, large patch-interior) in terms of relative abundance and raw species richness of total saproxylic beetles and bark and wood-borers. Tukey's H.S.D. test (alpha=0.05) was used for post-hoc multiple comparisons in ANOVA. The Shapiro-Wilk test was used to determine if data was normally distributed and the Levene's test was used to determine homogeneity of variance.

Using the software *EcoSim* (v. 7, 2001), individual-based rarefaction was used to compare species diversity, due to small sample size (Gotelli and Colwell, 2001; Gotelli and Entsminger, 2001; Buddle et al., 2005). Rarefaction shows the rate of accumulation of new species as new individuals are added, verifying that enough have been collected to make accurate species richness comparisons (Gotelli and Colwell, 2001; Buddle et al., 2005).

Indicator species analysis using PC-ORD (v. 4.17, 1999) determined which species had affinities for certain treatments (n=15, 125 species) (McCune and Mefford, 1999). Indicator species analysis assigns a probability to an indicator value using a Monte Carlo test of 1000 permutations (McCune and Grace, 2002).

Non-metric multidimensional scaling (NMS) ordination was used to create ordination plots reflecting species compositional differences between treatments by means of the Bray-Sorenson distance measure and the software PC-ORD (McCune and Mefford, 1999). NMS ordination is suited for non-normal discontinuous data typical of ecological work and avoids assumptions on linearity among variables (McCune and Grace, 2002). Un-transformed abundance and presence/absence data was analyzed. Starting configuration of a DCA ordination was used for the NMS ordination instead of random starting coordinates to lower stress levels and avoid local minima. Before a final ordination solution was performed by PC-ORD, a six-dimensional ordination was run to evaluate stress reduction and selection of the number of axes. A Monte Carlo test of 100 runs evaluated the strength and significance of the axes (McCune and Grace, 2002).

A canonical correspondence analysis (CCA) evaluated beetle community structure as explained by measured site characteristics with PC-ORD (McCune and Mefford, 1999). CCA constrains a species matrix to an environmental matrix by a multiple linear regression. Pooled Lindgren funnel and trunk-window trap data were untransformed. Row and column scores were standardized by centering and normalizing. A Monte Carlo test of 100 runs was employed to assess significance of the axes with the null hypothesis of no relationship between the species and environment matrix. Measured site characteristics considered for the CCA include deciduous tree density, coniferous tree density, deciduous snag density, coniferous snag density, % canopy openness, snag basal area, deciduous shrub density, coniferous shrub density, volume of logs and shrub density class.

Stand characteristics were also analyzed using ANOVA or Kruskal-Wallis tests by treatment (Large patch-interior, large patch-edge, 1/3 partial cut, 2/3 partial cut, clearcut) followed by Tukey post-hoc test or a Bonferonni adjusted Mann-Whitney test for non-parametric tests.

RESULTS

A total of 2246 saproxylic beetles were captured, consisting of 125 species and morphospecies in 15 Lindgren funnels and 15 trunk-window traps. Three hundred and twelve beetles and 41 species were bark and wood-borers. In Lindgren funnels, 1969 individuals and 108 species were captured, while in trunk-window traps 277 individuals and 56 species were collected (Appendix 3.1).

The saproxylic beetle species or morphospecies making up >2% of the total abundance collected include: *Melanophthalma* sp.1 (Lathridiidae) (51.1%), *Mordella* sp. 1 (Mordellidae) (4.9%), *Glishrochilus siepmanni* W.J. Brown (Nitidulidae) (4.1%), *Cerylon* sp. 1 (Cerylonidae) (3.5%), *Ampedus nigrinus*

(Herbst) (2.9%). Beetles of the closely related genera *Enicmus* or *Lathridius* (2.8%) (Lathridiidae) and Family Leiodidae (2.8%) were not identified to species.

Significantly more bark and wood-boring beetle individuals were collected from clearcuts compared to all other treatments (Table 3.1). Saproxylic beetle raw species richness, saproxylic beetle relative abundance and bark and wood-boring beetle species richness did not show treatment effects in the one-way ANOVA tests. However, the highest relative abundances and species richness of saproxylic beetles were consistently found in clearcuts and the lowest in interior of large patches. Very similar relative abundance and species richness of saproxylic and bark and wood-boring beetles were collected in 1/3 and 2/3 partial cut patches.

Clearcuts accumulated sapoxylic species at the fastest rate and had the highest number of species, while edges of large patches had the lowest rarified species richness (Fig 3.1a). There is a large amount of overlap in standard deviation among rarefaction curves which confirms the non-significance in ANOVA testing species richness by treatment. For bark and wood-boring beetle rarefaction curves, clearcuts had the highest number of individuals and species but the lowest species accumulation rate (Fig 3.1b). Interiors of large patches had the fewest individuals and the fastest species accumulation, closely followed by partial cuts.

In 1/3 partial cut patches, all 15 of the most abundant species in the total saproxylic beete data were collected (Fig. 3.2). In 2/3 partial cuts, no specimens of *Melandrya connectens* Newman (Melandryidae) were captured, although the 14 other most abundant species in the total data were trapped. In clearcuts and interiors of large patches, *Triplax dissimulator* (Crotch) (Erotylidae) and species from family Rhizophagidae were never collected. *Scotochroa buprestoides* (Kirby) (Melandryidae) was never captured at edges of large patches; a singleton was captured from the family Leiodidae. In the interior of large patches, no *M. connectens* nor *Clytus ruricola* (Olivier) (Cerambycidae) were caught, though a singleton of *S. buprestoides* was found.

The only significant indicator species present in the top 15 most abundant species was *Mordella* sp. 1 (Mordellidae) (mean: 35.5 ± 6.76, I.V.: 50, p=0.016).

Significant indictor species, *Mordella* sp. 1 and *Sphindus trinifer* (Casey) (Sphindidae) (mean: 29.7 ± 15.25, I.V.: 80, p=0.041), both occurred in maximum abundance in clearcut treatments.

A similar community structure was found in both saproxylic beetle relative abundance and presence/absence NMS ordinations (Fig. 3.3a and 3.3b). Relative abundance is weighted towards common species, while the presence/absence ordination gives equal weight to all species. The bark and wood-borers were not sampled in sufficient abundance to allow for stable ordinations.

The two-dimensional ordination of un-transformed relative abundance data explained 68.9% of the variance on the first two axes, which were significant (Fig. 3.3a). Clearcuts and interior of large patches are clustered at each end of the plot on axis 2. Partial cuts have a saproxylic species composition that is intermediate to each extreme and more similar to edges of large patches. The closer position of partial cut samples (both 1/3 and 2/3 partial cut treatments) in the ordination space indicates less variation in species composition of saproxylic beetle assemblages in these treatments than in both clearcut and uncut forests (interior or edge).

In the three-dimensional ordination of presence/absence data, all axes are significant and explain 71.6% of the variance. The partial cut patches have an intermediate species composition to clearcuts and interior of large patches, similar to the previous ordination. Two thirds partial cut patches are similar in composition to clearcuts while 1/3 partial cut patches are closer to interior of large patches.

In a CCA ordination, 26.2% of the variance is explained and axis 1 is significant (p=0.04) (Fig. 3.4). Variables with intraset correlations that were larger than 0.5 or smaller than -0.5 were graphed (Table 3.2, Fig. 3.4). Deciduous snag density has a correlation coefficient (axis 1: 0.49) just below the cut-off, but it was graphed because it is an important resource for saproxylic beetles. Weaker patterns can be expected for deciduous snags than live deciduous trees. Deciduous snag density explains variation in species composition for partial cut patches (Fig. 3.4). Deciduous tree density is important in structuring saproxylic beetle assemblages in partial cuts and interior of large patches. Percentage canopy openness and deciduous shrub density explain variation in species composition in clearcuts and edge of large patches.

The ANOVA and Kruskal-Wallis tests on stand characteristics by treatment demonstrate that canopy openness is significantly different in clearcuts compared to other treatments (Table 3.3). There is significantly higher log volume and shrub density in clearcuts compared to interior of large patches. Although non-significant, the highest snag densities and basal area occurred in 1/3 and 2/3 partial cuts and the lowest in clearcuts. Athough non-significant, the highest coniferous snag densities occurred in 1/3 cut patches and the highest deciduous snag density was in 2/3 partial cut patches.

DISCUSSION

Saproxylic beetles appear to readily use partial cuts, which had higher snag densities and snag basal areas than other treatments. Relative abundance and raw species richness patterns were similar for saproxylic and bark and wood-boring groups across treatments. Relative abundance and raw species richness were highest in clearcuts, intermediate in partial cuts and lowest in interior of large patches. Significantly more bark and wood-boring individuals were collected in clearcuts, over twice the number collected in partial cuts.

Different rarified species richness patterns were observed in clearcuts for saproxylic and bark and wood-boring beetles. Bark and wood-borers accumulated species at the fastest rate in interior of large patches and partial cuts, and the slowest in clearcuts, which begins to reach an asymptote, indicating few additional bark and wood-boring species will be collected from this habitat as new individuals are added. In contrast, highest rarified saproxylic beetle species richness was collected in clearcuts but were not significantly different than other treatments. Snag densities and basal areas were highest in partial cuts, providing increased habitat to bark and wood-boring species. Clearcuts had higher log volume but fewer snags than other treatments, which may reduce habitat for some bark and wood fauna. This indicates that other saproxylic beetle guilds, which are extremely abundant in the total data, such as fungivores and predators, may be less affected by snag availability than bark and wood-borers. Certain saproxylic beetles may be also using clearcuts as dispersal pathways but may not necessarily be suitable habitat.

Partial cuts may provide habitat for a greater range of species than clearcuts by keeping some characteristics of uncut forest. One-third partial cuts were the only treatment collecting the top 15 most abundant saproxylic beetle species in the total data; 2/3 partial cuts collected 14 species. The fungivorous species *Triplax dissimulator* was never collected in clearcuts and interior of large patches but was abundantly collected in 1/3 and 2/3 partial cuts. The genus *Triplax* is generally distributed in North America and larvae feed on soft bracket fungi (Arnett et al., 2002). Although little is known of habitat preferences of these beetles in North America. Mycetophilous beetles, which include *Triplax*, are considered indicators of well-preserved ecosystems in Europe (Franc, 1997). In European countries, numerous species of *Triplax* are endangered or threatened (Franc, 1997).

Species compositions in partial cuts and edges of large patches were intermediate to those of uncut and clearcut stands and retained species from both extremes. Both relative abundance and presence/absence ordinations of saproxylic assemblages displayed similar patterns with clearcuts and interior of large patches being clustered at each extreme of the plot with unique species compositions. The intensity of partial harvest influenced beetle composition in presence/absence ordination, where 2/3 partial cuts were similar in composition to clearcuts and 1/3 partial cuts were closer to interior of large patches. Forest interiors and partial cuts probably support some beetle species that are dependant on forested areas and not capable of surviving in clearcut areas.

Intermediate species composition of partial cuts in relation to uncut and clearcut forest has also been found with birds (Norton and Hannon, 1997; Lance and Phinney, 2001; Harrison et al., 2005). Beetles (Cook, 2002), carabids (Warriner et al., 2002), cerambycids (Warriner et al., 2002) and ground-dwelling arthropods (Hoonbok and Moldenke, 2005) have been found to increase in species richness in thinned or partially cut forest when compared to uncut forest.

Canopy openness best explained patterns of saproxylic species composition in ANOVA and had the highest intreaset correlation coefficient in CCA. In European studies, clearcuts containing remnant snags are hotspots for aspen-feeding saproxylic beetle diversity (Kaila et al., 1997; Martikainen, 2001; Sverdrup-Thygeson and Ims, 2002; Lindhe et al., 2005). Aspen-dependant beetles are adapted to natural disturbance and are known in Europe to prefer snags located in sunny open spaces like clearcuts (Kaila et al., 1997; Martikainen, 2001; Sverdrup-Thygeson and Ims, 2002; Lindhe et al., 2005). During seven years of saproxylic beetle collection using emergence traps in cut high-stumps of spruce, birch, aspen and oak, 2/3 of all saproxylic beetles favored semi or fully sun-exposed substrates, where most red-listed species were found (Lindhe et al., 2005). In North America, knowledge of species habitat preference is so weak that a similar coarse-grain analysis is not possible.

Dispersal, perception and host-searching behavior may be linked to collection patterns in flight-based traps. Saproxylic beetles are thought to be attracted to the long, dark silhouette of a snag while locating potential hosts in flight (Chenier and Philogene, 1989). The Lindgren funnel may be more visible to a beetle in flight in a clearcut compared to the interior of forests, where there are many obstructions to movement and vision. Low snag density and basal area in clearcuts reduces the number of potential hosts for beetles to land on and may increase the catch probability in the Lindgren funnel. For example, the wood-boring beetle *Clytus ruricola* was collected in all treatment patches except interior of large patches. Snag habitat was not limiting compared to other treatments; however tree density may impede movement and host-searching ability for this species. Very little is known in North America on saproxylic beetle life history and habitat preferences, which would explain patterns found for individual species. It is possible that many species could be already threatened by human influence without even being known to science, except by name.

Conclusions

Partial cuts appear to be readily used by saproxylic beetles and had high dead wood abundance. Similar to other studies (see introduction), intermediate species composition and relative abundance were collected in partial cuts, compared to cut and uncut forest. On a landscape scale, partial cuts reduce the effects of fragmentation by retaining characteristics of uncut forest and this may sustain species with dependence on late-successional host species, low dispersal capability or inability to survive in clearcut matrix. However, large scale disturbances such as fire are also necessary to preserve a large portion of the fauna. In Europe's boreal forest, threatened species have been found predominantly on aspen snags in clearcuts (Sverdrup-Thygeson and Ims, 2002; Lindhe et al., 2005), which are the main stand-replacing event substituting wildfire (Siitonen, 2001). In Chapter 2, higher larval densities were found in aspen snags located in habitat remnants within clearcuts. These habitat remnants also collected a greater relative abundance and species richness of adult beetles than clearcuts or forest interiors and demonstrated low variance in community structure. However, fragmentation may increase populations of disturbance-driven insects to the detriment of the forest interior specialists. This suggests diversification of forest and dead wood management may support a broader range of saproxylic beetles in the boreal forest than clearcut harvesting alone.

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Table 3.1: Results from one-way ANOVA testing for the effects of treatment patches (large patch-interior, large patch-edge, 1/3 partial cut, 2/3 partial cut, clearcut) on relative abundance and species richness (saproxylic, bark and wood-boring beetles) captured in pooled Lindgren funnels and trunk-window trap samples. Data (n=15) presented as means ± S.E. Post-hoc comparisons for ANOVA are represented by different letters using the Tukey post-hoc test ($\alpha<0.05$).

	Treatment patch						
	Lp-interior	**Lp-edge**	**1/3 partial cut**	**2/3 partial cut**	**Clearcut**	**$F_{4,14}$**	**P value**
Relative abundance saproxylic	93.3 ± 29.2	134 ± 27.1	174 ± 4.7	159.7 ± 20.5	188 ± 16.5	3.03	0.07
Relative abundance bark and wood-borers	12 ± 5.3b	19.3 ± 4.9b	17 ± 2.7b	16.3 ± 4.0b	39.3 ± 13.7a	6.55	**0.007**
Species richness saproxylic	24.3 ± 1.2	25 ± 1.2	34.7 ± 1.2	32.7 ± 5.5	36.3 ± 3.7	3.19	0.063
Species richness bark and wood-borers	7 ± 2.0	8.0 ± 1.7	9.3 ± 2.5	9.3 ± 4.2	10.3 ± 3.0	0.64	0.65

Fig. 3.1: Individual-based rarefaction estimates +/- 1 S.D. for species richness of saproxylic beetles (125 species) (A) and bark and wood-boring beetles (41 species) (B) for 5 sampled treatment patches (3 samples per treatment) (Large patch-interior, large patch-edge, 1/3 partial cut, 2/3 partial cut, clearcut), using pooled Lindgren funnels and trunk-window trap samples.

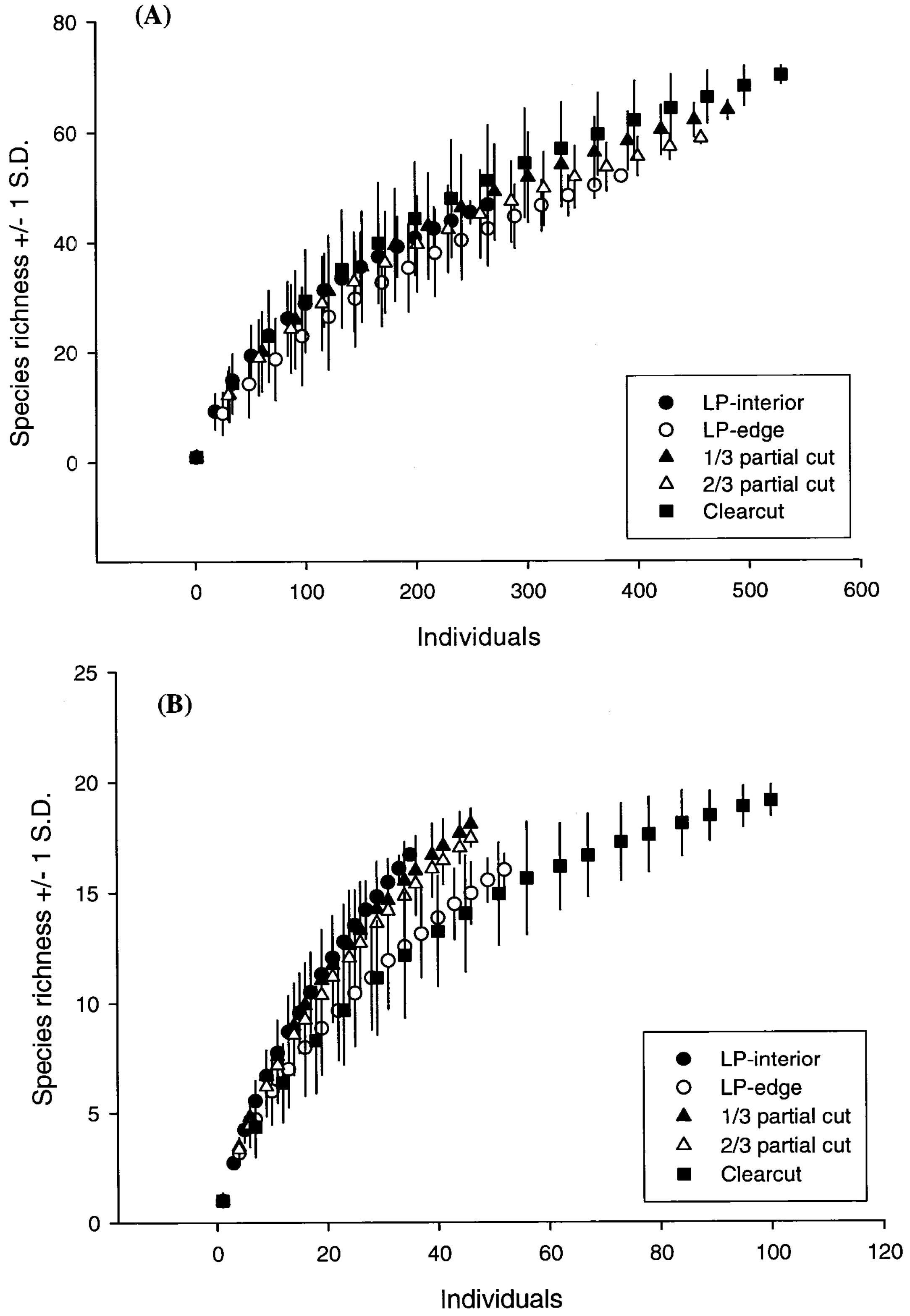

Fig 3.2: Rank-abundance curves where the 15 most abundant species from total saproxylic beetle data (pooled Lindgren funnels and trunk-window traps) are represented by bars and separated by treatment. The black bars represent significant ($p<0.05$) indicator species. Species codes with full species names are found in Appendix 3.1.

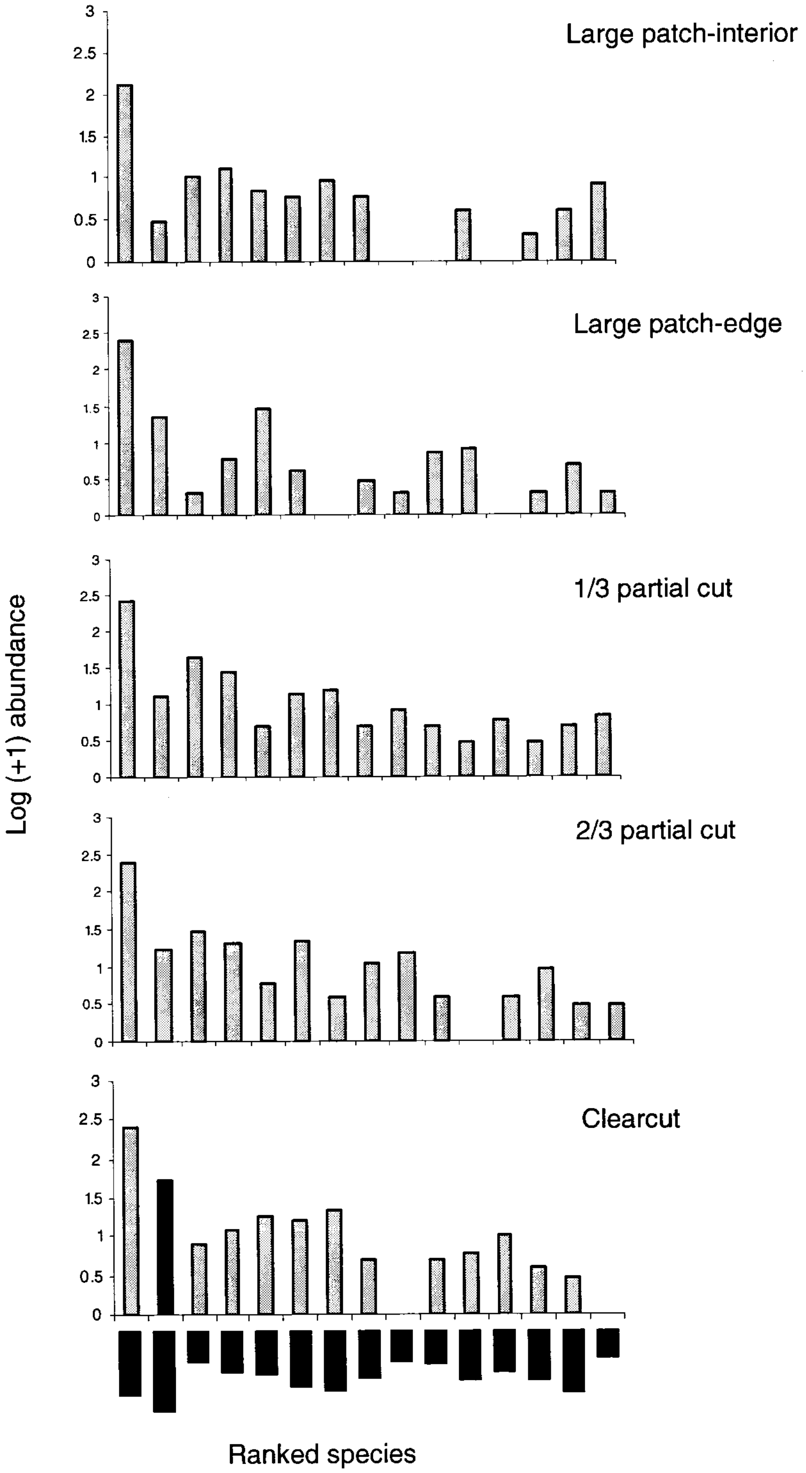

Fig. 3.3: Two-dimensional non-metric multidimensional scaling (NMS) ordination of untransformed saproxylic beetle data (19.75 = final stress, axis 1 p=0.049, axis 2=0.040) (A) and, 3-dimensional NMS presence/absence ordination of saproxylic beetle data (13.38 = final stress, axis 1: p=0.040, axis 2: p=0.049, axis 3: p=0.040) (B), collected in 15 pooled Lindgren funnels and trunk-window traps in treatment patches (large patch-interior, large patch-edge, 1/3 partial cut, 2/3 partial cut, clearcut)

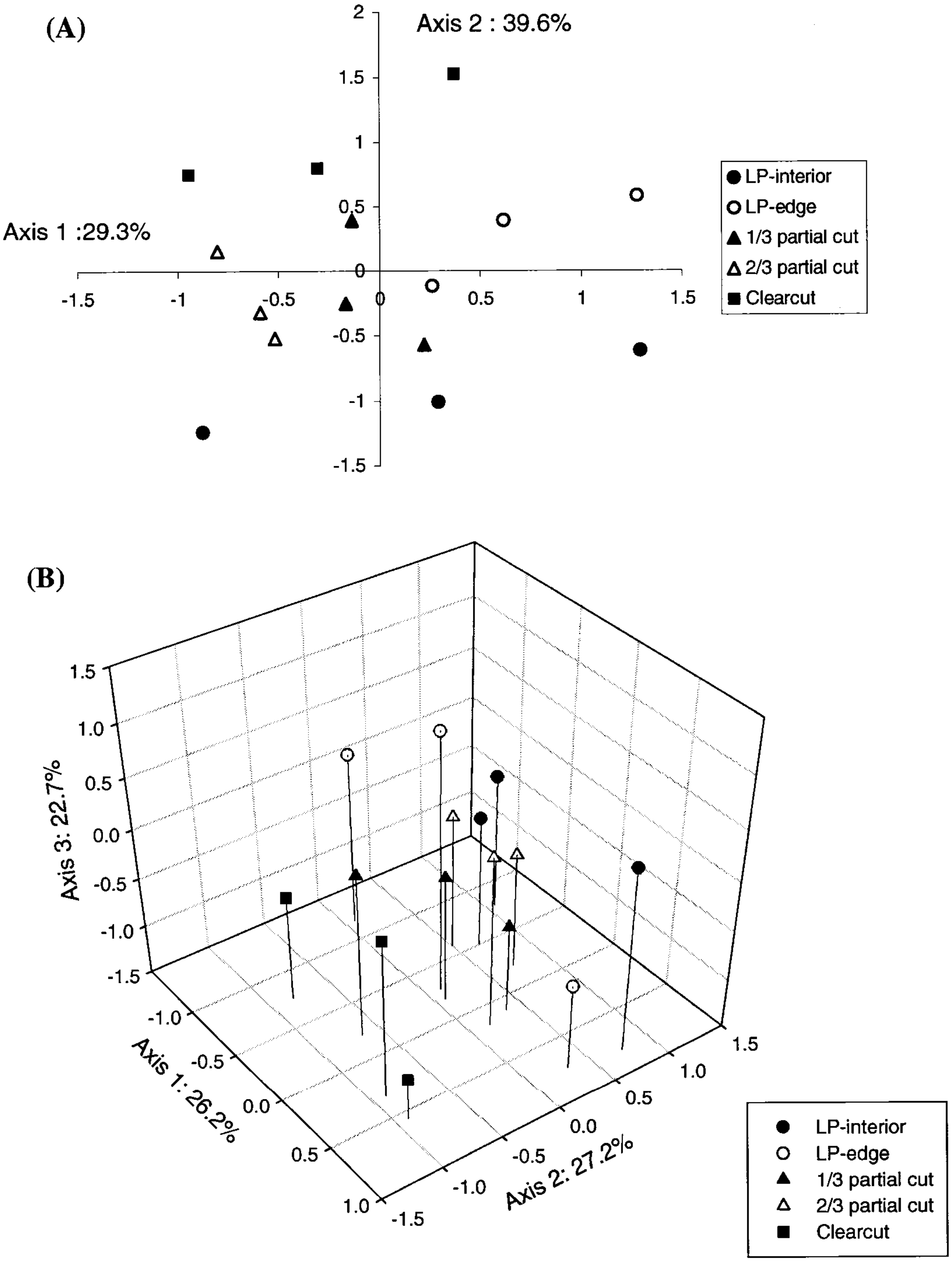

Fig 3.4: Canonical correspondence analysis of 10 measured stand characteristics on 125 species from samples of 15 pooled Lindgren funnels and trunk-window traps sampled in treatment patches (large patch-interior, large patch-edge, 1/3 partial cut, 2/3 partial cut, clearcut). Stand characteristics with correlations > 0.5 or < –0.5 are graphed. Monte Carlo test for species-environment correlation: axis 1: p= 0.04, axis 2: p=0.69.

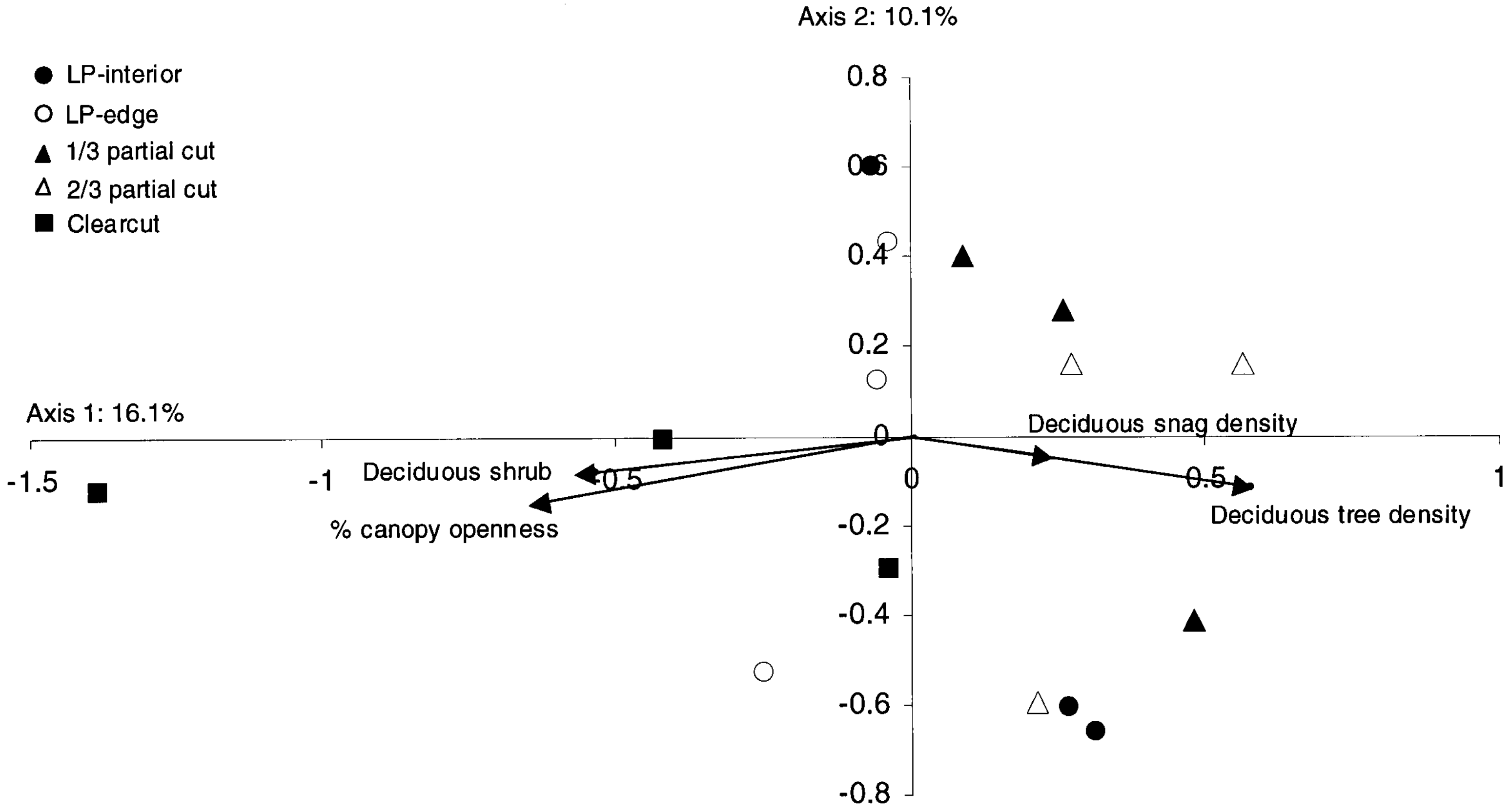

Table 3.2: Results and correlations from a CCA ordination of saproxylic beetles from 15 samples (pooled Lindgren funnels and trunk traps) of untransformed data (correlations > 0.5 or <-0.5 in bold)

	Axis	
	1	**2**
Eigenvalue	0.22	0.14
Species-env. correlation	0.10	0.10
Correlations		
Deciduous tree density	**0.62**	-0.16
Coniferous tree density	0.43	-0.11
Deciduous snag density	**0.49**	-0.13
Coniferous snag density	0.2	0.28
% canopy openness	**-0.65**	-0.22
Snag basal area	0.41	0.13
Deciduous shrub density	**-0.57**	-0.11
Coniferous shrub density	-0.46	0.23
Log volume	-0.26	-0.34
Shrub density class	-0.44	-0.02

Table 3.3: Results from one-way ANOVA and Kruskal-Wallis testing for the effects of treatment patches (large patch-interior, large patch-edge, 1/3 cut, 2/3 cut, clearcut) on site characteristics. Data (n=15) presented as means ± S.E. Post-hoc comparisons for ANOVA are represented by different letters using the Tukey post-hoc test. Post-hoc tests on Kruskal-Wallis results performed using Bonferroni adjusted Mann-Whitney tests.

Stand Characteristic								
ANOVA	**Lp-interior**	**Lp-edge**	**1/3 partial cut**	**2/3 partial cut**	**Clearcut**	**F, D.F.**	**F value**	**P value**
Deciduous snag basal area	14.62 ± 7.43	5.29 ± 1.29	6.76 ± 3.16	20.66 ± 11.51	1.43 ± 0.54	$F_{4, 4.325}$	2.60	0.18*
Deciduous shrub density	19.67 ± 5.81	19.33 ± 4.63	18.00 ± 3.22	21.33 ± 2.60	31.00 ± 1.53	$F_{4, 14}$	1.84	0.20
% canopy openness	16.31 ± 1.59b	18.81 ± 2.80b	19.3 ± 0.68b	24.55 ± 1.97b	62.15 ± 2.36a	$F_{4, 14}$	90.85	**<0.0001**
Kruskal-Wallis	**Lp-interior**	**Lp-edge**	**1/3 partial cut**	**2/3 partial cut**	**Clearcut**	**Chi^2, D.F.**	**Chi^2**	**P value**
Deciduous tree density	18.33 ± 6.36	10.00 ± 2.08	14.33 ± 2.67	17.00 ± 4.36	0.00 ± 0.00	$F_{4, 14}$	8.64	0.07
Coniferous tree density	6.67 ± 4.41	5.00 ± 2.52	6.67 ± 3.33	5.33 ± 1.67	0.67 ± 0.67	$F_{4, 14}$	3.14	0.54
Snag density	5.00 ± 2.08	3.33 ± 0.33	6.67 ± 1.45	6.67 ± 1.76	2.33 ± 0.67	$F_{4, 14}$	0.72	0.12
Deciduous snag density	3.67 ± 2.33	3.00 ± 0.00	3.67 ± 1.45	6.33 ± 1.86	2.33 ± 0.67	$F_{4, 14}$	5.09	0.28
Coniferous snag density	1.33 ± 0.88	0.33 ± 0.33	3.00 ± 1.73	0.33 ± 0.33	0.00 ± 0.00	$F_{4, 14}$	4.71	0.32
Snag basal area	20.27 ± 11.27	11.67 ± 6.44	24.61 ± 9.15	21.94 ± 10.82	1.43 ± 0.54	$F_{4, 14}$	6.60	0.16
Log volume	0.008 + 0.003	0.008 ± 0.002	0.03 ± 0.01	0.02 + 0.004	0.07 ± 0.02	$F_{4, 14}$	11.60	**0.02****
Coniferous shrub density	0.33 ± 0.33	5.67 ± 2.91	0.67 ± 0.33	0.00 ± 0.00	3 ± 1.53	$F_{4, 14}$	7.83	0.98
Density class	1.33 ± 0.33	2.50 ± 0.29	2.33 ± 0.33	2.00 ± 0.00	3.33 ± 0.33	$F_{4, 14}$	10.18	**0.04****

* Welch's F statistic and p-value used to correct for inequality of variances

\+ Post-hoc tests on Kruskal-Wallis results yielded detected no differences when Bonferroni adjusted

**No significant differences detected between treatments using Bonferroni adjusted pairwise comparisons with the Mann-Whitney test

Appendix 3.1: Saproxylic beetles captured in 15 Lindgren funnels and 15 trunk-window traps in treatment patches (large patch-interior large patch-edge, 1/3 partial cut, 2/3 partial cut, clearcut) in Abitibi, Quebec.

					Lindgren funnels					**Trunk-window traps**					
Family	**Genus**	**Species**	**Author**	**Code**	**1/3 cut**	**2/3 cut**	**Clearcut**	**LP-edge**	**LP-interior**	**1/3 cut**	**2/3 cut**	**Clearcut**	**LP-edge**	**LP-interior**	**Total**
Alleculidae	*Androchirus*	*erythropus*	(Kirby)	Aner	0	1	0	0	1	0	0	0	0	0	**2**
Alleculidae	*Hymenorus*	*niger*	(Melsheimer)	Hyni	0	1	1	0	0	0	0	0	0	0	**2**
Alleculidae	*Isomira*	*quadristriata*	(Couper)	Isqu	0	2	5	4	4	1	0	0	0	0	**16**
Alleculidae	*Mycetochara*	*bicolor*	(Couper)	Mybi	0	2	0	0	1	0	0	0	0	0	**3**
Alleculidae	*Mycetochara*	*foveata*	(LeConte)	Myfo	0	1	0	0	0	0	0	0	0	0	**1**
Anobiidae	*Calymmaderus*	sp. 1		Cani	0	0	0	0	0	4	0	0	1	0	**5**
Anobiidae	*Probium*	*sericeum*	(Say)	Prse	0	0	6	0	0	0	0	0	0	0	**6**
Anobiidae	*Ptilinus*	*ruficornis*	Say	Ptru	0	1	0	0	0	0	1	0	0	0	**2**
Anthribiidae	*Euparius*	*marmoneus*	(Olivier)	Euma	0	0	1	0	0	0	0	0	0	0	**1**
Apionidae	sp. 1			Apio sp 1	0	0	0	1	1	0	0	0	0	0	**2**
Buprestidae	*Agrilus*	*anxius*	Gory	Agan	0	0	0	0	0	0	1	0	0	0	**1**
Buprestidae	*Dicerca*	*tenebrica*	(Kirby)	Dite	0	0	2	0	0	0	0	0	0	0	**2**
Cephaloidae	*Cephaloon*	*ungulare*	LeConte	Ceun	1	0	0	0	0	0	0	0	0	0	**1**
Cerambycidae	*Anthophylax*	*attenuatus*	(Haldeman)	Anat	1	0	2	1	0	1	0	0	0	0	**5**
Cerambycidae	*Clytus*	*ruricola*	(Olivier)	Clru	5	2	5	7	0	0	2	0	0	0	**21**
Cerambycidae	*Evodinus*	*monticola*	(Randall)	Evmo	1	1	0	0	0	0	0	0	0	0	**2**
Cerambycidae	*Stictoleptura*	*canadensis*	(Olivier)	Stca	0	2	3	1	0	0	1	1	1	3	**12**
Cerambycidae	*Trachyisida*	*mutabilis*	(Newman)	Trmu	0	0	1	0	0	0	0	0	0	0	**1**
Cerambycidae	*Trigonarthris*	*minnesotana*	(Casey)	Trmi	0	0	0	0	0	0	1	0	0	0	**1**
Cerylonidae	*Cerylon*	sp. 1		Ceryl	24	16	12	6	13	3	4	0	0	0	**78**
Ciidae	*Cis*	*fuscipes*	Mellié	Cifu	0	0	0	0	0	0	1	0	0	0	**1**
Ciidae	sp. 5			Ciid sp 5	0	0	0	0	0	1	0	1	0	0	**2**

					Lindgren funnels					**Trunk-window traps**					
Family	**Genus**	**Species**	**Author**	**Code**	**1/3 cut**	**2/3 cut**	**Clearcut**	**LP-edge**	**LP-interior**	**1/3 cut**	**2/3 cut**	**Clearcut**	**LP-edge**	**LP-interior**	**Total**
Clambidae	*Clambus*	sp. 1		Clam	0	0	0	0	0	1	0	0	0	0	**1**
Cleridae	*Chariessa*	*pilosa*	(Forster)	Chpi	0	1	1	0	0	0	0	0	0	0	**2**
Cleridae	*Cymatodera*	*bicolor*	(Say)	Cybi	0	1	1	0	0	0	0	0	0	0	**2**
Cleridae	*Madioniella*	*dislocatus*	(Say)	Madi	0	0	1	2	0	1	0	2	0	0	**6**
Cleridae	*Zenodosus*	*sanguineus*	(Say)	Zesa	2	1	0	4	6	0	0	0	0	0	**13**
Colydiidae	*Lasconotus*	*borealis*	Horn	Labo	0	0	0	1	0	0	0	0	0	0	**1**
Colydiidae	*Synchita*	*fuliginosa*	Melsheimer	Syfu	0	0	0	0	1	0	0	0	0	0	**1**
Corylophidae	*Molamba*	*fasciata*	(Say)	Mofa	0	0	0	1	1	0	0	0	0	0	**2**
Corylophidae	sp. 1			Cory sp 1	0	1	0	1	3	1	0	0	0	0	**6**
Cryptophagidae	*Atomaria*	sp. 1		Atom sp	0	0	3	0	1	0	0	0	0	0	**4**
Cryptophagidae	*Cryptophagus*	sp. 1		Crypt sp 1	0	0	1	0	1	0	0	0	0	0	**2**
Cryptophagidae	*Cryptophagus*	sp. 2		Crypt sp 2	0	0	0	2	0	0	0	0	0	0	**2**
Cucujidae	*Cucujus*	*clavipes*	Fabricius	Cucl	0	1	0	0	0	1	0	0	0	0	**2**
Curculionidae	*Cossonus*	sp. 5		Cur sp 5	0	0	1	0	0	0	0	0	0	0	**1**
Curculionidae	sp. 3			Cur sp 3	0	0	2	1	0	0	0	0	0	0	**3**
Elateridae	*Agriotella*	*debilis*	LeConte	Agde	0	0	1	0	0	0	0	0	0	0	**1**
Elateridae	*Agriotes*	*fucosus*	(LeConte)	Agfu	3	2	1	2	1	0	0	0	0	0	**9**
Elateridae	*Ampedus*	*apicatus*	(Say)	Amap	3	8	4	2	0	0	1	0	0	2	**20**
Elateridae	*Ampedus*	*evansi*	W.J. Brown	Mest	1	0	0	0	0	0	0	0	0	0	**1**
Elateridae	*Ampedus*	*fusculus*	(LeConte)	Amfu	0	0	0	1	0	0	0	0	0	0	**1**
Elateridae	*Ampedus*	*laurentinus*	W.J. Brown	Amla	0	0	1	0	0	0	0	0	0	0	**1**
Elateridae	*Ampedus*	*nigrinus*	(Herbst)	Amni	4	5	13	26	6	1	1	5	0	3	**64**
Elateridae	*Ampedus*	*pullus*	Germar	Ampu	0	1	17	0	0	0	0	0	0	0	**18**
Elateridae	*Ampedus*	sp. 1		Am sp 1	0	0	2	1	0	0	0	0	0	0	**3**
Elateridae	*Athous*	*productus*	(Randall)	Atpr	0	0	1	0	0	0	1	0	0	0	**2**
Elateridae	*Athous*	*rufifrons*	(Randall)	Atru	2	0	0	3	1	1	0	0	1	0	**8**

					Lindgren funnels					Trunk-window traps					
Family	Genus	Species	Author	Code	1/3 cut	2/3 cut	Clearcut	LP-edge	LP-interior	1/3 cut	2/3 cut	Clearcut	LP-edge	LP-interior	Total
Elateridae	*Ctenicera*	*insidiosa*	(LeConte)	Ctin	0	0	1	0	0	0	0	0	0	0	**1**
Elateridae	*Ctenicera*	*resplendens*	(Randall)	Ctre	0	0	3	0	0	0	0	0	0	0	**3**
Elateridae	*Dalopius*	sp. 1		Dal sp 1	3	1	2	5	4	2	2	1	0	0	**20**
Elateridae	*Danosoma*	*brevicorne*	(LeConte)	Dabr	1	2	2	0	0	0	0	0	0	0	**5**
Elateridae	*Denticollis*	*denticornis*	(Kirby)	Dede	3	0	0	0	4	1	2	0	0	0	**10**
Elateridae	*Liotrichus*	*spinosa*	(LeConte)	Ctsp	0	1	0	0	0	0	0	0	0	0	**1**
Elateridae	*Melanotus*	*castanipes*	(Paykull)	Meca	3	10	5	3	6	2	1	0	0	0	**30**
Elateridae	*Pseudanostirus*	*hieroglyphicus*	(Say)	Cthi	2	7	2	0	0	0	0	0	0	0	**11**
Elateridae	*Pseudanostirus*	*propolus*	(LeConte)	Ctpr	2	3	0	2	2	0	1	0	0	0	**10**
Elateridae	*Pseudanostirus*	*triundulatus*	(Randall)	Cttr	1	0	1	1	0	1	0	0	0	0	**4**
Elateridae	*Selatosomus*	*appropinquans*	(Randall)	Ctap	0	0	1	0	0	0	0	0	0	0	**1**
Elateridae	*Selatosomus*	*aratus*	(LeConte)	Sear	0	0	2	0	0	1	0	0	1	0	**4**
Elateridae	*Selatosomus*	*nitidula*	(LeConte)	Ctni	4	4	5	4	0	0	0	0	0	0	**17**
Elateridae	sp. 1			Elat sp 1	0	0	1	0	0	0	0	0	0	0	**1**
Endomychidae	*Endomychus*	*biguttatus*	Say	Enbi	1	1	3	1	1	0	0	0	0	0	**7**
Endomychidae	*Mycetina*	*perpulcha*	(Newman)	Mype	0	0	3	1	0	0	0	0	0	0	**4**
Endomychidae	*Phymaphora*	*pulchella*	Newman	Phpu	5	2	1	1	3	1	0	0	0	0	**13**
Erotylidae	*Triplax*	*dissimulator*	(Crotch)	Trdi	8	15	0	2	0	0	0	0	0	0	**25**
Erotylidae	*Triplax*	*frosti*	Casey	Trfr	0	1	0	0	0	0	0	0	0	0	**1**
Erotylidae	*Triplax*	*thoracica*	Say	Trth	0	0	0	1	0	0	2	0	0	0	**3**
Erotylidae	*Tritoma*	*pulchra*	(Say)	Trpu	0	0	0	0	0	5	5	0	0	0	**10**
Eucinetidae	*Eucinetus*	sp. 1	LeConte	Euci sp 1	0	0	1	0	0	0	0	0	0	0	**1**
Eucinetidae	*Eucinetus*	*terminalis*	LeConte	Eute	1	2	1	1	0	1	0	0	0	0	**6**
Eucmemidae	*Isoripis*	*obliqua*	(Say)	Isob	0	0	0	0	0	1	0	0	0	0	**1**
Eucnemididae	*Deltometopis*	*amoenicornis*	(Say)	Deam	0	0	3	0	0	0	0	0	0	0	**3**
Eucnemididae	*Dromaeolus*	*harringtoni*	Horn	Drha	1	0	4	0	0	0	0	0	0	0	**5**

					Lindgren funnels					Trunk-window traps					
Family	**Genus**	**Species**	**Author**	**Code**	**1/3 cut**	**2/3 cut**	**Clearcut**	**LP-edge**	**LP-interior**	**1/3 cut**	**2/3 cut**	**Clearcut**	**LP-edge**	**LP-interior**	**Total**
Eucnemididae	*Microrhagus*	sp. 1		Micr sp 1	0	1	1	0	0	0	0	0	0	0	**2**
Eucnemididae	*Nematodes*	*penetrans*	(LeConte)	Nepe	0	0	0	0	0	1	0	0	0	0	**1**
Helodidae	*Cyphon*	sp. 1		Cyph sp 1	2	1	1	0	0	0	0	0	0	0	**4**
Helodidae	*Nycteus*	*oviformis*	(LeConte)	Nyov	0	0	1	0	1	0	0	0	0	0	**2**
Histeridae	*Cylistix*	sp. 1		Cyli	0	0	0	0	0	0	2	1	0	0	**3**
Laemophloeidae	*Laemophloeus*	sp. 1	(Say)	Laem sp 1	0	2	0	3	11	0	0	0	0	0	**16**
Lampyridae	*Lucidota*	*corrusca*	(Linné)	Luco	1	0	6	2	1	2	0	0	1	0	**13**
Lampyridae	*Pyractomena*	*borealis*	(Randall)	Pybo	0	0	5	1	0	0	1	1	0	0	**8**
Lathridiidae	*Enicmus or lathridius*	spp.		Lathrid	14	21	16	4	6	0	1	0	0	0	**62**
Lathridiidae	*Melanophthalma*	sp. 1		Melano	182	214	260	247	131	84	30	0	0	0	**1148**
Leiodidae	spp.			Leiodid	7	2	22	1	9	9	2	0	0	0	**52**
Lycidae	*Dictyopterus*	*aurora*	(Herbst)	Diau	0	1	1	1	0	0	0	0	0	0	**3**
Lycidae	*Leptoceletes*	*basalis*	LeConte	Ceba	1	0	1	0	0	0	0	0	0	0	**2**
Lycidae	*Plateros*	sp. 1		Plat sp 1	0	0	3	0	0	0	0	0	0	0	**3**
Melandryidae	*Dircaea*	*liturata*	(LeConte)	Dili	1	0	1	1	0	1	0	1	1	0	**6**
Melandryidae	*Echodes*	*sericea*	(Haldeman)	Ecse	0	2	0	1	1	1	1	0	0	0	**6**
Melandryidae	*Melandrya*	*connectens*	Newman	Meco	1	0	5	2	4	2	0	1	6	0	**21**
Melandryidae	*Melandrya*	*striata*	Say	Mest	0	1	3	0	0	3	2	0	0	0	**9**
Melandryidae	*Orchesia*	*castanea*	(Melsheimer)	Orca	1	0	3	0	0	0	0	0	0	0	**4**
Melandryidae	*Orchesia*	*ovata*	Laliberté	Orov	0	0	0	0	0	2	1	0	0	0	**3**
Melandryidae	*Scotochroa*	*buprestoides*	(Kirby)	Scbu	6	4	9	0	1	0	0	1	0	0	**21**
Melandryidae	*Serropalpus*	*substriatus*	Haldeman	Sesu	1	0	0	0	1	0	0	0	0	0	**2**
Mordellidae	*Mordella*	sp. 1		Mord sp 1	13	14	51	21	3	0	3	4	1	0	**110**
Mordellidae	*Tomoxia*	*lineella*	Leconte	Toli	0	0	0	0	0	1	0	0	1	1	**3**
Mycetophagidae	*Mycetophagus*	sp. 2		Myc sp 2	0	0	1	0	0	0	0	0	0	0	**1**

					Lindgren funnels					Trunk-window traps					
Family	**Genus**	**Species**	**Author**	**Code**	**1/3 cut**	**2/3 cut**	**Clearcut**	**LP-edge**	**LP-interior**	**1/3 cut**	**2/3 cut**	**Clearcut**	**LP-edge**	**LP-interior**	**Total**
Nitidulidae	*Epuraea*	*flavomaculata*	Mäklin	Epfl	0	2	0	0	0	2	0	0	0	0	**4**
Nitidulidae	*Epuraea*	*planulata*	Erichson	Eppl	1	1	0	0	1	2	0	0	0	0	**5**
Nitidulidae	*Glishrochilus*	*sanguinolentus*	(Olivier)	Glsa	3	5	0	0	1	1	0	0	0	0	**10**
Nitidulidae	*Glishrochilus*	*siepmanni*	W.J. Brown	Glsi	38	29	8	2	10	5	1	0	0	0	**93**
Pyrochroidae	*Dendroides*	*concolor*	(Newman)	Deco	1	0	1	0	1	1	0	0	0	0	**4**
Rhipiphoridae	*Pelecotoma*	*flavipes*	Melsheimer	Pefl	0	0	0	0	0	1	0	1	0	0	**2**
Rhizophagidae	*Rhizophagus*	sp. 1		Rhi	1	1	0	2	8	3	1	0	0	0	**16**
Salpingidae	*Rhinosimus*	*viridiaeneus*	Randall	Rhvi	0	1	0	1	0	0	0	0	0	0	**2**
Scolytidae	*Crypturgus*	*pusillus*	(Gyllenhal)	Crpu	0	0	0	0	1	0	0	0	0	0	**1**
Scolytidae	*Dryocoetes*	*autographus*	(Ratzeburg)	Drau	0	0	0	2	2	0	0	0	0	0	**4**
Scolytidae	*Hypothenemus*	*dissimilis*	(Zimmermann)	Hydi	0	0	0	0	1	0	0	0	0	0	**1**
Scolytidae	sp. 4			Tiny-sco 4	0	0	0	1	0	0	0	0	0	0	**1**
Scolytidae	*Xyloborus*	*sayi*	(Hopkins)	Xysa	1	0	0	1	9	0	0	0	0	0	**11**
Scraptiidae	*Canifa*	sp. 1		Can sp 1	0	0	6	2	0	0	0	0	0	0	**8**
Scraptiidae	*Canifa*	sp. 2		Can sp 2	0	0	2	1	1	0	0	0	0	0	**4**
Scydmaenidae				Scyd	0	0	0	0	0	2	0	2	0	3	**7**
Silvanidae	*Dendrophagus*	*cygnaei*	Mannerheim	Decy	0	0	0	0	2	0	0	0	0	0	**2**
Silvanidae	*Silvanidae*	sp. 1		Sil sp 1	4	4	0	0	0	0	0	0	0	0	**8**
Sphindidae	*Odontosphindus*	*denticollis*	LeConte	Odde	1	1	1	0	2	0	0	0	0	0	**5**
Sphindidae	*Sphindus*	*trinifer*	Casey	Sptr	0	0	4	1	0	0	0	0	0	0	**5**
Tenebrionidae	*Neatus*	*tenebrioides*	(Palisot de Beauvois)	Nete	0	0	0	0	0	0	1	0	0	0	**1**
Tetratomidae	*Penthe*	*obliquata*	(Fabricius)	Peob	0	0	1	0	0	0	0	0	0	0	**1**
Tetratomidae	*Penthe*	*pimelia*	(Fabricius)	Pepi	1	0	0	1	0	0	0	0	0	0	**2**
Trogossitidae	*Grynocharis*	*quadrilineata*	(Melsheimer)	Gyqu	0	0	0	0	0	1	0	0	0	0	**1**
Trogossitidae	*Tenebroides*	sp. 1		Tene	0	0	0	0	0	0	1	0	0	0	**1**

Family	Genus	Species	Author	Code	Lindgren funnels 1/3 cut	2/3 cut	Clearcut	LP-edge	LP-interior	Trunk-window traps 1/3 cut	2/3 cut	Clearcut	LP-edge	LP-interior	Total
Trogossitidae	*Thymalus*	*marginicollis*	Chevrolat	Thyma	1	0	0	0	1	0	0	0	0	0	**2**

CHAPTER 4: GENERAL CONCLUSION

New information has been obtained on saproxylic beetles inhabiting south-eastern mixedwood boreal forest in the Abitibi region of Quebec, where logging has extensively fragmented the landscape. I examined saproxylic beetle responses, from an ecosystem management perspective, in two silvicultural systems that may help preserve saproxylic fauna by mimicing boreal forest natural dynamics. Such harvesting practices provide diversified forest conditions that may maintain ecological functions, sustainability and biodiversity (Hunter, 1993; Gauthier et al., 1996; Bergeron and Harvey, 1997; Lähde et al., 1999; Harvey et al., 2002; Bergeron et al., 2002).

Chapter 2 investigated habitat use and aspen-host use of saproxylic and bark and wood-boring beetles in forest habitat remnants (small patches and corridors) inside even-aged clearcut landscapes. Habitat remnants are believed to resemble the patchy remnant vegetation structure of natural post-fire residual trees and snags (Work et al., 2003; Gandhi et al., 2001). Chapter 3 focused on stands harvested with partial cutting, theorized to imitate natural succession and gap dynamics, by comparing assemblages with clearcut and uncut forest.

The hypothesis that biodiversity may be better preserved when harvesting mimics more closely natural disturbance is supported by the results of Chapter 2 and 3. The results also support that the diversification of forest management may conserve a broader range of species than clearcutting alone. Unforturnately, a paucity of information exists on the life history and habitat preferences of saproxylic beetles, in North America, such that little biological information can be added to these findings.

In Chapter 2, higher species richness and relative abundance of saproxylic and bark and wood-boring beetle were collected in habitat remnants and the lowest of these variables was collected in interior of large patches. Although non-significant, higher larval densities were collected from habitat remnants, compared to uncut forest. Habitat remnants also conserved the most species of the 20 most abundant adult beetles in the total data and had highest snag densities.

Ordinations displayed highly variable species composition for large patches (edges and interior) and less variation for clearcuts and habitat remnants; significant indicator species only occurred in clearcuts and remnant patches.This suggests habitat greater habitat specificity for some saproxylic beetles on remnant habitats and clearcuts than uncut forest.

In Chapter 3, partial cuts had high dead wood abundance and were readily used by dispersing saproxylic beetles. Saproxylic beetle relative abundance and species composition was intermediate, in 1/3 and 2/3 partial cut patches, to that of clearcut and uncut forest. The species that were the most abundant in the total data were collected more often in partial cuts in than other treatments. Partial cut forest had high densities and basal areas of deciduous and coniferous snags. Partial cuts may reduce the effects of fragmentation by retaining characteristics of uncut forest, sustaining species with dependence on later successional host species with low dispersal capability or inability to survive in clearcut matrix. However, some forest interior specialists may not find suitable living conditions in partial cuts. In Chapter 2, coniferous snag densities were significantly higher in forest interiors, and species dependant on shady conditions and coniferous dead wood may not be preserved in small patches and narrow strips. It is recommended to retain large patches of forest in addition to practicing alternative harvesting in clearcut areas.

For both chapters, canopy openness was an important factor determining beetle species composition and abundance patterns. Increased canopy openness tended to increase captures irrespective of quantity of snag habitat. In Fennoscandia, threatened saproxylic beetle species have been found predominantly on aspen snags within clearcuts (Sverdrup-Thygeson and Ims, 2002; Linde et al., 2005), which is the main stand-replacing event substituting wildfire (Siitonen, 2001). Different assemblages of beetles have been found between burned and clearcut sites (Ahnlund and Lindhe, 1992; Niemelä, 1997). Large-scale fire disturbances creating an abundance of high-quality dead wood may also be necessary to preserve a large portion of the fauna.

Suitable quantities and quality of dead wood is highly ephemeral and a high spatial and temporal connectivity is needed to support a wide range of saproxylic diversity in harvested landscapes. Both remnants habitats and partial cuts produce high abundances of dead wood, supporting diverse saproxylic fauna. In Chapter 2, clearcutting and fragmentation into small habitat may increase populations of disturbance-driven insects to the detriment of the forest interior specialists. In Chapter 3, partial cuts reduce the effects of fragmentation to increase habitat for some interior species but not all. This suggests diversification of forest and dead wood management may support a broader range of saproxylic beetles in the boreal forest than clearcut harvesting alone.

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