University of Alberta

Boreal Mixed-wood Beetles and the Cumulative Ecological Consequences of Disturbance

by

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To my wife, fellow ecologist and best friend,

Julienne,

thank you for your love and patience.

ABSTRACT

Boreal forests of Canada, and elsewhere, are increasingly stressed by multiple, potentially interacting disturbances. In addition to natural disturbances like wildfire, anthropogenic stressors associated with increasing demands for natural resources have become critical elements of the disturbance regime in many areas. Thus, biodiversity conservation and sustainable forest management will increasingly depend on our understanding of the cumulative ecological consequences of disturbance.

I examined the combined effects of wildfire and industrial forestry practices on boreal mixed-wood ground beetles and saproxylic beetles, and on the ecological function of one saproxylic species. Ground beetle responses to the individual and combined effects of wildfire, forest harvesting and herbicide-use were species-specific, but disturbance combinations led to a greater decrease in the compositional variability of the entire ground beetle assemblage. For saproxylic beetle assemblages, the combination of wildfire and forest harvesting (postfire salvage logging) reduced species richness and altered species composition to a greater extent that either disturbance alone. Postfire salvage logging also altered the trophic structure of the saproxylic beetle assemblage and was particularly detrimental for wood- and bark-boring species. Through a series of experiments, the abundance of one such species, *Monochamus scutellatus scutellatus*, was linked to decomposition processes in burned forests. Together, the results of these studies suggest that disturbance combinations should be avoided whenever possible because they may impact not only beetle diversity, but also decomposition processes in forests recovering from wildfire.

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CHAPTER 1

Introduction

1.1 Biodiversity, "taxonomic impediment" and a "special preference" for beetles

When asked what could be inferred about the nature of the Creator from studying creation, the distinguished evolutionary biologist J. B. S. Haldane (1892-1964) is reported to have answered that the Creator had "an inordinate fondness for beetles" (Hutchinson 1959). This widely-quoted statement has given rise to a long-standing debate because the line cannot be found in any of Haldane's written work (Gould 1993). In fact, according to Gould (1993), Haldane's closest recorded statement comes from an address to the British Interplanetary Society in which, according to the society's secretary, Haldane said, "the fact that there are 400,000 species of beetles on this planet, but only 8000 species of mammals" suggests that "the Creator, if He exists, has a special preference for beetles".

Regardless of the exact phrasing and circumstances of this famous quip, there is undeniable insight in the words. In terms of numbers of species, beetles, the Order Coleoptera, comprise the largest component of global biodiversity with more than 340,000 described species (Groombridge 1992; Marshall 2006) and estimates of those yet to be described ranging into the millions (Erwin 1982; Gaston 1991; Stork 1988). In other words, roughly one fifth of every known species of plant and animal on Earth is a beetle (Evans and Bellamy 1996). Thus, the study of beetles is arguably one of the most significant elements of biodiversity research. A general understanding of beetle diversity could hardly be irrelevant to understanding life's overall diversity, while such understanding of other much less diverse taxa might easily be rooted in special circumstance and irrelevant to beetles.

Coleopteran diversity at once represents an important challenge and an exciting opportunity for those engaged in the study of biodiversity. The challenge stems largely from an imbalance between taxonomic workloads and available resources. Taxonomy – the theory and practice of identifying, describing, naming and classifying of organisms – is a necessary prerequisite to all other biological enquiry. At present, the enormous workload facing beetle taxonomists, indeed all invertebrate taxonomists, is disproportionate to available taxonomic resources (*e.g.*, funding, specifically trained individuals, adequate keys, accurate reference collections, *etc.*) (Boero 2001; Giangrande 2003; Huber and Langor 2004). Given the current estimates of both taxonomic resources and undescribed species, Wilson (1988) suggested that it would take 25,000 taxonomist lifetimes just to catch up. For many biodiversity studies, such challenges often result in the necessary exclusion of lesser-known species or groups (*e.g.*, Staphylinidae: Aleocharinae from beetle studies), and this may ultimately hinder acquisition of general understanding. Currently, however, there is a growing awareness of the need to address this "taxonomic impediment" as an important first step towards global biodiversity conservation (Convention on Biological Diversity 2000; Global Taxonomy Initiative 2001; Giangrande 2003; Klopper *et al.* 2002). Whether or not practical outcomes will follow awareness of global taxonomic issues remains to be seen.

Along with taxonomic challenges, the study of beetles also represents considerable and highly attractive research opportunities. For many common beetle groups, the basic taxonomic framework has been established and there are reasonable guides available for identification of known species. In addition to the prospect of discovering and describing new species, ecological explorations of beetles represent fertile fields for scientific investigation. For the majority of described species, basic life-history information is either lacking or is inferred from detailed studies of relatively few species. For example, wood- and bark-boring beetles (Cerambycidae, Buprestidae and Curculionidae: Scolytinae, Cossoninae, Molytinae, *etc.*) are generally considered to be involved in decomposition of woody debris and forest nutrient cycling (Gullan and Cranston 1994; Perry 1994; Speight *et al.* 1999). However, this assumption is supported by little direct evidence involving only one or two "pest" species (Edmonds and Eglitis 1989). Moreover, understanding of the complex relationships between an array of beetle species and cellulolytic fungi thought to be “involved” in decomposition processes is far from complete (Speight *et al.* 1999). Even for more well-studied beetle groups like the Carabidae (ground beetles), considerable knowledge gaps exist for species-specific habitat and diet requirements as well as inter- and intra-specific interactions between adults and larvae (Ball and Bousquet 2001; Lindroth 1961-1969; Thiele 1977). Thus, any research that focuses on the basic biology and ecology of beetles possesses significant potential to advance scientific understanding.

Although the vast global diversity of beetles (described and undescribed) may help to stimulate concern for beetle conservation and taxonomy, the paucity of knowledge regarding species-specific survival requirements and ecological functions should not be overlooked. Despite considerable debate (McCann 2000), there is a growing consensus that ecosystem-level responses to environmental stress are controlled, at least in part, by the diversity and particular characteristics of the plant, animal and microbial species present in any given ecosystem (Naeem *et al.* 1994; Naeem *et al.* 1999). Present-day estimates of species extinction rates are unprecedented in the fossil record (Bloom 1995; Pimm *et al.* 1995; Riciardi and Rasmussen 2000; Smith *et al.* 1993) and human-domination of global ecosystems has been implicated as the central driver in the present "biodiversity crisis" (Ehrlich and Wilson 1991; Vitousek *et al.* 1997; Wilson 1992). Such estimates of extinction are necessarily based on observations of well-studied groups of vertebrates (*e.g.*, birds and mammals) (Smith *et al.* 1993), but this does not relieve insufficiently-studied groups, like beetles, from risk. In Europe, for example, a disproportionately large number of saproxylic beetles (species associated with decaying wood) are currently threatened with extirpation or extinction (Grove 2002). Consequently, the lack of a clear understanding of the ecological functions of beetles and the other "little things that run the world" (Wilson 1987) suggests that scientific advances in the study of both beetle taxonomy and ecology will become increasingly important in biodiversity conservation arenas.

In Canada, societal awareness of biodiversity conservation culminated in the signing of the Convention on Biological Diversity at the Earth Summit in Rio de Janeiro in 1992. In doing so, Canada (and other signatories) committed "...to conserve biological diversity, to sustainably use its components and to share equitably the benefits arising from the use of genetic resources" (Convention on Biological Diversity 2000). Canada was among the first countries to ratify the Convention on

Biological Diversity and efforts to meet these commitments are now increasingly apparent in federal policy (*e.g.*, Canadian Biodiversity Strategy 1992, Species at Risk Act 2003).

1.2 Sustainable management in Canada's boreal forest

Biodiversity conservation is now recognized as a critical element of sustainable forest management, especially in Canada's boreal region (National Forest Strategy Coalition 2004). Canada is home to *c.* 30% of the world's circumpolar boreal forests, with an area of *c.* 310 million ha extending eastward from the Yukon, northern British Columbia and Northwest territories, across the northern regions of the Prairie Provinces, Quebec and Ontario, to Newfoundland and Labrador (Natural Resources Canada 2005). In general, this region is recognized by its dominant tree species, which include white spruce (*Picea glauca* [Moench] Voss), black spruce (*P. mariana* [P.Mill.] B.S.P.), trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*P. balsamifera* L.) and jack pine (*Pinus banksiana* Lamb.), with elements of balsam fir (*Abies balsamea* [L.] P.Mill.), larch (*Larix laricina* [Du Roi] K. Koch) and paper birch (*Betula papyrifera* Marsh.). Although subject to recognizable (subsistence) forestry since European colonization, industrial forestry activity grew dramatically in the Canadian boreal zone in the last half of the 20th Century and has been a serious source of ecosystem disturbance in Alberta since only the early 1990s (Schneider 2002).

The boreal forest is also characterized by a post-glaciation history of highly stochastic natural disturbances like wildfire and insect outbreaks (Bonan and Shugart 1989; Rowe and Scotter 1973). Fluctuations in frequency and severity of such disturbances, coupled with variable moisture and nutrient regimes, have resulted in heterogeneous landscapes comprised of varying stand types (species composition) and age-classes (Bonan and Shugart 1989; Johnson *et al.* 1998). This habitat heterogeneity, in turn, supports a diverse assemblage of more than 93,000 described species of plants, animals and micro-organisms (Natural Resources Canada 2005).

Modern boreal forest landscapes are increasingly shaped by management activities associated with industrial resource extraction. In many areas, effects of multiple overlapping anthropogenic disturbances are already apparent. For example, in many parts of Alberta it is increasingly common to find evidence of multiple natural resource extraction activities in the same area, often occurring sequentially on the same sites (Schneider 2002). The cumulative ecological consequences of such stressors are largely unknown, but will no doubt be complex and difficult to predict for many organisms. This uncertainty is compounded by the fact that such anthropogenic stressors are occurring on a backdrop of existing natural disturbance regimes and global climate change. Thus, attaining the simultaneous goals of sustainable forest management and biodiversity conservation in Canada's boreal forests (and elsewhere) will increasingly depend on our understanding of the individual and combined effects of natural and anthropogenic disturbances. Although the published literature is replete with studies of single disturbances (*e.g.,* Hunter 1999), relatively little work has been directed towards improving our understanding the cumulative ecological consequences of multiple, potentially interacting, disturbances.

1.3 Thesis objectives and organization

The overall goal of my dissertation is to examine the ecological consequences of multiple disturbances in boreal ecosystems in order to provide recommendations for sustainable forest management and biodiversity conservation. To achieve this goal, I used a combination of approaches including field surveys and experiments as well as both community- and species-based analyses. All field surveys and experiments were located in and around the "Chisholm Fire", which occurred May 23 – June 4, 2001 approximately 200 km northwest of Edmonton, Alberta, Canada, near the hamlet of Chisholm (Figure 1.1). Exact study site locations are provided in Table 1.1. A detailed synopsis the severity and extent of this wildfire as well as associated climate and fuel conditions are provided in Quintilio *et al.* (2001).

As a group, beetles were selected for this study because (1) they are central to the study of overall biodiversity (see above); (2) previous research has established that Canadian species are highly sensitive to disturbances caused by forestry activity (*e.g.*, Niemelä *et al.* 1993); (3) they can be sampled efficiently to produce large, statistically meaningful datasets; and (4) compared to some other groups (*e.g.*, Diptera, Hymenoptera), they are relatively easier to deal with taxonomically.

For clarity, I have divided the dissertation into 5 chapters, organized around the thesis that beetles can be used to effectively illustrate impacts of multiple ecosystem disturbances on biodiversity and that such disturbances can influence the structure of communities and significantly affect ecological function. The first chapter provides a general introduction to the problem and outlines the rationale for the overall study. Chapter 2 is a community- and species-level analysis of boreal forest ground beetle responses to the individual and combined effects of wildfire, forest harvesting and herbicide-use. In chapter 3, I explore the effects of postfire salvage logging on saproxylic beetle assemblages and their trophic structure. In chapter 4, I report the results of a series of field and laboratory experiments aimed at investigating the link between one saproxylic beetle species, *Monochamus s. scutellatus* (Say) (Coleoptera: Cerambycidae), and decomposition processes in burned boreal forests that may be impacted by postfire salvage logging. Finally, chapter 5 provides a synthesis of the key findings of the thesis research, study limitations and some recommendations for application in forest management and future research.

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Table 1.1: Precise location (latitude, longitude) of each study site. Treatment codes are GREEN = green; HARV = harvested, BURN = burned, SALV = salvaged and HERB = herbicide.

Treatment	Replicate	Coordinates	
GREEN	1	N 54° 54.47	W 114° 04.46
GREEN	2	N 55° 04.54	W 114° 05.92
GREEN	3	N 55° 14.91	W 114° 43.47
GREEN	4	N 54° 54.71	W 114° 03.91
GREEN	5	N 55° 17.87	W 115° 06.48
GREEN	6	N 55° 13.63	W 114° 42.53
HARV	1	N 55° 41.06	W 115° 48.48
HARV	2	N 55° 41.19	W 115° 49.21
HARV	3	N 55° 41.48	W 115° 48.20
HARV	4	N 55° 17.87	W 115° 05.49
HARV	5	N 55° 17.94	W 115° 06.68
HARV	6	N 55° 17.66	W 115° 06.50
BURN	1	N 54° 54.13	W 114° 07.58
BURN	2	N 55° 06.49	W 114° 09.19
BURN	3	N 55° 10.50	W 114° 30.24
BURN	4	N 54° 54.28	W 114° 06.75
BURN	5	N 54° 56.35	W 114° 06.50
BURN	6	N 55° 08.54	W 114° 12.36
SALV	1	N 54° 54.42	W 114° 07.74
SALV	2	N 54° 54.48	W 114° 05.99
SALV	3	N 55° 01.41	W 114° 22.84
SALV	4	N 54° 55.78	W 114° 06.71
SALV	5	N 55° 01.85	W 114° 22.28
SALV	6	N 55° 01.34	W 114° 23.11
HERB	1	N 54° 04.51	W 114° 20.51
HERB	2	N 54° 05.14	W 114° 20.29
HERB	3	N 54° 05.71	W 114° 20.31
HERB	4	N 55° 04.31	W 114° 20.21
HERB	5	N 55° 07.23	W 114° 21.73
HERB	6	N 55° 06.20	W 114° 20.57

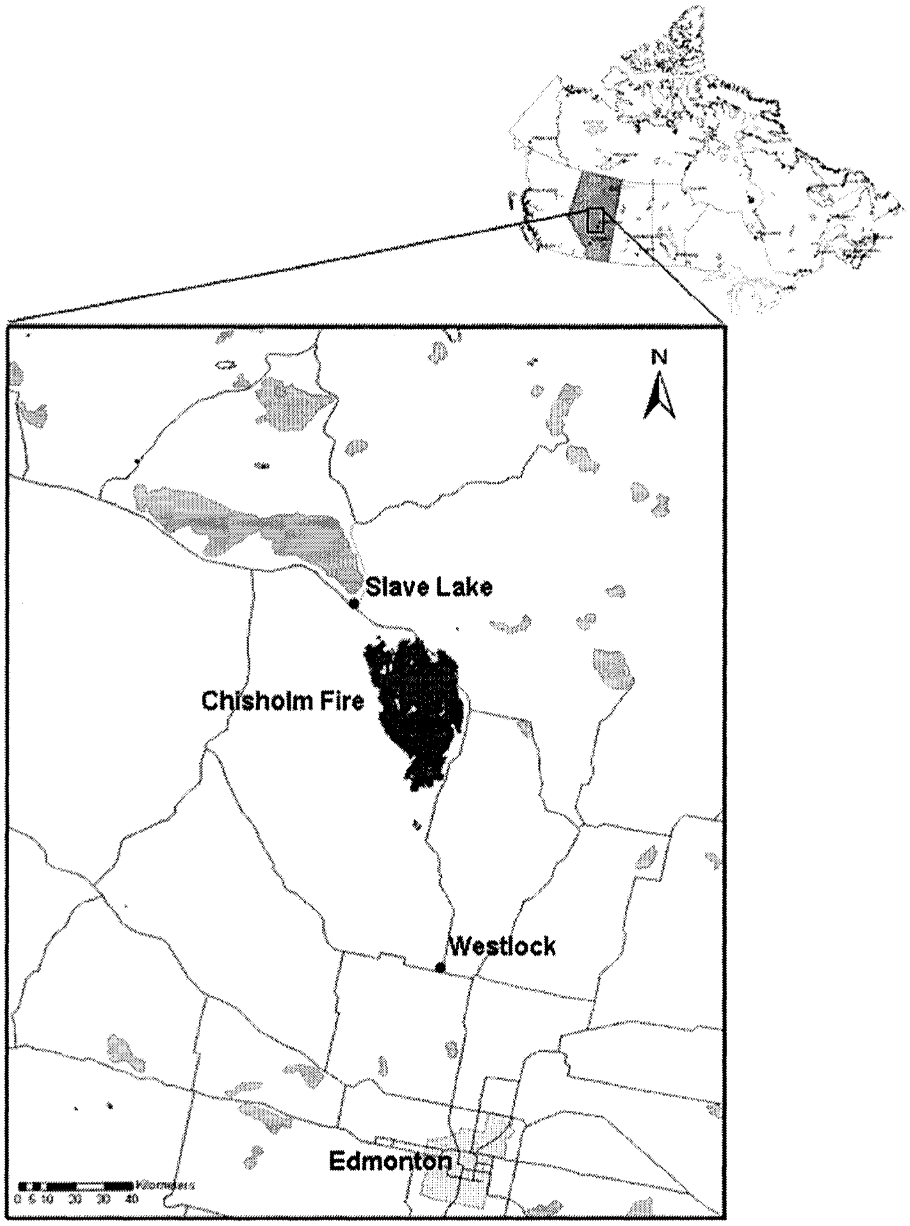

Figure 1.1: Map of the study area showing the location of the Chisholm fire.

CHAPTER 2

Biodiversity and multiple disturbances: boreal forest ground beetle (Coleoptera: Carabidae) responses to wildfire, harvesting and herbicide

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A version of this chapter has been accepted for publication:
Cobb, T. P., Langor, D. W., and Spence, J. R. 2006. Biodiversity and the cumulative effects of disturbance: boreal forest ground beetle (Coleoptera: Carabidae) responses to wildfire, harvesting and herbicide. Canadian Journal of Forest Research (in press).

2.1 Summary

In this chapter, I examined the short-term (2 yrs) responses of boreal forest ground beetles (Coleoptera: Carabidae) to the individual and combined effects of wildfire, harvesting and herbicide use. Both community- and species-level analysis demonstrated remarkable differences in ground beetle responses to wildfire and forestry-related disturbances and suggested that while some species may appear to benefit from disturbance combinations (*e.g., Sericoda quadripunctata*, *Pterostichus adstrictus*), these effects are detrimental to others (*e.g., Sericoda bembidioides*). In addition, I found that variability in ground beetle species composition was significantly reduced by disturbance combinations suggesting that multiple disturbances may lead to a simplification of this assemblage. Ground beetle responses were correlated with changes in several habitat parameters such as amount of woody debris, exposed bare ground and plant species richness, suggesting avenues for future study and potential mitigation. Overall, however, the results of this study suggest that

efforts to avoid compounding disturbances on any given site should be considered in the development of current and future forest management guidelines.

2.2 Introduction

Throughout the boreal region, wildfires and other natural disturbances play important roles in shaping the forest landscape and maintaining biodiversity (Bergeron *et al.* 2001; Johnson *et al.* 1998). Variation in the timing and severity of forest fires creates a mosaic of different postfire successional habitats that support a diverse assemblage of organisms. Not surprisingly, many boreal species display adaptations to a regime of regular disturbance by fire. For example, some pine species, like jack pine (*Pinus banksiana* Lamb.) and lodgepole pine (*P. contorta* Dougl. ex Loud.), possess serotinous cones that are closed with resin and remain in the crown until opened by extreme heat (Johnson and Gutsell 1993; Muir and Lotan 1985; Radeloff *et al.* 2004; Teich 1970), while other plants like fireweed (*Epilobium angustifolium* L.) are able to quickly disperse into burned areas to take advantage of increased nutrient availability (Rowe 1983). Several bird species, including black-backed (*Picoides arcticus* Swainson) and American three-toed (*P. dorsalis* Baird) woodpeckers, are strongly associated with recently burned forests (Hoyt and Hannon 2002; Hutto 1995; Morissette *et al.* 2002), presumably attracted by the increased availability of insect prey. These "pyrophilous" (fire-loving) insects are abundant in early postfire forests (Evans 1971; Wikars 1997), and this group provides some of the most striking examples of fire adaptations. The black fire beetle, *Melanophila acuminata* (DeGeer) (Coleoptera: Buprestidae), for example, has a pair of specialized infrared-detecting metathoracic organs enabling it to locate fire-killed trees (Evans 1962, 1966; Schmitz *et al.* 1997).

The knowledge that many boreal forest organisms are adapted to regular disturbances has led to development of the "natural disturbance model" as a guide to more sustainable forest management (Attiwill 1994; Hunter 1993). This model suggests that biodiversity and continued function of inadequately understood boreal forest ecosystems will be best preserved by forest management activities that emulate natural disturbances. However, given the complexities of natural disturbances and species responses to them, there remain many unanswered questions about what exactly to emulate (Spence 2001). Moreover, in addition to natural disturbances, boreal ecosystems face many simultaneous, and potentially interacting environmental stressors with uncertain ecological consequences (Kennedy 2002; Schneider 2002). In western North America (and elsewhere), industrial forest management, fire suppression, global climate change, and increasing economic demand for both timber and non-timber resources (*e.g.,* oil, natural gas, mineral deposits) have become important components of the disturbance regime. Combined effects of these anthropogenic disturbances with wildfire and other natural disturbances will undoubtedly be complex and difficult to ascertain for many species. Generally, responses to disturbance combinations will most likely depend on the spatial and temporal scales at which studied organisms operate. Nonetheless, simultaneous goals for conservation of boreal ecosystems, their constituent biodiversity and for sustainable forest management will depend on gaining a better understanding of the ecological consequences of combining natural and anthropogenic disturbances.

In this study, I examined the short-term response of boreal mixed-wood ground beetles (Coleoptera: Carabidae) to the individual and combined effects of wildfire, forest harvesting, and the silvicultural application of herbicide that was used to reduce competition in replanted areas. Ground beetles were selected for this investigation because the group is diverse and abundant in boreal ecosystems, taxonomically well known in northern Holarctica, relatively easy to sample (Spence and Niemelä 1994), and previous work has shown that many species are responsive to habitat changes (Gandhi *et al.* 2004; Holliday 1992; Koivula and Vermeulen 2005; Lövei and Sunderland 1996; Niemelä *et al.* 1988; Niemelä *et al.* 1994; Saint-Germain *et al.* 2005; Wikars 1995; Work *et al.* 2004). Using both community- and species-level analyses, my objectives were to: (1) compare the effects of forestry-related disturbances (anthropogenic) with those of wildfire (natural); (2) determine if the combined effects of natural and anthropogenic disturbances were greater than either disturbance type alone; and (3) relate changes in ground beetle assemblages to changes in habitat parameters that may differ among disturbance types.

2.3 Methods

2.3.1 Study site

This study was conducted in and around a large-scale wildfire (*c.* 120,000 ha) that occurred May 23 – June 4, 2001 approximately 200 km northwest of Edmonton, Alberta, Canada, near the hamlet of Chisholm (N54°55′, W114°10′). Extreme weather conditions and drought-related fuel levels resulted in severe crown fire behaviour that left very few unburned residual patches and little to no remaining duff layer in many areas (Quintilio *et al.* 2001). Prior to the fire, the area was a boreal mixed-wood forest with both pure and mixed stands of white spruce (*Picea glauca* [Moench] Voss), black spruce (*P. mariana* [P.Mill.] B. S. P.), trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*P. balsamifera* L.) and jack pine (*Pinus banksiana* Lamb.), with minor elements of balsam fir (*Abies balsamea* [L.] P.Mill.), larch (*Larix laricina* [Du Roi] K. Koch) and paper birch (*Betula papyrifera* Marsh.). This landscape also encompassed a wide range of managed forest stands (*e.g.*, harvested areas and white spruce plantations) as well as unmanaged forest stands of varying ages and types.

2.3.2 Experimental design

I focused on mixed stands of mature (100-120 years old) white spruce (60% of canopy composition) and trembling aspen (40%). To address the objectives outlined above, I selected sites according to five different stand treatments: (1) GREEN – "green", reference sites that had not been burned or harvested in >100 yrs; (2) HARV – unburned, "harvested" sites that were clear-cut logged in 2001; (3) BURN – "burned" sites that were consumed by the Chisholm fire; (4) SALV – sites that were burned by the Chisholm fire and then "salvage" logged during the winter of 2001/2002; and (5) HERB – heavily disturbed "herbicide" sites that had been harvested in 1999, replanted with white spruce in 2000, burned by the Chisholm fire, and then treated with a broad-spectrum herbicide (Vision® application rate of 1.5 $kg^{-1}ha^{-1}$). The application of herbicide to conifer plantations to kill competing hardwoods is widely used in Canadian boreal forests and elsewhere (Sullivan and Sullivan 2003) to reduce competition with naturally regenerating trembling aspen in freshly harvested sites. For the purpose of this study, BURN and HARV sites represented singly disturbed sites whereas SALV and HERB sites represented multiply disturbed sites. For each of these stand treatments, I selected 6 sites (total = 30) on the basis of both pre- and post-disturbance stand characteristics (age, tree species composition, stem density, soil characteristics and accessibility), determined from forest inventory maps (Alberta Vegetation Inventory) followed by ground verification. Sites consisted of individual stands of trees (3-30 ha) separated by a minimum of 1 km.

2.3.3 Ground beetle sampling

Ground beetles were sampled by continuous pitfall trapping during the summer months (May 1- Aug 28) of 2002 and 2003. Pitfall traps (Spence and Niemelä 1994) consisted of an outer sleeve constructed from 1-L white plastic containers (11.2 cm diameter) placed flush with the surface of the ground, and a tight-fitting, plastic inner cup (0.5 L). Traps were charged with ~150 ml of silicate-free ethylene glycol (ACDelco™ Dex-cool® Extended Life Antifreeze/Coolant) and covered by a plywood roof (15 cm X 15 cm) elevated (2-3 cm) on two nails to reduce the amount of rain and debris from entering the trap. Near the centre of each site (estimated from forest inventory maps), I placed four pitfall traps at the corners of a 25 m X 25 m square (total number of pitfall traps = 120). This inter-trap distance was chosen to reduce depletion effects and increase the independence of samples (Digweed *et al.* 1995). No pitfall trap was < 50 m from any discernable edge or water body. Ground beetles (and other arthropods) were removed biweekly from all traps, and then preserved in 70% ethanol. Species-level identifications were made using keys provided in Lindroth

(1961-1969) and nomenclature follows that of Bousquet (1991). Voucher specimens are deposited in the E. H. Strickland Entomological Museum (University of Alberta) in Edmonton, Alberta and the Royal Alberta Museum in Edmonton, Alberta.

Many studies have examined the advantages and disadvantages of sampling ground beetles using pitfall traps (see Adis 1979; Luff 1975; Spence and Niemelä 1994 for a general discussion). While all sampling techniques are biased in one way or another, for many studies of epigaeic arthropod assemblages, there are no reasonable alternatives to pitfall trapping (Spence and Niemelä 1994). Here, I use pitfall traps as recommended by Niemelä *et al.* (1986) and Niemelä *et al.*(1990) to compare the relative catch rates of ground beetle species across a range of disturbed and undisturbed forest habitats. I have attempted, as much as possible, to account for additional factors that may bias ground beetle catch data by using the same method across all stand treatments, sampling continuously during the summer months, and providing detailed habitat measurements.

2.3.4 Habitat measurements

To assist with the interpretation of ground beetle data, I recorded a range of different environmental parameters. During biweekly visits to each site I recorded the maximum and minimum temperature (max/min thermometer placed 1 m above the ground) and collected a small (*c.* 5 g) sample of mineral soil (0-3 cm depth) in order to obtain a soil moisture estimate (Kalra and Maynard 1991). Thermometers were left out between sample years so that the minimum winter temperature could also be recorded.

In addition, I obtained site-level estimates of ground characteristics (percent cover by plants, litter, or bare ground), understorey plant species richness, and woody debris. Around each pitfall trap, I established a 1 m^2 plot in which we identified all understorey plant species using Johnson *et al.* (1995) and determined plant species richness, as well as % cover by plants, litter (organic debris), and bare ground (exposed mineral soil). Three replicate samples of fine woody debris (FWD; pieces of dead wood < 5 cm diameter) were collected from each site using a randomly placed 0.25 m^2 quadrate and collecting all surface woody debris pieces within the quadrate. These samples were then brought back to the laboratory, oven-dried at 70°C to a constant mass, and then weighed to the nearest 1 g. Coarse woody debris (CWD; pieces of dead wood > 5 cm diameter) volume estimates were obtained by recording the type (snag = standing dead tree > 1.5 m height, stump = vertical piece < 1.5 m height, or log = fallen or leaning > 45°), diameter (mid point), and length (or height) for all pieces found within two 5 m-radius plots centred on 2 pitfall traps (selected randomly) at each site. Volume estimates for stumps and logs (or portions) within each plot were calculated as the volume of a cylinder using diameter and length measurements. Snag volume was calculated using base diameter, height (measured with a clinometer), and an estimated top diameter assuming a taper function of 1.2 cm per meter of height (Spies and Franklin 1991).

2.3.5 Data analysis

Ground beetle species richness for each stand treatment was estimated by rarefaction (Gotelli and Colwell 2001). Rarefaction accounts for variable sampling effort (*i.e.,* number of individuals or samples) by estimating species richness based on random subsamples of individuals drawn from the original dataset. Rarefaction curves were generated using non-standardized catches of each species. For all other analyses, ground beetle catch data were standardized by sampling effort (total individuals/trap*day) to account for occasional sample loss (*c.* 3%) due to trap disturbance by animals and to limit the potential influence of seasonal and yearly variability (*i.e.,* life-history).

I compared overall ground beetle catch rates across stand treatments using 1-factor ANOVA. To examine species-level responses to the stand treatments, we used a separate 1-factor ANOVA for each species because multivariate data did not meet the "variance-covariance" assumption required for MANOVA (Box's $M = 321.46$, $p < 0.0001$) (Norman and Streiner 2000). Therefore, species-level ANOVA's were performed on the top 12 most abundant species (> 95% of the total catch) using a Bonferroni correction ($\alpha = 0.05/12$). Where ANOVA's were significant, Tukey's HSD *post hoc* tests were used to compare stand treatment means. Catch rates of individual species were $\log_{10}(x + 1)$ transformed when necessary to meet the ANOVA assumptions of normality and homoscedasticity (Zar 1996).

To compare ground beetle species assemblages across stand treatments, I used nonmetric multidimensional scaling (NMS). This non-parametric, unconstrained ordination technique is effective for revealing gradients in ecological data with complex species responses and has the advantage of avoiding the assumption of linear relationships among variables (Clarke 1993; McCune and Grace 2002). For this analysis, I used Sørensen (Bray-Curtis) dissimilarity as the distance measure and pitfall trap-level data consisting of standardized catch rates for all species. Further transformations (*e.g.*, $log_{10}(x + 1)$) yielded similar results and were therefore deemed unneccessary.

Similarity in species composition among stand treatments was evaluated using multi-response permutation procedures (MRPP) and rank-transformed Sørensen (Bray-Curtis) distance (Mielke *et al.* 1976; Zimmerman *et al.* 1985). Dispersion (the amount of scatter) within each stand treatment grouping in the NMS was determined from the dissimilarity matrix by calculating the average dissimilarity in species composition between all traps within a given site. Stand-level dispersion for each treatment was then evaluated using 1-factor ANOVA followed by Tukey's HSD *post hoc* tests.

Effects of measured habitat characteristics on beetle species composition were evaluated using multivariate regression tree (MRT) analysis (De'ath 2002). This multivariate version of classification and regression tree analysis (De'ath and Fabricius 2000) models the relationship between multiple species data and environmental characteristics and has been shown to be particularly useful in ground beetle studies (Koivula 2005; Koivula and Vermeulen 2005; Pihlaja *et al.* 2006; Work *et al.* 2004). MRT progressively splits species data to form clusters of sites that are related by multiple regression to a set of measured environmental variables. Each binary split is chosen to minimize the dissimilarity between sites within clusters, and each cluster represents a particular assemblage of species. Starting with a split that divides the entire data set into two clusters, the process continues until an overly large dendrogram or "tree" is grown. The size of this tree is then reduced or "pruned" based on a cross-validation stopping rule determined by the goals of the analysis (*i.e.*, exploration, description, or prediction). For this analysis, I again used Sørensen (Bray-Curtis) dissimilarity as the distance measure and the final tree was selected by cross validation using the 1-SE rule (Breiman *et al.* 1984), which selects the smallest tree within one standard error of the most predictive tree (*i.e.*, the smallest predicted mean square error).

Finally, I used Indicator species analysis (Dufrêne and Legendre 1997) to further describe the ground beetle species assemblage associated with each stand treatment (NMS) and node (MRT). This analysis generates an indicator value for each species based on its catch rate and relative frequency in a particular set of sites (*i.e.*, stand treatment for the NMS and cluster of sites for the MRT). Indicator values range from 0 (no indication) to 100 (perfect indication) and were evaluated against a Monte Carlo test statistic (1000 permutations).

Several different software packages were used to run the above analyses. Rarefaction curves were generated using EstmateS 7.5 (Colwell 2005). ANOVA's and Tukey's HSD *post hoc* tests were performed using SPSS for Windows 11.5 (SPSS 2002, LEAD Technologies Inc. 2002). NMS ordination and Indicator Species Analyses were performed using PC-Ord (McCune and Mefford 1999). R 2.0.1 (R Development Core Team 2004) was used for the MRT. For all analyses, except species-level ANOVA's (see above), we employed a rejection coefficient of 0.05.

2.4 Results

I collected a total of 19,050 ground beetles representing 55 species during this study (Appendix 2-A). SALV sites yielded the largest catch of ground beetles (6672 individuals, 35.0% of total catch) followed by BURN sites (5295 individuals, 27.8%), HERB sites (3855 individuals, 20.2%), GREEN sites (2016 individuals, 10.6%), and HARV sites (1212 individuals, 6.4%). *Sericoda quadripunctata* (DeGeer) was the most commonly collected species (7036 individuals, 36.9% of total catch), followed by *Pterostichus adstrictus* Eschscholtz (6425 individuals, 33.7% of total catch), and *Sericoda bembidioides* Kirby (1236 individuals, 6.5% of total catch). Data from each sampling year were pooled for analyses because overall treatment patterns were similar between years.

2.4.1 Species richness and abundance

Species richness, as estimated by rarefaction, was higher in disturbed sites than in control sites (Figure 2.1). Based on a subsample of 1200 beetles, sites within the SALV stand treatment had the highest average species richness (27.2), followed by HERB (26.7), BURN (26.3), HARV (25.0), and GREEN (19.1). This pattern was also reflected in the overall abundance of ground beetles as catch rates were higher in burned than in unburned sites (Figure 2.2). More specifically, the effect of stand treatment on catch rates of the entire ground beetle assemblage was significant (ANOVA, $F_{4,25} = 19.161, p < 0.001$) with BURN, SALV, and HERB having greater catch rates than GREEN and HARV sites (Tukey's HSD).

2.4.2 Species responses

Despite the highly conservative Bonferroni adjustment to the alpha level ($\alpha = 0.0042$), the effect of stand treatment on catch rates of the top 12 most abundant species was significant for all but 3 species (ANOVA; Table 2.1). Examination of the mean catch rates for each species across stand treatment revealed several distinct response patterns (Tukey's HSD; Figure 2.3). First, *Sericoda quadripunctata*, *Bembidion grapii* Gyllenhal and *Pterostichus adstrictus* responded positively to the effect of fire as their mean catch rates were significantly greater in burned treatments (BURN, SALV, and HERB) than in unburned treatments (GREEN and HARV). For these three species, the multiple disturbance treatments (SALV and HERB) did not dramatically alter their mean catch rates although *S. quadripunctata* showed a significantly positive response to SALV and *P. adstrictus* responded negatively to HERB. Second, *Scaphinotus marginatus* (Fischer von Waldheim) and *Platynus decentis* (Say) responded negatively to all disturbance treatments, whereas *Patrobus foveocollis* (Eschscholtz) responded negatively to all burned treatments (BURN, SALV, HERB). While this effect was not statistically significant for *P. decentis* ($p = 0.0097$) given the Bonferroni adjusted alpha level, its response pattern suggested that it was negatively affected by any disturbance type we investigated. *Sericoda bembidioides* Kirby and *Stereocerus haematopus* (Dejean) exhibited a third pattern of response as both responded negatively to the multiple disturbance treatments. Catch rates for these two species were highest in the sites with a single disturbance, BURN for *S. bembidioides* and HARV for *S. haematopus*, and were significantly reduced in sites with multiple disturbances (SALV and HERB). No significant effect of stand treatment was found for *Calathus ingratus* Dejean and *Calathus advena* (LeConte). Finally, catch rates of *Calosoma calidum* (Fabricius) were highest in HERB sites and catch rates of *Amara obesa* (Say) were highest in SALV sites, suggesting that both of these species responded positively to the effects of multiple disturbances.

2.4.3 Species composition

Ground beetle species composition varied significantly between stand treatments in the NMS ordination (MRPP; $T = -34.233$, $A = 0.631$, $p < 0.001$) (Figure 2.4). The NMS solution was achieved after 100 iterations and had a final stress of 10.259. The variance explained by the ordination was 89.8% (axis 1 = 78.9%, axis 2 = 10.9%). Separation in species composition was greatest between burned (BURN, SALV and HERB) and unburned (GREEN and HARV) stand treatments (MRPP; $T = -61.275$, $A = 0.558$, $p < 0.001$), suggesting that fire had the strongest effect on the overall species composition. Among the unburned sites, there was significant separation in species composition between GREEN and HARV stand treatments (MRPP; $T = -13.758$, $A = 0.204$, $p < 0.001$). Among the burned sites (BURN, SALV and HERB), separation in species composition between stand treatments was still significant, but there was considerably more overlap (MRPP; $T = -9.319$, $A = 0.160$, $p < 0.001$).

Indicator species analysis revealed a total of 19 species as significant indicators of stand treatment (Table 2.2). *Scaphinotus marginatus* was the strongest indicator of the GREEN stand treatment, followed by *Platynus decentis*, *Carabus chamissonis* Fischer von Waldheim, *Agonum retractum* LeConte, and *Trechus apicalis*

Motschulsky. For the HARV treatment, only *Stereocerus haematopus* was a significant indicator, whereas for the BURN stand treatment, *Sericoda bembidioides* was the strongest indicator species followed by *Harpalus laevipes* Zetterstedt, and *Elaphrus americanus* Dejean. Sites within the SALV treatment had the largest number of significant indicators (7), with the strongest being *Amara obesa* followed by *Agonum placidum* (Say), *Bembidion quadrimaculatum dubitans* (LeConte), *Sericoda quadripunctata*, *Bembidion mutatum* Gemminger & Harold, *Amara torrida* (Panzer), and *Pterostichus adstrictus*. For sites within the HERB treatment, *Calosoma calidum* was the strongest indicator followed by *Calosoma frigidum* Kirby and *Syntomus americanus* (Dejean).

The amount of dispersion (or mean dissimilarity) in species composition varied significantly between stand treatments (ANOVA; $F_{4,25} = 20.207, p < 0.001$) (Figure 2.5). Comparison across stand treatments (Tukey's HSD) showed that intra-stand variation in species composition did not differ significantly between BURN, HARV and GREEN sites. In contrast, dispersion was significantly lower in sites that had received more than one disturbance (SALV and HERB).

2.4.4 Habitat and ground beetle assemblage structure

Cross-validated MRT analysis of all 55 ground beetle species (Figure 2.6) and 13 measured habitat parameters (Table 2.3) consistently produced a tree with 5 terminal nodes (groups A-E). This tree explained 93.6% of the total variance in the ground beetle dataset and the cross-validated relative error value was 0.277, indicating that the model had some predictive power (0: perfect predictor; ~1: poor predictor;

De'ath 2002). The first split (bare ground) explained 47.7% of the variance, followed by 23.1%, 11.4% and 11.4% for amount of coarse woody debris (CWD), plant species richness, and amount of fine woody debris (FWD), respectively.

Ground beetle species compositional structure, illustrated by proportion of total catch for the top 12 most abundant species, varied strongly across the 5 groups in the MRT (Figure 2.6; groups A-E). The first group (group A) included 13 sites (3 BURN, 5 SALV and 5 HERB) that had some (> 1%) exposed bare ground and indicator species analysis revealed that *Amara obesa* was a significant indicator of this group even though the species assemblage at these sites was clearly dominated by *Sericoda quadripunctata* and *Pterostichus adstrictus*. Group B contained 3 sites (all BURN) that in addition to having no bare ground also had CWD volumes in excess of 184.6 m^3/ha. This group was also dominated by *S. quadripunctata* and *P. adstrictus* although no significant indicator species were detected. Groups C (2 sites; 1 HERB and 1 SALV) and D (3 sites; all HARV) both had CWD volumes less than 184.6 m^3/ha and fewer than 5.5 understorey plant species per m^2 on average, but were divided on the basis of group D having more FWD ($\geq$ 1.94 kg/m^2) than group C. No significant indicator species were detected for group D, but *S. quadripunctata* and *Calosoma calidum* emerged as significant indicators of group C. The remaining 9 sites (group E; 6 GREEN and 3 HARV) were characterized as having lower volumes of CWD (<184.6 m^3/ha) and higher average understorey plant species richness ($\geq$ 5.5 species/m^2). The ground beetle assemblage in group E was dominated by *Scaphinotus marginatus* and *Calathus ingratus*, which were both identified as significant indicators of this set of sites.

2.5 Discussion

2.5.1 Effects of wildfire

Studies on the effects of fire on forest arthropods suggest that assemblages may be altered by direct mortality of resident species (Ahlgren 1974; Paquin and Coderre 1997; Wikars and Schimmel 2001), an influx of disturbance-adapted colonizers (Beaudry *et al.* 1997; Evans 1971; Holliday 1984; Saint-Germain *et al.* 2004; Wikars 1995; Wikars 1997), and indirect effects of habitat succession (Ahlgren 1974; Buddle *et al.* 2000; Holliday 1991; Richardson and Holliday 1982; Saint-Germain *et al.* 2005). In the present study, I found that burned sites had greater species richness and higher overall catch rates than unburned sites regardless of what other treatments were applied. I also found that species composition patterns were clearly dominated by the effects of fire. These results were largely attributable to the response of three species, *S. quadripunctata*, *S. bembidioides*, and *P. adstrictus*. These three species accounted for over 75% of the total catch and all three responded positively to the effects of fire.

Both *S. quadripunctata* and *S. bembidioides* have previously been described as pyrophilous (Evans 1971), requiring burned substrates for at least part of their life cycle (Lindroth 1961-1969). Exactly what attracts these species to burned forests remains unclear, although Koivula *et al.* (2006) showed that the presence of both *S. quadripunctata* and *S. bembidioides* was strongly linked to increased fire severity. Whatever attracts these species to burned areas, the response appears to be short-lived as my data (Appendix 2-A) and that of other studies (Holliday 1991; Koivula *et al.* 2006; Wikars 1995) show that their presence declines dramatically 2-4 years after a fire.

In addition to *S. quadripunctata* and *S. bembidioides*, I also found that *P. adstrictus* and *B. grapii* were strongly and positively affected by fire. Neither of these two species has been described as pyrophilous, although Muona and Rutanen (1994) also noted an increase in the abundance of *P. adstrictus* and *B. grapii* after prescribed burning of coniferous forests in Finland. Both of these species prefer open areas with sparse vegetation and moderately dry soil (Lindroth 1961-1969), which may help to explain their preference for the burned sites in our study as these sites had reduced plant cover and lower average soil moisture (Table 3). In addition, increased volume of CWD in burned sites (BRN; Table 3) may also help to explain the increased catch rates of *P. adstrictus* as the first two instars of this species inhabit logs (Goulet 1974).

2.5.2 Effects of forest harvesting

At the community level, effects of forest harvesting on ground beetle assemblages were similar to effects of fire in that both disturbances led to an increase in species richness and significantly altered species composition relative to the controls. However, fire led to a much greater increase in species richness than harvesting and the species composition found in harvested and burned stands was distinct at least during the first two years after disturbance. In a study comparing the short-term response of ground beetles to fire and clear-cut harvesting of black spruce forests of Québec, Saint-Germain *et al.* (2005) also noted strong differences in species composition especially with respect to species dominance. At present, it is not clear how long differences in ground beetle species composition between burned and harvested boreal forests may last, although previous studies indicate that assemblages of ground-dwelling spiders, beetles (Buddle *et al.* 2006; Buddle *et al.* 2000) and songbirds (Hobson and Schieck 1999) converge in species composition 30 years after disturbance.

The differences I found in species composition between undisturbed and harvested sites were driven by several species. For example, catch rates of S. *marginatus* and *P. decentis* were reduced in harvested sites suggesting that both species were negatively impacted by forest harvesting. Niemelä *et al.* (1993) and Spence *et al.* (1996) noted that both of these species were scarce in or absent from sites recovering from forest harvesting even after 27 years, suggesting that the short-term negative response we detected may persist over a longer period of time. While both species are considered to be forest specialists (Lindroth 1961-1969), the reduction in *P. decentis* may be linked to its preference for resting in moist leaf litter or under decayed logs, and the reduction in *S. marginatus* is likely linked to decreased availability of its mollusc prey (Hylander *et al.* 2004). Interestingly, both *P. decentis* and *S. marginatus* catches were also reduced in burned sites, suggesting that disturbance of any kind may be detrimental to these two species.

Several less commonly collected species also appeared to be negatively impacted by harvesting. *C. chamissonis*, *A. retractum* and *T. apicalis* accounted for a meagre 1.4 % of the total ground beetle catch, but I found that all three species were significant indicators of the undisturbed stand treatment (Table 2.2), and collected fewer individuals in harvested sites than in undisturbed sites (Appendix 2-A). Spence *et al.* (1996) also noted the negative effect of forest harvesting on *C. chamissonis* and a related species of *Trechus*. According to descriptions in Lindroth (1961-1969), all three of these species appear to be true forest specialists associated with damp, somewhat shaded areas among dead leaves. While catches of these species were too low to permit direct statistical comparisons in my study, the role that they play in determining patterns of overall species composition should not be overlooked as they may be highly sensitive to habitat change. Evidence on saproxylic insects in heavily managed Finnish boreal forests suggests that rare or uncommonly collected species may indeed be those most threatened by habitat change (Siitonen and Martikainen 1994).

In the present study, not all species were negatively affected by harvesting. One species, *S. haematopus*, showed a significant and positive response to forest harvesting and was found to be the only significant indicator of the harvested stand treatment. Previous work has shown that this species is not detrimentally affected by clear-cut logging (Niemelä *et al.* 1993), but the reason for its tolerance is not clear. Little is currently known about the habitat requirements of this species although Lindroth (1961-1969) described it as being abundant on the tundra, associated with dry, sandy soils. My analyses may offer additional insight as I found that this species was most common in sites that had little (if any) exposed bare ground, relatively low plant diversity, moderately moist soils, and high levels of fine woody debris covering the ground (Figure 2.6 and Table 2.3). Furthermore, I collected several teneral individuals in harvested stands (unpublished data), suggesting that *S. haematopus* was also breeding successfully in this habitat.

2.5.3 Effects of multiple disturbances

Finally, I compared ground beetle assemblages in sites that had been either burned (BURN) or harvested (HARV), with those that had been disturbed by both fire and forestry-related disturbances. Specifically, I examined ground beetle responses to postfire salvage logging (SALV) and an herbicide treatment (HERB), which had been harvested prior to the fire, replanted with white spruce and then treated with herbicide to reduce competition with naturally regenerating trembling aspen.

Recently, there have been increasing efforts to examine the ecological effects of postfire salvage logging on boreal forest biota (Donato *et al.* 2006b; Fraser *et al.* 2004; Koivula *et al.* 2006; Lindenmayer *et al.* 2004; Macdonald 2007, Morissette *et al.* 2002; Nappi *et al.* 2004; Phillips *et al.* 2006). Studies on the effects of this practice on ground beetles emphasize the unique nature of this disturbance relative to harvesting unburned stands (Phillips *et al.* 2006) and suggest that populations of pyrophilous species (Koivula *et al.* 2006) may be particularly sensitive. In my study, species responses to postfire salvage logging were variable. Catch rates of *S. quadripunctata* and *A. obesa* were significantly greater in SALV sites than in BURN sites. In addition, *P. adstrictus*, *B. mutatum* and *B. quadrimaculatum dubitans* also appeared to prefer SALV sites, as all emerged as significant indicators of salvage logging in our analysis. One common element among all of these species is that they are associated with open areas, with sparse or no vegetation, and moderately dry soil (Lindroth 1961-1969), suggesting that they may all benefit from the creation of these conditions in salvage logged sites (Table 2.3). However, I also found that catch rates of another pyrophilous species, *S. bembidioides*, were significantly reduced in SALV sites, which suggests a negative response to the combined effects of fire and harvesting. The degree to which such negatively affected species may be able to withstand widespread salvage logging efforts by seeking refuge in unsalvaged stands (Koivula *et al.* 2006) or fire residuals (Gandhi *et al.* 2004) remains unclear.

Effects of herbicide treatments, such as the competitive release treatment investigated here, on non-target organisms have been studied extensively (for a general review, see Sullivan and Sullivan 2003). In an experimental study, Duchesne *et al.* (1999) reported that the application of herbicide in areas replanted with white spruce did not affect the overall catch of ground beetles, but reduced the abundances of *P. decentis*, *P. adstrictus* and *A. retractum* while increasing the catch of other species, such as *C. calidum*. Response patterns for these species were identical in my study (Figure 2.3 and Appendix 2-A), but in addition to *C. calidum*, I also found *C. frigidum* and *S. americanus* to be significant indicators of the HERB sites. While the occurrence of *S. americanus* in these sites is probably due to its preference for sunny areas with sparse low vegetation (Lindroth 1961-1969), the increase in *C. calidum* and *C. frigidum* seems perplexing. Both *Calosoma* species are well-known predators of Lepidoptera (Lindroth 1961-1969), and the herbicide application has been reported to reduce the abundances of herbivorous insects (Sullivan and Sullivan 2003). However, similar to the Duchesne *et al.* (1999) study, I found that 1 year after the treatment was applied, plants like raspberry and prickly rose had partially recovered (Table 2.3), suggesting that the Lepidoptera community may have recovered as well. In addition, *S. haematopus* was also significantly reduced in the HERB sites. As *S. haematopus* appears to benefit from the effects of forest harvesting, its lower catch rates in both

SALV and HERB sites suggest that the effects of multiple disturbances may be detrimental for this species.

At the community level, the over-powering effect of fire was such that I detected no difference in species richness or total ground beetle catch rates between sites that had simply been burned and those that had been multiply disturbed. This effect was also apparent in comparisons of species composition, as my ordination analysis showed considerable overlap between BURN, SALV and HERB stand treatments (Figure 2.4). Interestingly, differences in the order of disturbance (SALV = burned then harvested; HERB = harvested, then burned) were not apparent in the compositional response. However, the amount of dispersion or compositional variability in the SALV and HERB sites was significantly lower than in sites disturbed only by fire or harvesting alone. This result suggests that the combined effects of fire and forestry-related disturbances may simplify, and to some extent homogenize, the ground beetle assemblage not through a reduction in overall catch or species loss, but rather through a reduction of the amount of compositional variation between sites (or even between traps within sites). The ecological consequences of this reduction in variability are beyond the scope of my study. However, if biodiversity is the variety and variability within and among living things and the ecological complexes in which they occur (Wilson 1992), then this form of biodiversity loss clearly warrants further examination.

2.5.4 Implications for biodiversity conservation and sustainable forest management

Rising societal demands for timber resources combined with current and predicted increases in wildfire activity in many parts of the circumpolar boreal forest (Flannigan *et al.* 1998; Overpeck *et al.* 1990; Stocks *et al.* 1998) suggest that the frequency of disturbance combinations such as those investigated here will continue to rise. Given the relative novelty of industrial forestry in North American boreal ecosystems compared to wildfire, I reasoned that boreal mixed-wood ground beetles would be better adapted to fire than to harvesting and that the combined effects of these disturbances could be cumulative. In general, my analyses showed remarkable differences in ground beetle responses to wildfire and forestry-related disturbances and suggest that while some species may appear to benefit from the combined effects of wildfire and forestry-related disturbances, these effects may be detrimental to others and may lead to a simplification of the entire assemblage.

The ecological consequences of such biodiversity loss remain unclear. Efforts to determine the relationship between biodiversity and the stability of ecological function are at the heart of a long-standing debate in ecology (McCann 2000). While demonstration of the diversity-stability link has been elusive (Grime 1997; Naeem 2002a, 2002b), mounting evidence supports the hypothesis that biodiversity loss could alter the performance of ecosystems (Grime 1997; Naeem 2002b; Naeem *et al.* 1999; Sala *et al.* 2000; Sankaran and McNaughton 1999; Tilman 1996; Tilman and Downing 1994). Therefore, in this era of rapid climate change, increasing natural resource exploitation, and accelerating species extinctions (Ehrlich and Wilson 1991; Smith *et* *al.* 1993; Vitousek *et al.* 1997), the loss of compositional variability associated with combining natural and anthropogenic disturbances detected here warrants further research.

Many of the ground beetle responses I detected were correlated with changes in several key habitat parameters that suggest avenues for mitigating the effects of forestry-related practices. Specifically, the presence of exposed bare ground, understorey plant species richness, and amounts of both coarse and fine woody debris explained a substantial portion of the total variability in ground beetle species composition. For example, 47.7% and 23.1% of the total variance in ground beetle species composition was explained by the presence of exposed bare ground and the amount of coarse woody debris, respectively. While these findings may be interpreted as a potential mitigation "thresholds" for forest management strategies aimed at conserving ground beetle species composition, they should be interpreted with caution for two reasons. First, my study was limited temporally to the first two years after disturbance suggesting that more work needs to be done to determine whether such differences in habitat characteristics may persist over longer time scales. Second, I have presented results for a particular ground beetle assemblage, namely the assemblage associated with boreal spruce-aspen mixed-wood forests of a particular age and density, so it is difficult to generalize these findings to other organisms, other forest types and across wider spatial scales. Nonetheless, these results indicate that more detailed studies of these particular habitat variables may provide considerable insight into how to best conserve this and other portions of boreal forest biodiversity. Until the effects of disturbance combinations on boreal forest biota are better understood, I recommend that efforts to avoid compounding disturbances on any given site should be considered in the development of forest management guidelines.

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Table 2.1: Summary of ANOVA results for the effect of stand treatment on the top 12 most abundant species. Significant tests ($p < 0.0042$, Bonferroni adjustment) are in bold.

Species	$F_{4,25}$	**MS**	*p*
Sericoda quadripunctata (DeGeer)	39.40	40.930	**< 0.0001**
Pterostichus adstrictus Eschscholtz	26.69	19.620	**< 0.0001**
Sericoda bembidioides Kirby	7.24	3.390	**0.0005**
Calathus ingratus Dejean	3.36	0.592	0.0250
Scaphinotus marginatus (Fischer von Waldheim)	47.21	0.143	**< 0.0001**
Platynus decentis (Say)	4.20	0.019	0.0097
Stereocerus haematopus (Dejean)	8.93	0.159	**< 0.0001**
Patrobus foveocollis (Eschscholtz)	4.79	0.011	**0.0005**
Calathus advena (LeConte)	1.99	0.058	0.1274
Bembidion grapii Gyllenhal	8.55	0.005	**< 0.0001**
Calosoma calidum (Fabricius)	7.84	0.011	**0.0003**
Amara obesa (Say)	6.93	0.006	**0.0006**

Table 2.2: Significant indicator species for each stand treatment (GREEN = green/control; HARV = harvested; BURN = burned; SALV = salvaged; and HERB = herbicide). Indicator values are presented as percent of perfect indication (Dufrene and Legendre 1997) and significance ($p < 0.05$) was determined using Monte Carlo randomization (1000 permutations).

Species	Stand Treatment	Indicator Value (obs.)	Indicator value from randomization	
			Mean (± SE)	*p*
Scaphinotus marginatus (Fischer von Waldheim)	GREEN	87.8	28.1 (0.31)	0.001
Platynus decentis (Say)	GREEN	62.9	36.2 (0.29)	0.007
Carabus chamissonis Fischer von Waldheim	GREEN	56.1	21.6 (0.33)	0.012
Agonum retractum LeConte	GREEN	53.6	28.9 (0.28)	0.017
Trechus apicalis Motschhulsky	GREEN	50.2	31.4 (0.31)	0.042
Stereocerus haematopus (Dejean)	HARV	63.8	34.6 (0.23)	0.002
Sericoda bembidioides Kirby	BURN	59.3	29.7 (0.32)	0.015
Harpalus laevipes Zetterstedt	BURN	52.6	27.1 (0.27)	0.010
Elaphrus americanus Dejean	BURN	41.5	17.8 (0.31)	0.041
Amara obesa (Say)	SALV	62.8	28.6 (0.27)	0.002
Agonum placidum (Say)	SALV	50.2	26.3 (0.22)	0.003
Bembidion quadrimaculatum dubitans (LeConte)	SALV	46.4	17.5 (0.27)	0.025
Sericoda quadripunctata (DeGeer)	SALV	41.0	26.8 (0.15)	0.004
Bembidion mutatum Gemminger & Harold	SALV	40.3	23.1 (0.26)	0.042
Amara torrida (Panzer)	SALV	38.0	15.3 (0.27)	0.024
Pterostichus adstrictus Eschscholtz	SALV	34.9	27.2 (0.10)	0.021
Calosoma calidum (Fabricius)	HERB	68.6	28.0 (0.28)	0.002
Calosoma frigidum Kirby	HERB	63.0	18.2 (0.30)	0.004
Syntomus americanus (Dejean)	HERB	45.7	20.2 (0.27)	0.013

Table 2.3: Summary of habitat conditions recorded for each stand treatment (GREEN = green/control, HARV = harvested, BURN = burned, SALV = salvaged; HERB = herbicide). Values are means (±SE) for $n = 6$ sites. The five most common understorey plant species within each stand treatment are listed in order of decreasing dominance.

	Stand Treatments				
Parameter	GREEN	HARV	BURN	SALV	HERB
CWD (m^3/ha)	94.98 (±21.6)	90.76 (±15.0)	329.56 (±47.6)	90.75 (±18.6)	85.27 (±27.1)
snag (%)	21.82 (±7.2)	0.96 (±1.0)	81.45 (±3.8)	7.25 (±6.1)	0.00 (±0.0)
log (%)	75.33 (±8.1)	84.64 (±4.0)	17.50 (±4.1)	71.62 (±11.1)	78.96 (±5.1)
Stump (%)	2.85 (±1.6)	14.40 (±3.5)	1.06 (±0.7)	21.14 (±6.2)	21.04 (±5.1)
FWD (kg/m^2)	0.36 (±0.1)	3.57 (±0.2)	0.29 (±0.1)	1.54 (±0.2)	0.42 (±0.1)
T_{max} summer (°C)	29.81 (±0.7)	31.83 (±1.3)	33.65 (±0.8)	35.17 (±1.1)	35.36 (±1.0)
T_{min} summer (°C)	2.87 (±0.4)	0.23 (±0.5)	1.33 (±0.4)	1.98 (±0.5)	1.88 (±0.3)
T_{min} winter (°C)	-33.67 (±1.0)	-33.33 (±1.9)	-34.67 (±3.2)	-30.33 (±1.5)	-29.17 (±0.7)
Soil moisture (%)	29.40 (±6.3)	31.07 (±1.7)	17.80 (±2.3)	17.07 (±2.5)	15.92 (±1.0)
Plant richness (sp/m^2)	11.83 (±1.8)	4.50 (±1.1)	5.67 (±1.0)	4.50 (±0.4)	4.67 (±0.6)
plant cover (%)	77.50 (±5.9)	21.33 (±9.5)	60.83 (±13.0)	25.00 (±5.6)	37.50 (±10.9)
litter (%)	22.50 (±5.88)	78.67 (±9.49)	17.17 (±6.81)	31.67 (±7.03)	10.00 (±4.28)
bare ground (%)	0.00 (±0.00)	0.00 (±0.00)	22.00 (±13.66)	43.33 (±7.15)	52.5 (±12.23)
Dominant plants	Moss (various)	Grass (various)	Fireweed (*Epilobium angustifolium*)	Fireweed (*Epilobium angustifolium*)	Grass (various)
	Wild sarsaparilla (*Aralia nudicaulis*)	Trembling aspen (*Populus tremuloides*)	Moss (various)	Trembling aspen (*Populus tremuloides*)	Raspberry (*Rubus idaeus*)
	Prickly rose (*Rosa acicularis*)	Raspberry (*Rubus idaeus*)	Trembling aspen (*Populus tremuloides*)	Raspberry (*Rubus idaeus*)	Prickly rose (*Rosa acicularis*)
	Bunch berry (*Cornus canadensis*)	Fireweed (*Epilobium angustifolium*)	Bicknell's geranium (*Geranium bicknelli*)	Grass (various)	Bunch berry (*Cornus canadensis*)
	Moose berry (*Viburnum edule*)	Moss (various)	Prickly rose (*Rosa acicularis*)	Bicknell's geranium (*Geranium bicknelli*)	Trembling aspen (*Populus tremuloides*)

Abbreviations: Coarse woody debris (CWD); fine woody debris (FWD); maximum temperature (T_{max}); Minimum temperature (T_{min}).

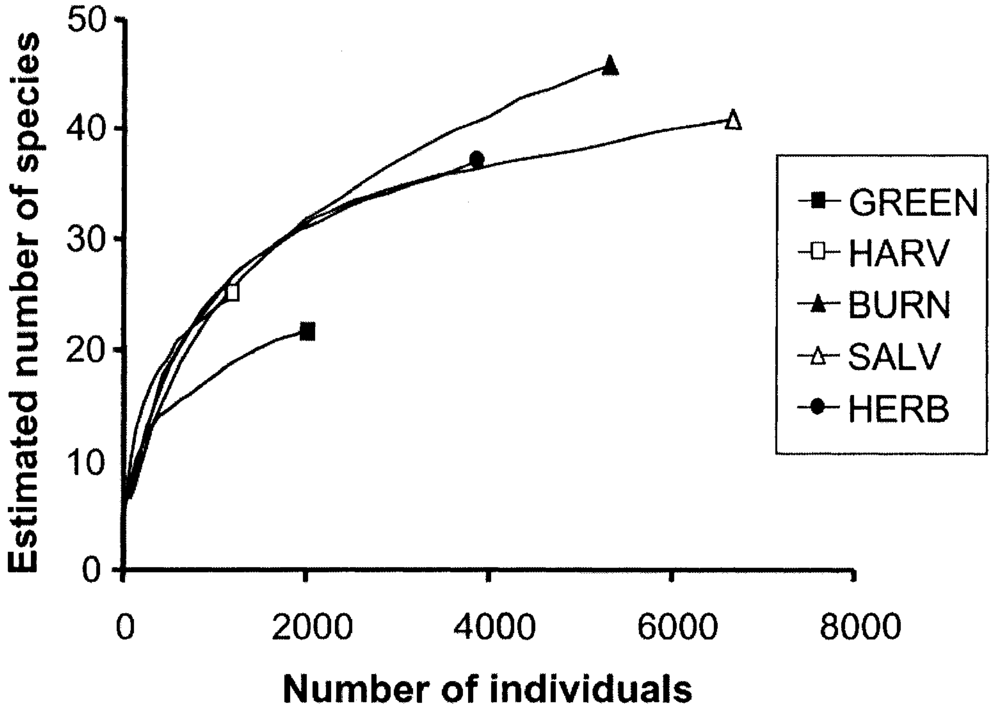

Figure 2.1: Rarefaction estimates of ground beetle species richness for GREEN = green/control (filled squares), HARV = harvested (open squares), BURN = burned (filled triangles), SALV = salvage logged (open triangles), and HERB = herbicide (filled circles) stand treatments.

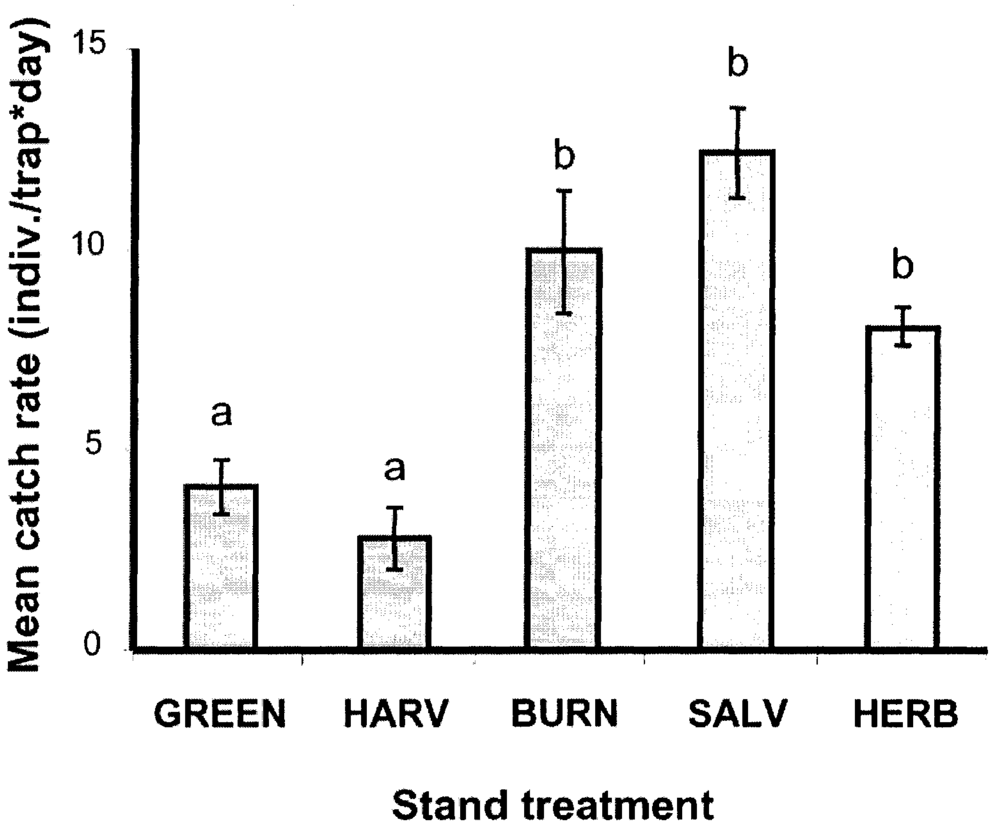

Figure 2.2: Standardized catch (individuals / trap*day) of all ground beetles across the five stand treatments (GREEN = green/control; HARV = harvested; BURN = burned; SALV = salvage logged; HERB = herbicide). Different lower case letters indicate significant differences between stand treatments (Tukey's HSD, $p < 0.05$). Bars represent ± 1SE for $n = 6$ sites.

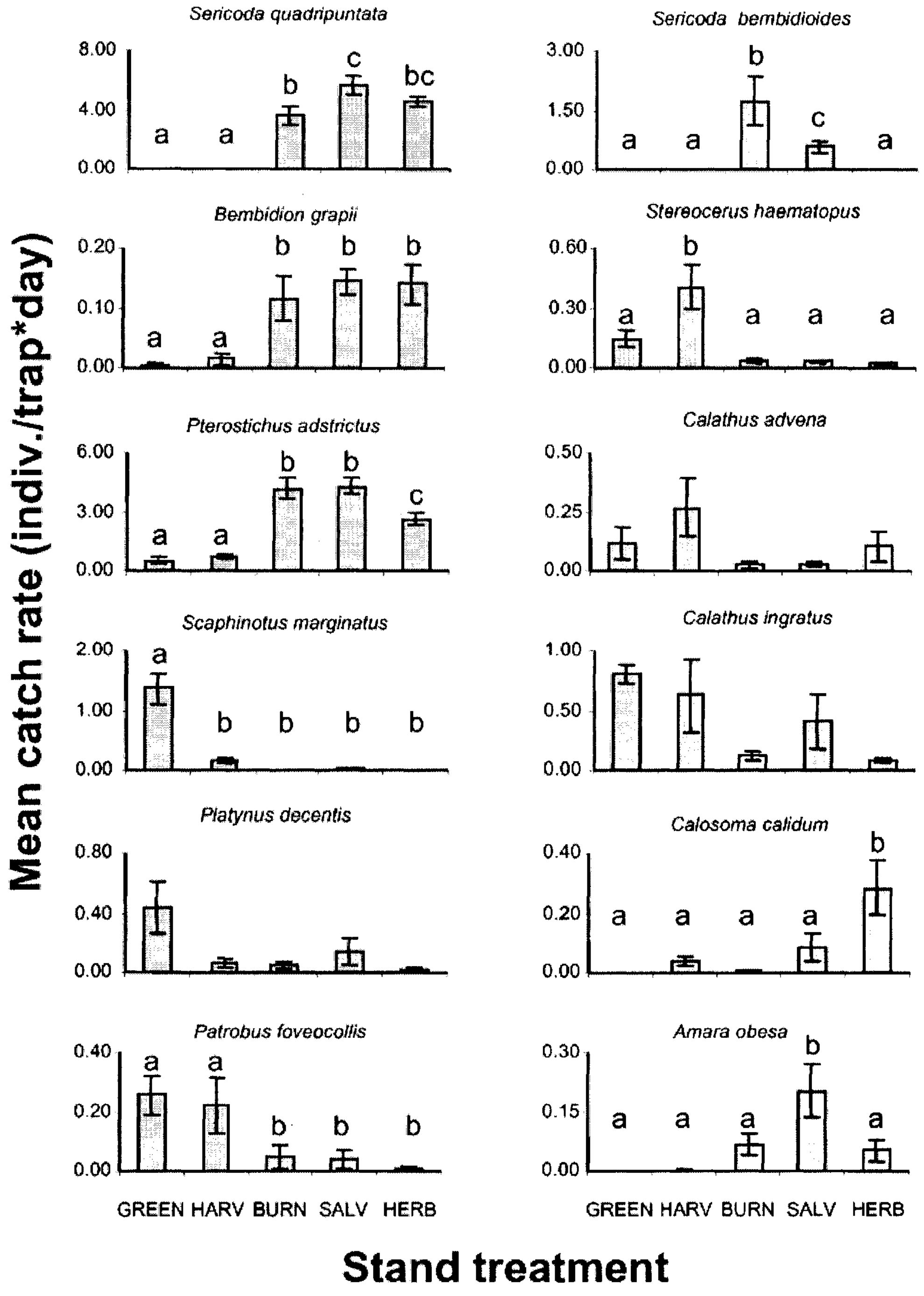

Figure 2.3: Standardized catch (individuals / trap*day) of the top 12 most abundant ground beetle species across the five stand treatments (GREEN = green/control; HARV = harvested; BURN = burned; SALV = salvage logged; HERB = herbicide). Different lower case letters indicate significant differences between stand treatments (Tukey's HSD; $p < 0.05$) for each species. Error bars are ± 1SE for $n = 6$ sites.

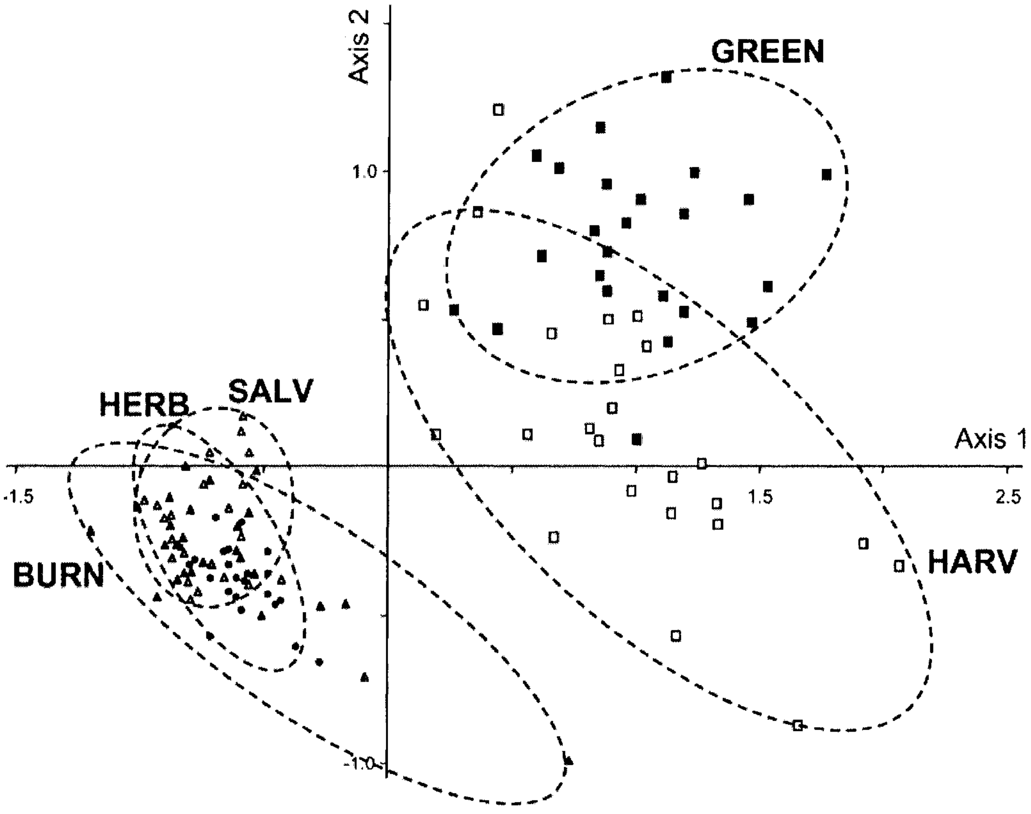

Figure 2.4: Non-metric multidimensional scaling (NMS) ordination of trap-level ground beetle catch rates. Data are coded to show the effects of stand treatment (GREEN = green/control, filled squares; HARV = harvested, open squares; BURN = burned, filled triangles; SALV = salvage logged, open triangles; HERB = herbicide, filled circles) on carabid species assemblages. Confidence ellipses (95%) for each stand treatment are provided to illustrate groupings.

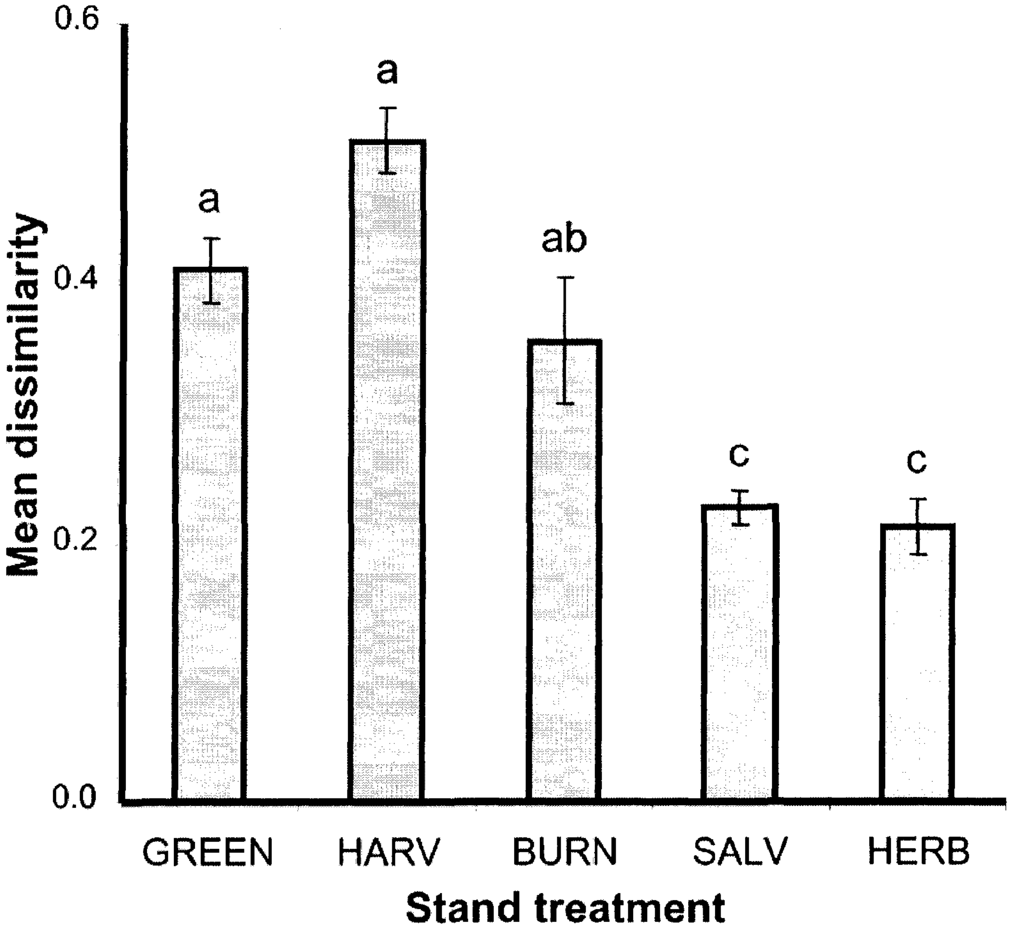

Figure 2.5: Mean dispersion (or dissimilarity) in ground beetle species assemblages between sites within each stand treatment (GREEN = green/control; HARV = harvested; BURN = burned; SALV = salvage logged; HERB = herbicide). Bars represent ± 1SE for n = sites. Different lower case letters indicate significant differences (Tukey's HSD, $p < 0.05$).

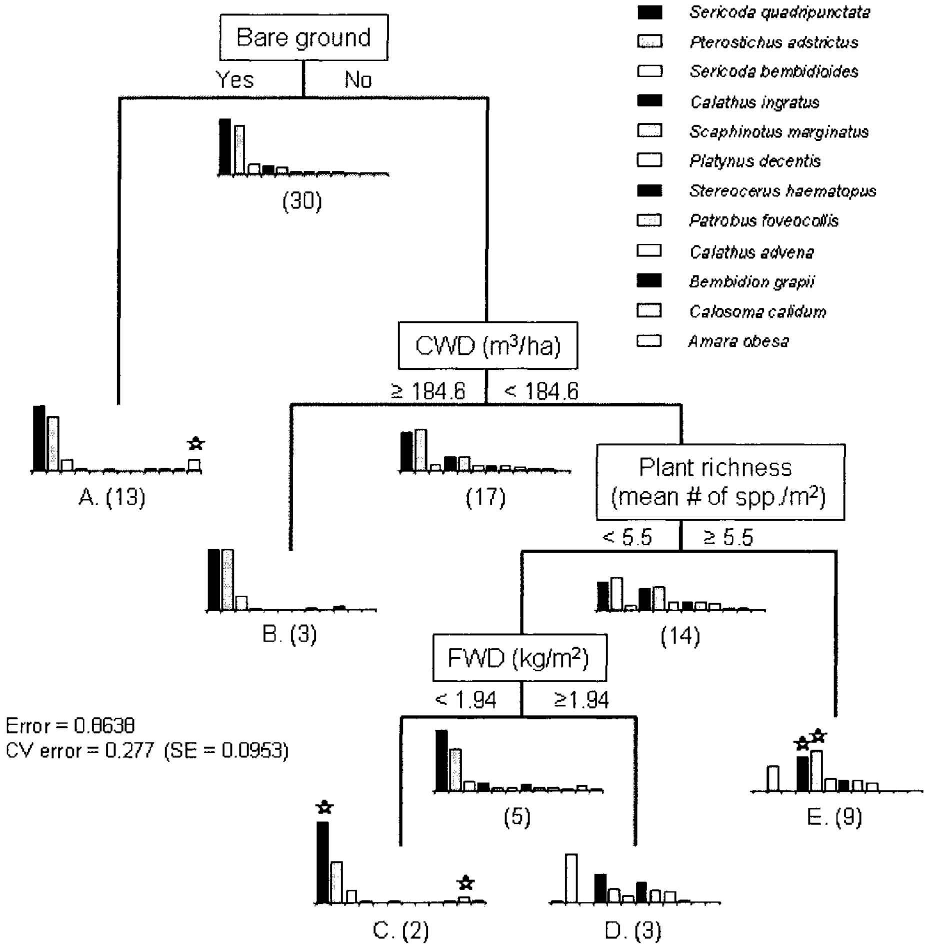

Figure 2.6: Multivariate regression tree for standardized ground beetle data (individuals / trap*day). Sørensen (Bray-Curtis) distance was used for splitting. Barplots at each node show the proportion of total catch (0-50%) for the top 12 most abundant species and the number of sites is shown in parentheses; cyclical shadings (black, grey, white) indicate the various species and run from left to right across each barplot. Significant indicator species ($p < 0.05$) for groups A-E are denoted by stars.

Appendix 2-A: Ground beetle species distribution (total catch) across all stand treatments (GREEN = green/control; HARV = harvested; BURN = burned; SALV = salvaged; HERB = herbicide) in each collection year.

	2002					2003					
Species	**GREEN**	**HARV**	**BURN**	**SALV**	**HERB**	**GREEN**	**HARV**	**BURN**	**SALV**	**HERB**	Total
Agonum cupreum Dejean	0	0	0	1	0	1	0	0	11	5	**18**
Agonum cupripenne (Say)	0	0	0	1	0	0	0	0	0	0	**1**
Agonum gratiosum (Mannerheim)	5	0	3	17	1	0	0	0	0	0	**26**
Agonum placidum (Say)	0	1	10	28	12	0	2	0	3	2	**58**
Agonum retractum LeConte	24	6	3	8	2	44	16	4	6	1	**114**
Amara apricaria (Paykull)	0	0	1	1	0	0	0	0	0	1	**3**
Amara erratica (Duftschmid)	0	0	0	0	0	0	1	0	0	1	**2**
Amara lacustris LeConte	0	0	1	0	0	0	0	0	0	0	**1**
Amara latior (Kirby)	1	0	1	4	1	0	0	0	0	0	**7**
Amara littoralis Mannerheim	0	0	0	1	0	0	1	0	0	2	**4**
Amara lunicollis Schiodte	0	0	2	1	3	0	2	1	2	0	**11**
Amara obesa (Say)	0	0	23	33	5	0	1	14	76	21	**173**
Amara patruelis Dejean	0	0	1	0	0	0	0	0	0	0	**1**
Amara quenseli (Schonherr)	0	0	3	1	0	0	0	0	3	0	**7**
Amara torrida (Panzer)	0	0	1	2	0	0	0	0	1	0	**4**
Badister obtusus LeConte	0	0	0	0	0	1	0	0	0	0	**1**
Bembidion bimaculatum (Kirby)	0	0	12	6	1	0	0	1	2	1	**23**
Bembidion grapii Gyllenhal	0	0	25	21	15	2	8	37	57	58	**223**
Bembidion mutatum Gemminger & Harold	0	3	1	8	6	0	0	0	7	2	**27**
Bembidion nigripes (Kirby)	0	0	2	0	0	0	0	0	0	0	**2**
Bembidion nitidum (Kirby)	0	0	1	0	0	0	0	0	3	0	**4**
Bembidion quadrimaculatum dubitans (LeConte)	0	0	1	4	1	0	0	0	1	0	**7**
Bembidion rupicola Kirby	0	0	1	1	0	0	0	0	0	0	**2**
Bembidion timidum (Leconte)	0	0	0	1	0	0	0	0	0	0	**1**
Calathus advena (LeConte)	41	76	9	10	10	17	33	5	5	45	**251**
Calathus ingratus Dejean	198	145	41	144	21	202	128	20	79	11	**989**
Calosoma calidum (Fabricius)	0	1	19	44	119	0	0	3	3	6	**195**
Calosoma frigidum Kirby	0	0	1	0	9	0	0	0	0	6	**16**
Carabus chamissonis Fischer von Waldheim	5	0	2	1	0	15	0	0	0	1	**24**
Chlaenius alternatus Horn	0	0	0	0	0	0	0	0	0	1	**1**
Cymindis cribricollis Dejean	2	2	6	4	2	0	0	3	1	7	**27**
Dicheirotrichus cognatus (Gyllenhal)	0	0	0	0	0	0	1	2	0	0	**3**
Elaphrus americanus Dejean	0	0	6	2	0	0	0	3	0	0	**11**
Elaphrus clairvillei Kirby	0	0	1	1	0	0	0	5	6	0	**13**
Harpalus fulvilabris Mannerheim	1	7	6	3	1	5	11	8	17	4	**63**
Harpalus laevipes Zetterstedt	0	0	40	39	7	0	0	30	12	5	**133**
Harpalus lewisii LeConte	0	0	3	5	2	0	0	3	4	1	**18**
Harpalus somnulentus Dejean	0	0	2	0	0	0	0	0	0	1	**3**
Loricera pilicornis (Fabricius)	1	0	1	0	1	0	0	0	0	0	**3**
Notiophilus aquaticus (Linné)	0	0	1	0	0	0	0	0	0	5	**6**
Patrobus foveocollis (Eschscholtz)	71	39	11	16	3	55	57	3	6	1	**262**
Platynus decentis (Say)	84	4	15	61	3	138	29	8	17	2	**361**
Poecilus lucublandus (Say)	0	0	1	4	0	0	0	0	0	0	**5**
Pterostichus adstrictus Eschscholtz	104	54	1160	984	516	160	282	1036	1329	800	**6425**
Pterostichus brevicornis (Kirby)	0	0	0	0	0	0	0	1	1	0	**2**
Pterostichus pensylvanicus LeConte	0	1	6	5	3	1	3	3	4	4	**30**
Pterostichus punctatissimus (Randall)	0	5	0	0	0	11	8	1	0	1	**26**
Pterostichus riparius (Dejean)	1	5	0	0	0	0	2	0	0	0	**8**
Scaphinotus marginatus (Fischer von Waldheim)	332	34	0	5	0	335	21	1	8	0	**736**
Sericoda bembidioides Kirby	0	0	659	408	5	0	0	85	78	1	**1236**
Sericoda quadripunctata (DeGeer)	2	1	1076	1904	1158	0	4	840	1118	933	**7036**
Stereocerus haematopus (Dejean)	33	58	17	12	4	40	127	1	4	5	**301**
Syntomus americanus (Dejean)	0	0	1	5	6	0	0	0	0	0	**12**
Tachyta angulata Casey	0	1	0	0	0	0	0	0	0	0	**1**
Trechus apicalis Motschhulsky	40	22	1	5	0	44	10	0	7	4	**133**
Total beetles	**945**	**465**	**3177**	**3801**	**1917**	**1071**	**747**	**2118**	**2871**	**1938**	**19050**
Total species	**17**	**19**	**42**	**39**	**27**	**16**	**21**	**25**	**30**	**31**	

CHAPTER 3

Saproxylic beetles and postfire salvage logging: the synergistic effects of wildfire and forest harvesting

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3.1 Summary

In this chapter, I examined the effects of postfire salvage logging on saproxylic beetle assemblages to determine whether the combined effects of wildfire and forest harvesting on the same sites are cumulative. Specifically, I compared the diversity, species composition and trophic structure of saproxylic beetle assemblages among freshly burned, logged and salvaged boreal mixed-wood forest stands (six replicates of each stand type). Postfire salvage logging reduced beetle species richness and was particularly detrimental for wood- and bark-boring species. Compared to undisturbed sites, species composition was displaced further by the combined effects of wildfire and harvesting than by either disturbance alone. I also found strong differences in trophic structure across stand treatments that were linked to changes in coarse woody debris quantity and quality (*e.g.*, decay stage). Collectively, these findings suggest that the combined effects of wildfire and forest harvesting on saproxylic beetles are

synergistic such that current and predicted increases in postfire salvage logging activity may have serious consequences for North American forest biodiversity.

3.2 Introduction

Saproxylic species as those that are "dependent, during some part of their life cycle, upon the dead or dying wood of moribund or dead trees (standing or fallen), or upon wood-inhabiting fungi, or upon the presence of other saproxylics" (Speight 1989). Under this broad definition, saproxylic insects, particularly beetles, are arguably one of the largest components of forest biodiversity (Grove 2002a). Research from various parts of the world suggests that 20-25% of the entire forest fauna can be considered saproxylic (*e.g.,* Berg *et al.* 1994; Hammond *et al.* 1996; Siitonen 2001). Saproxylic beetles alone are thought to outnumber the world's terrestrial vertebrate species by two to one (Parker 1982) and this estimate is most likely conservative, given that Speight's (1989) definition includes both direct and indirect associations with dead wood. In addition to species richness, ecological diversity of this group is also impressive. For example, saproxylic beetles can be classified according to at least five trophic groups including wood/bark borers, fungivores, detritivores, scavengers and predators (Grove 2002a; Hammond 1997; Jonsell *et al.* 1998; Siitonen 2001).

The diversity of saproxylic insects has largely been attributed to microhabitat sensitivity and a high degree of spatial and temporal variability of such microhabitats as trees die and decay (Grove 2002b; Hammond 1997; Hammond *et al.* 2001, 2004; Jonsell *et al.* 1998; Lindhe *et al.* 2005; Martikainen *et al.* 2000; Schiegg 2000; Siitonen 2001). Many studies from northern Europe (Jonsell *et al.* 1998; Jonsson and

Kruys 2001; Kaila *et al.* 1997; Martikainen *et al.* 2000; Siitonen 2001; Siitonen *et al.* 2000; Similä *et al.* 2002), Australia (Grove 2002a; Yee *et al.* 2001) and Canada (Hammond *et al.* 2001, 2004; Jacobs *et al.* 2006) have demonstrated the sensitivity of this group of insects to changes in the quantity and quality of dead wood. As a result, there has been increased awareness of the potential for saproxylic insects to act as ecological indicators in managed forests (Ehnström 2001; Grove 2002a, 2002b; Siitonen 2001) and a growing concern for their conservation (Ås 1993; Berg *et al.* 1994; Ehnström 2001; Gibb *et al.* 2006; Grove *et al.* 2002; Hammond *et al.* 2004; Jonsell *et al.* 1998; Kaila *et al.* 1997; Martikainen 2001; Similä *et al.* 2002; Speight 1989; Yee *et al.* 2001). For example, in Fennoscandia, reductions in dead wood volume resulting from a lengthy history of highly efficient fire suppression and intensive forest management have been directly implicated in the decline of many rare and threatened saproxylic insect species (Ehnström 2001; Esseen *et al.* 1992, 1997; Heliövaara and Väisänen 1984; Siitonen 2001; Siitonen and Martikainen 1994; Wikars 1992; Wikars 1995). Thus, the incorporation of "biological legacy elements" such as dead wood into current forest ecosystem management practices is gaining wider acceptance (Franklin *et al.* 1997; Hagan and Grove 1999; Lee *et al.* 1997).

In contrast with western European forests, stand-replacing wildfires continue to be a dominant source of dead wood in many parts of North America. In Canada, for example, more than 7500 wildfires occur annually, covering an average of 2.8 million ha (range 0.7 – 7.6 million ha/yr) (Natural Resources Canada 2005). These numbers are expected to increase as various climate change scenarios predict increases in wildfire activity over the next 50 to 100 years (Overpeck *et al.* 1990; Stocks *et al.*

1998), especially in western North America (Flannigan *et al.* 1998; Flannigan and van Wagner 1991; Li *et al.* 2000). Consequently, it may be reasoned that saproxylic insects are not at risk in North America. However, such reasoning is called into question by increasing economic pressure to salvage burned timber from wildfires across most of North America (Lindenmayer 2006; Lindenmayer and Noss 2006; Sessions *et al.* 2004).

Postfire salvage logging is now a common practice in North American forests despite considerable debate about its ecological consequences (Donato *et al.* 2006a; Donato *et al.* 2006b; Stokstad 2006) and general lack of postfire management policy and guidelines (Lindenmayer 2006; Lindenmayer *et al.* 2004; Nappi *et al.* 2004; Purdon *et al.* 2002; Schmiegelow *et al.* 2006). In Alberta, for example, over 20% of the timber harvested in 1999 came from large-scale postfire salvage logging (Schneider 2002). Justification for salvage operations generally involves recouping economic losses prior to serious deterioration of wood quality (Lindenmayer 2006; Lindenmayer and Noss 2006; Morissette *et al.* 2002; Schmiegelow *et al.* 2006), but may also include reducing the risk of future wildfire and enhancing stand regeneration (Sessions *et al.* 2004). While many studies have compared the effects of wildfire and traditional (non-salvage) forest harvesting (Hunter 1999), considerably fewer studies have examined the combined effects of these two disturbances on the same sites (McIver and Starr 2000, 2001). At present, the ecological consequences of compounding disturbances are not yet fully understood, although evidence is mounting to suggest that salvage logging alters bird (Hutto 1995, 2006; Morissette *et al.* 2002; Nappi *et al.* 2004)) and ground beetle assemblages (Cobb *et al.* 2006; Koivula and

Spence 2006; Koivula *et al.* 2006; Phillips *et al.* 2006) and negatively affects postfire plant regeneration (Donato *et al.* 2006b; Fraser *et al.* 2004; Greene *et al.* 2006). However, responses of saproxylic insects to postfire salvage logging have not been investigated, despite their significant contribution to overall forest biodiversity and clear association with dead wood.

In this study, I examined the short-term effects of postfire salvage logging on saproxylic beetle assemblages to determine whether the combined effects of wildfire and forest harvesting are cumulative. Specifically, my objectives were (1) to compare the diversity, species composition and trophic structure of saproxylic beetle assemblages in freshly burned, logged and salvaged boreal mixed-wood forest stands; (2) to determine which species or groups of species may be of particular conservation concern if economic emphasis on salvage logging continues to increase in western North America; and (3) to discuss these findings in the context of various characteristics of coarse woody debris in these habitats, in order to assist in developing ecologically sensitive postfire management guidelines.

3.3 Methods

3.3.1 Study area and design

Field work for this study was conducted approximately 200 km northwest of Edmonton, Alberta, Canada within the mid-boreal upland ecoregion. This ecoregion ranges in elevation from 400 – 800 m (a.s.l.) and is characterized by well-drained and gray luvisolic soils (Strong and Leggat 1981). During the data collection periods (April – September, 2002 and 2003), mean daily temperature was 18.5°C (2002) and

16.8°C (2003) and the mean monthly precipitation was 19.5 mm (2002) and 33.5 mm (2003). Dominant forest types in the study area include pure and mixed stands of white spruce (*Picea glauca* [Moench] Voss), black spruce (*P. mariana* [Mill] B.S.P.), trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*P. balsamifera* L.) and jack pine (*Pinus banksiana* Lamb.), with minor elements of balsam fir (*Abies balsamea* [L.] Mill.), larch (*Larix laricina* [Du Roi] K. Koch) and paper birch (*Betula papyrifera* Marsh.). My work focused on mixed stands of white spruce (c. 60% of canopy composition) and trembling aspen (c. 40%) located in and around the boundaries of a severe, large-scale wildfire (*c.* 120,000 ha) that occurred May 23 – June 4, 2001 near the hamlet of Chisholm, Alberta, Canada (N54°55′, W114°10′). Quintilio *et al.* (2001) provide a detailed synopsis of the severity and extent of this fire as well as associated climate and fuel conditions.

I selected six sites in each of the four following disturbance categories: (1) GRN – "green", reference sites that had not been burned or harvested in >100 yrs; (2) BRN – sites that were "burned" by the wildfire; (3) HAR – unburned, "harvested" sites that were clear-cut logged in 2001; and (4) SAL – sites that were burned by the wildfire and then "salvaged" during the winter of 2001/2002. Sites were individual stands of trees (3-30 ha) separated by a minimum distance of 1 km. Sites were selected initially from forest inventory maps (Alberta Vegetation Inventory, Alberta Sustainable Resource Development, 2000) on the basis of pre-disturbance stand characteristics (age, tree species composition, stem density, soil characteristics) and final site selection was made after ground verification of stand characteristics.

3.3.2 Beetle sampling and identification

Sampling stations for all sites were established at a random distance (0-50 m) and direction from the estimated center of each site. Saproxylic beetles were sampled using flight-intercept traps (Hammond 1997; Kaila 1993) constructed from a thin (0.3 cm) piece of clear plastic (20 cm x 30 cm) connected to a heavy cloth funnel and a plastic sample cup (100 ml) that was charged with *c.* 30 ml of silicate-free ethylene glycol. A total of 120 traps were attached perpendicularly to white spruce trees and stumps. In GRN and BRN sites, 4 traps/site (25 m apart) were attached to standing white spruce trees at approximately 1.5 m above the ground, whereas in HAR and SAL sites, the traps (4/site, 25 m apart) were attached to stumps (0.5 m height) due to the scarcity of available trees. To control for the possible confounding effect of trap height, an additional 2 traps/site were placed at the base of the standing trees in the GRN and BRN sites. All traps were serviced biweekly during the frost-free months (April to September) of 2002 and 2003 to remove all collected beetles and replace the ethylene glycol.

With few exceptions (notably Ptiliidae and Staphylinidae: Aleocharinae), beetle specimens were identified to the species level using available keys, collections and taxonomic expertise (see Acknowledgements). Family and generic nomenclature follows Arnett and Thomas (2001) and Arnett *et al.* (2002) and species nomenclature follows Bousquet (1991). Each beetle taxon was assigned to one of 5 trophic groups (Fg = fungivore, Po = predator or opportunistic feeder of other saproxylic insects, Wb = wood/bark borer, Sd = saprovore/detritivores, or ? = unknown or uncertain of the life stage found in dead wood) based on available life history information for both adults and larvae (Arnett and Thomas 2001; Arnett *et al.* 2002; Hammond 1997; Hammond *et al.* 2001; Stehr 1991). A synoptic collection of all species is housed within collections at the Spence-laboratory (University of Alberta, Edmonton, Alberta, Canada) and at the Northern Forestry Centre (Canadian Forest Service, Edmonton, Alberta, Canada)

3.3.3 Coarse woody debris measurements

To examine variation in saproxylic beetle assemblages associated with dead wood characteristics, I conducted detailed surveys of the coarse woody debris (CWD; pieces of dead wood > 5 cm diameter) at each site. Specifically, I established two 5 m-radius plots, centered on 2 randomly selected flight-intercept traps at each site. For each piece of CWD encountered in a plot, I recorded the diameter, length (or height), type (snag = standing dead tree > 1.5 m height, stump = vertical piece < 1.5 m height, or log = fallen or leaning > 45^o) and species (when possible). In addition, each piece was described according to burn severity and decay stage (Table 3.1). Volume estimates for stumps and logs (or portions) within each plot were calculated as the volume of a cylinder using diameter and length measurements. Snag volume was calculated using base diameter, height (measured with a clinometer), and an estimated top diameter assuming a taper function of 1.2 cm diameter per m of height (Spies and Franklin 1991).

3.3.4 Data analyses

Beetle species richness was estimated for each stand treatment by rarefaction using non-standardized catches of each species and the software package EstmateS 7.5 (Colwell 2005). Rarefaction accounts for variable sampling effort (*i.e.,* number of individuals or samples) by estimating species richness based on random subsamples of individuals drawn from the original dataset (Gotelli and Colwell 2001). Curves generated by this procedure were examined for differences in species richness at given subsamples of beetles. For all other analyses, total catches for each species were standardized by sampling effort (individuals/trap*day) to account for occasional sample losses (*c.* 3%) due to trap disturbance by animals and to limit the potential influence of seasonal and yearly variability associated with species-specific life-history parameters.

Saproxylic beetle species assemblages were compared across stand treatments using nonmetric multidimensional scaling (NMS), multi-response permutation procedures (MRPP) and indicator species analysis. These analyses were performed using PC-Ord for Windows (version 4.14; McCune and Mefford 1999). NMS is a non-parametric, unconstrained ordination technique that is effective for revealing gradients in ecological data with complex species responses (McCune and Grace 2002) and has the advantage of avoiding the assumption of linear relationships among variables (Clarke 1993; McCune and Grace 2002). For NMS ordination, I used Sørensen (Bray-Curtis) dissimilarity as the distance measure and stand-level data consisting of standardized total catch rates for all species. MRPP was used to evaluate similarity in species composition among stand treatments in the ordination (Mielke *et* *al.* 1976; Zimmerman *et al.* 1985). MRPP provides a measure of the within-group agreement (or stand treatment in our analysis) as well as the degree of separation between groups (McCune and Grace 2002). The species assemblage associated with each stand treatment was further described using indicator species analysis (Dufrêne and Legendre 1997). This analysis generates an indicator value for each species based on its catch rate and relative frequency in a particular set of sites and ranges from 0 (no indication) to 100 (perfect indication). Indicator values for each species were evaluated against a Monte Carlo test statistic (1000 permutations).

One-factor analysis of variance (ANOVA; SPSS for Windows 11.5, LEAD Technologies, Inc. 2002) was used to examine the effect of stand treatment on mean catch rates of all saproxylic beetles as well as catch rates of the three main trophic groups (fungivores, predators, and wood/bark borers). Data were $\log_{10}(x+1)$ transformed prior to analysis when necessary to meet the ANOVA assumptions of normality and homoscedasticity (Zar 1996). Where ANOVA's were significant, differences between stand treatments were compared using Tukey's HSD *post hoc* tests (Zar 1996).

Finally, relationships between measured CWD characteristics and saproxylic beetle trophic structure were evaluated using multivariate regression tree (MRT) analysis (De'ath 2002) performed with R 2.0.1 (vegan and mvpart packages; R Development Core Team 2004). MRT is a multivariate version of classification and regression tree analysis (De'ath and Fabricius 2000) effective for modelling the relationship between multiple species data and environmental characteristics. This technique has been particularly effective for beetle studies (Jacobs *et al.* 2006; Koivula

2005; Koivula and Vermeulen 2005; Pihlaja *et al.* 2006; Work *et al.* 2004). MRT progressively divides the species data to form clusters of sites that are related by multiple regression to a set of measured environmental variables (CWD parameters in our study). Each binary division is chosen to minimize the dissimilarity between sites within clusters, and each cluster represents a particular assemblage of species. For this analysis, I again used Sørensen (Bray-Curtis) dissimilarity as the distance measure and the final tree was selected by cross validation using the 1-SE rule (Breiman *et al.* 1984) that selects the smallest tree within one standard error of the most predictive tree (*i.e.,* the smallest predicted mean square error).

3.4 Results

3.4.1 Total catch

A total of 15,751 beetles were collected in this study. Of these, 10,454 were determined to be saproxylic and consisted of 245 taxa, mostly identified to the species level (Appendix 3-A). This total includes all individuals within the subfamily Aleocharinae (Staphylinidae) as well as 13 other taxa that could not be reliably identified to the species level given available literature and local expertise. Fungivores (78 spp.) were numerically dominant in this collection with 4777 individuals, followed by wood- and bark-borers (60 spp.) and predators (96 spp.) with 2485 and 2427 individuals, respectively. Saprovores / detritivores (3 spp., 40 individuals) and those species whose trophic status could not be determined (8 taxa, 725 individuals) were excluded from the analyses. HAR sites yielded the largest catch of saproxylic beetles

(31.9% of total catch) followed by BRN sites (31.7%), SAL sites (25.9%) and GRN sites (10.5%).

3.4.2 Species richness and composition

Saproxylic beetle species richness, as estimated by rarefaction, was lower in SAL than in all other treatments (Figure 3.1). Based on a subsample of 850 individuals (the maximum number common to all treatments), HAR treatment had the highest average species richness (102.4 spp.) followed by the BRN treatment (96.2 spp.), the GRN treatment (93.0 spp.) and the SAL treatment (80.8 spp.).

NMS ordination analysis showed strong differences in saproxylic beetle species composition between stand treatments (Figure 3.2; MRPP; $T = -13.28$, $A = 0.24$, $p < 0.001$). The final NMS solution (stress = 13.11, 2-dimensional) explained 83.2% of the total species variance (axis 1 = 51.1%, axis 2 = 32.1%) and was achieved after 109 iterations. Comparison of the reference stand treatment (GRN) with the disturbed stand treatments (HAR, BRN and SAL) showed that there was a greater degree of separation in species composition between GRN and SAL sites (MRPP; $T = -7.05$, $A = 0.22$, $p < 0.001$) than between GRN and BRN sites (MRPP; $T = -6.82$, $A = 0.17$, $p < 0.001$) or between GRN and HAR sites (MRPP; $T = - 6.15$, $A = 0.12$, $p < 0.001$).

Indicator species analysis revealed a total of 44 species as significant indicators of stand treatment including 17 Fungivores (Fg), 12 Wood/bark borers (Wb) and 15 Predators (Po) (Table 3.2). The strongest indicator species were *Polygraphus rufipennis* (Kirby) for GRN sites, *Trypodendron lineatum* (Olivier) for HAR sites, *Monochamus scutellatus* (Say) for BRN sites and *Sphaeriestes virescens* (LeConte) for SAL sites, all with indicator values in excess of 65%. A closer examination of the list of significant indicator species revealed distinct differences in the distribution of trophic groups associated with each stand treatment (Table 3.2). BRN and HAR sites contained a mix of all three functional groups (BRN = 3 Wb, 2 Po, 1 Fg; HAR = 6 Wb, 3 Po, 11 Fg), while no fungivores were found to be significant indicators of GRN sites (GRN = 3 Wb, 3 Po, 0 Fg) and no wood/bark borers were significant indicators of SAL sites (SAL = 0 Wb, 7 Po, 5 Fg).

Mean catch rate of saproxylic beetles (all trophic groups combined) varied significantly across stand treatments (ANOVA; $F_{3,20} = 4.99, p = 0.011$), with HAR sites having a greater mean catch rate than all other stand treatments (Tukey's HSD; $p < 0.010$) (Figure 3.3). The effect of stand treatment was also significant for each of the three trophic groups (ANOVA; Fg, $F_{3,20} = 9.18, p = 0.001$; Po, $F_{3,20} = 6.47, p = 0.003$; Wb, $F_{3,20} = 6.44, p = 0.003$), although response patterns differed among groups (Figure 3.3). Mean catch rate of fungivores was highest in HAR sites followed by SAL sites and then BRN and GRN sites. For predators, the mean catch rate was highest in SAL sites and lowest in GRN sites, whereas for wood/bark borers, the mean catch rate was highest in HAR sites and lowest in SAL sites.

3.4.3 Coarse woody debris and saproxylic trophic structure

Differences in trophic structure of the saproxylic beetle assemblage were closely related to differences in several measured characteristics of the CWD in each stand treatment (Figure 3.4). Cross-validated MRT analysis of 234 saproxylic beetle taxa (all Fg, Po and Wb) and 7 measured CWD characteristics (Table 3.3) consistently produced a tree with 6 terminal nodes (groups A-F). This tree explained 85% of the total variance in the saproxylic beetle dataset. The relatively low cross-validated error value (CV error = 0.40), indicated that this model had some predictive power as well (0: perfect predictor; *c.* 1: poor predictor; De'ath 2002). The first division explained 41% of the total variance and was based on whether or not the CWD was burned. Not surprisingly, this characteristic separated BRN and SAL sites from GRN and HAR sites. BRN and SAL sites were further separated by total volume of CWD, which explained an additional 26% of the total variance. An additional 12% of the variance was explained by the volume of CWD in the earliest decay stage (Decay Stage 1) which separated GRN from HAR sites. The volume of CWD in Decay stage 3 further explained a small amount of variation (3%) among sites of the GRN stand treatment, while the volume of CWD in decay stage 6 explained an additional 3% of the variation among sites of the HAR stand treatment.

Saproxylic beetle trophic structure, illustrated by the proportion of the total catch represented by fungivores, predators and wood/bark borers, varied strongly across the 6 groups in the MRT (Figure 3.4; groups A-F). SAL sites (group A) were dominated by predators and fungivores, but contained very few wood/bark borers, whereas BRN sites (group B) were comprised of a relatively equal distribution of all three trophic groups. In contrast, GRN sites (groups C and D) were dominated by wood/bark borers and HAR sites (groups E and F) were dominated by fungivores.

3.5 Discussion

3.5.1 Saproxylic beetle diversity and species composition

Saproxylic beetle species richness was lower in salvage logged sites than in all other sites, and their species composition differered from undisturbed sites to a greater extent than those that had experienced either fire or harvesting alone. These findings suggest that wildfire and harvesting have synergistic effects when combined on the same sites. The ecological consequences of losing saproxylic species or altering their assemblages are difficult to predict because the precise functional roles of the majority of species have not yet been sufficiently studied (Grove 2002a). Although there have been few direct studies (*c.f.*, Edmonds and Eglitis 1989), most species are believed to be involved in dead wood decomposition (Edmonds and Eglitis 1989; Speight *et al.* 1999), suggesting that altering the diversity and composition of this assemblage may impact nutrient cycling in forests recovering from wildfire. Moreover, food-web dynamics may also be impacted as saproxylic beetles are an important part of the prey base for the Black-backed woodpecker (*Picodes arcticus* Swainson) and the American three-toed woodpecker (*Picoides dorsalis* Baird), which are associated with burned forests (Hoyt and Hannon 2002; Hutto 1995, 2006; Nappi *et al.* 2004). Protection of habitats for rare and threatened saproxylic beetles in northern Europe has been recommended for the conservation of the White-backed woodpecker (*Dendrocopos leucotos* [Bechstein]), which is critically endangered in Finland and Sweden (Martikainen *et al.* 1998).

Many species of plants (Rowe 1983), birds (Drapeau *et al.* 2000; Hoyt and Hannon 2002; Hutto 1995, 2006; Martikainen *et al.* 1998; Morissette *et al.* 2002;

Nappi *et al.* 2004) and insects (Evans 1966, 1971; Koivula *et al.* 2006; Muona and Rutanen 1994; Saint-Germain *et al.* 2004; Saint-Germain *et al.* 2005; Schmitz *et al.* 1997; Wikars 1995; Wikars 2002) are closely associated with early postfire successional forests. For insects, dependence on fire and early postfire forests may be due to increased nutritional quality of woody substrates, reduced predation or reduced competition (Wikars 1997). Consequently, it may be reasoned that such pyrophilous ("fire-loving"), saproxylic species may be highly sensitive to postfire salvage logging. In my study, three well-known pyrophilous species, namely *Melanophila acuminata* (DeGeer) (Buprestidae), *Monochamus scutellatus* (Say) (Cerambycidae) and *Sericoda bembidioides* Kirby (Carabidae) were significant indicators of the BRN stand treatment. *Melanophila acuminata* is best known for its attraction to infrared radiation (Evans 1971, 2005; Schmitz and Bleckmann 1998; Schmitz *et al.* 1997; Schmitz and Trenner 2003) and *M. scutellatus* is believed to be attracted by volatile chemicals in conifer oleoresin and smoke (Allison *et al.* 2001; Chénier and Philogène 1989a, 1989b; Gardiner 1957a, 1957b). Considerably less is known about *S. bembidioides*, except that it is common for a short time (1-2 years) in burned coniferous forests of western North America (Koivula *et al.* 2006; Lindroth 1961-1969) especially where fire severity is high (Koivula *et al.* 2006). While all three of these species were relatively common in BRN sites in our study, very few were collected in SAL sites (Appendix 3-A) suggesting that pyrophilous, saproxylic species may be particularly sensitive to postfire salvage logging. However, this may only be true for some species as we also found that another pyrophilous species, *Sericoda quadripunctata* (DeGeer) was a significant indicator of the SAL stand treatment. Interestingly, *S.*

quadripunctata may benefit from the production of logging debris associated with salvage operations as oviposition and larval development of this species have been observed in crevices of small pieces of burned dead wood (Burakowski 1986).

3.5.2 Saproxylic beetle trophic structure

A closer examination of the responses of three saproxylic beetle trophic groups to postfire salvage logging suggested that this practice may not only impact the diversity and species composition of this assemblage, but may also affect its trophic structure. Hammond *et al.* (2004), in their study of *Populus* forests in Canada, also noted a link between saproxylic beetle trophic structure and successional stage (stand age). In my study, abundance of predators, fungivores and wood/bark borers differed between burned, harvested and postfire salvage logged treatments.

Predators were generally favoured by salvage logging as demonstrated by their greater mean catch rate in SAL sites and by the fact that the majority of the significant indicators of the SAL treatment belonged to this trophic group. It is possible that increased prey resources in SAL sites may account for this result; however, for most species, there is insufficient life history information to either support or refute this hypothesis. For example, the strongest indicator of the SAL stand treatment was *Sphaeriestes virescens* (LeConte) (Salpingidae). While both adults and larvae of this species are thought to be predators of other saproxylic insects (Arnett *et al.* 2002; Hammond 1997; Young 1991), the biology of this species has not yet been sufficiently studied to adequately explain its occurrence in SAL sites (Arnett *et al.* 2002; Young 1991). Additional insight may be gained from the fact that SAL sites in my study had a substantial volume of *Populus* woody debris (33.7 m^3ha^{-1}), mostly in the form of logs, and that Hammond (1997) successfully reared *S. virescens* from *Populus* logs.

Responses of fungivores to postfire salvage logging were variable, although mean catch rates were significantly lower in SAL sites than in HAR sites. An examination of the list of significant indicator species from this trophic group showed that 5 species were favoured by salvage logging, whereas 12 were negatively affected. *Henoticus serratus* (Gyllenhal) (Cryptophagidae) was one of the species apparently favoured by salvage logging and previous work has shown that this species is highly associated with burned substrates especially in the presence of the ascomycete fungus, *Trichoderma* sp. (Wikars 1997, 2002). Several species within this fungal genus have previously been isolated from burned white spruce logs (Lumley *et al.* 2001), suggesting that the abundance of this substrate in SAL sites (Table 3.3) is linked to the abundance of *H. serratus*. In comparison, fungivorous beetle species that were negatively affected by salvage logging included *Clambus pubescens* Redtenbacher (Clambidae) and *Melanopthalma villosa* (Zimmerman) (Latridiidae), which were previously found to be associated with mature forests (Hammond *et al.* 2004). In my study, *C. pubescens* was highly associated with HAR sites and *M. villosa* was associated with BRN sites (Table 3.2), suggesting that the habitat requirements of these species may be more liberal than originally thought. However, these contrasting results further underscore the suggestion by Hammond *et al.* (2004) that more detailed studies on the biology of these species in North America are required to fully elucidate their habitat requirements.

Wood- and bark-boring species in my study were those most negatively affected by salvage logging. In fact, 87% of all wood/bark boring species found in BRN sites showed reduced catches in SAL sites (Appendix 3-A). Notable examples include two pyrophilous species already mentioned, *M. scutellatus* and *M. acuminata*, but similar responses were seen for the cerambycids *Acmaeops proteus* (Kirby), *Pachyta lamed liturata* Kirby, *Rhagium inquisitor* (L.), *Spondylis upiformes* (Mann.), *Stictoleptura canadensis* (Oliver) and the recently-described *Tetropium nanum* Laplante. The generally negative impact of postfire salvage logging on this trophic group is most likely related to the removal of snags from SAL sites as many species are known to oviposit and develop in snags, especially following fire (Evans 1962; Hanks 1999; Hanks *et al.* 1998; Linsley 1959; Rose 1957; Saint-Germain *et al.* 2004; Yanega 1996). Moreover, the abundance of wood- and bark-boring species has been shown to be greater in snags than in logs (Hammond *et al.* 2004). Thus, by relying on snags, wood- and bark-boring species may be particularly sensitive to postfire salvage logging.

3.5.3 Coarse woody debris and saproxylic beetles

Many studies have demonstrated a clear link between the quality and quantity of dead wood and saproxylic beetle assemblages (*e.g.,* Grove 2002a, 2002b; Hammond 1997; Hammond *et al.* 2001, 2004; Martikainen 2001; Siitonen 2001; Similä *et al.* 2002). In addition to total volume of dead wood, this work has shown that the type (*i.e.,* snag, stump or log), species, size, and connectivity (in time and space) of woody debris are important factors for saproxylic beetles. In my study, changes in trophic structure of the saproxylic beetle assemblage were related mostly to the effects of fire itself, but also to two main CWD parameters, namely total volume and decay stage.

The volume of woody debris in the earliest stage of decay (Decay Stage 1) was an important parameter for distinguishing saproxylic assemblages associated with GRN and HAR stand treatments. More specifically, I found that clear-cut harvesting increased the amount of woody debris in Decay Stage 1 (mostly as logs and stumps), which was associated with a shift in the trophic structure from one dominated by wood/bark borers (GRN sites) to one that was dominated by fungivores (HAR sites). Additional variation between sites within the GRN and HAR stand treatments was attributed to the volume of woody debris in more advanced stages of decay (Decay Stages 3 and 6). Thus, in unburned sites, the variety of decay stages present appears to be important in defining saproxylic beetle assemblages.

In contrast, I found that variation among assemblages associated with BRN and SAL sites was closely linked to total volume of coarse woody debris, regardless of decay. In fact, 26% of the total variation between saproxylic beetles associated with SAL and BRN sites was attributed to this parameter. By removing a large proportion of the snags (Table 3.3), postfire salvage logging in my sites resulted in the total volume of woody debris being $< 179.3\ m^3\ ha^{-1}$ (compared to $329.6\ m^3\ ha^{-1}$ for BRN; Table 3.3). This change in total volume of CWD was associated with a reduced contribution of wood/bark borers to the overall trophic structure, suggesting a potential "threshold" that may be important for conserving wood- and bark-boring species in early postfire forests.

While such "thresholds" for woody debris characteristics are required for development of postfire management guidelines aimed at conserving saproxylic beetle assemblages, this finding should be interpreted with caution for two key reasons. First, this analysis only explained a portion of the overall variance in the saproxylic beetle assemblage. For example, total CWD volume explained 26% of the variance between BRN and SAL sites, suggesting that an additional 74% was attributed to factors beyond the scope of our analysis. A second caveat is that my study was limited both spatially and temporally for the purpose of simultaneously comparing the short-term response of saproxylic beetles to a range of different stand treatments in a single forest type (*i.e.,* boreal spruce-aspen mixed-wood). Thus, my study provides insight into the response of a particular saproxylic beetle assemblage, not this assemblage as a whole. More work needs to be done to determine whether or not the coarse woody debris parameter "thresholds" that I found are important in other forest types, other geographical areas, and across longer time scales.

3.5.4 Conclusions

In a recent review, Lindenmayer and Noss (2006) suggested that a key obstacle to understanding the impacts of salvage logging was to determine whether the effects of this practice were different from, and potentially more detrimental than, other forms of logging that are not preceded by a major disturbance. Collectively, my results show that the effects of wildfire and forest harvesting on the same sites may be synergistic for saproxylic beetles. I found that different trophic groups of saproxylic beetles responded very differently to postfire salvage logging than to wildfire or traditional (non-salvage) logging. Moreover, by altering the quantity and quality of dead wood in burned forests, postfire salvage logging may negatively impact saproxylic beetle diversity as well as alter species composition and trophic structure of this assemblage in early postfire successional forests.

The published literature is replete with studies about the ecological consequences of individual disturbances in forest ecosystems (Hunter 1999; Stelfox 1995). However, modern forest ecosystems face a multitude of both natural and anthropogenic environmental stressors that are often acting simultaneously on the same sites (Bedford and Preston 1988; Kennedy 2002; Schneider 2002). In addition to natural disturbances like wildfire and insect outbreaks, anthropogenic stressors associated with increased resource extraction (*e.g.,* timber, oil and gas, mineral deposits), pollution and global climate change have become increasingly important parts of the disturbance regime in virtually all forests (Perry 1994). Thus, research about the ecological consequences of multiple disturbances is urgently needed.

In many parts of North America, large portions of forest flora and fauna have evolved under a historical regime of regular disturbance by wildfire (Bergeron *et al.* 2001; Hunter 1993; Johnson *et al.* 1998), and saproxylic insects comprise a large proportion of this fauna (Grove 2002a; Speight 1989). The loss of rare and threatened saproxylic species from European forests may offer a glimpse of the future should forest management in North America continue along its present path (Martikainen 2001; Martikainen *et al.* 1998; Siitonen and Martikainen 1994). While my study builds on earlier findings of the North American saproxylic beetle fauna (Hammond 1997; Hammond *et al.* 2001, 2004; Jacobs *et al.* 2006), it is clear that much more work needs to be done to better understand the basic biology of this sensitive and important part of forest biodiversity. Until the consequences of multiple disturbances, such as postfire salvage logging, are sufficiently understood, postfire management policy should be tempered by caution rather than be driven by economics alone (Lindenmayer and Noss 2006; Nappi *et al.* 2004; Schmiegelow *et al.* 2006).

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Table 3.1: Classification system used to describe the type, decay stage, and burn severity of woody debris encountered at each site (adapted from Lee *et al.* 1995; Pedlar *et al.*2002).

Category	Description
Type	
Stump	Standing < 1.5 m
Log	Fallen or leaning > 45°
Snag	Standing > 1.5 m
Decay stage	
1	Wood hard; bark, branches, and twigs present and intact; upright or elevated on support points
2	Wood hard; twigs mostly lacking; < 50% of bark missing
3	Some branches remaining; > 50% bark missing; wood soft in places
4	Little to no bark remaining; no branches; wood fungi present; wood soft, small crevices, small pieces lost
5	Large wood fragments lost; outline of trunk deformed; vascular plants beginning to colonize
6	Wood mostly broken down; log completely moss covered and colonized by various vascular plants
7	Humification nearly 100%; hard to define as log, outline indeterminable; no evidence of hard wood
Burn severity	
0	Unburned
1	< 50% of total length scorched; some bark remaining; cambium intact and moist
2	> 50% of total length scorched; some bark remaining; cambium variable
3	> 50% of total length scorched; little to no bark; cambium dry
4	> 70% of total length scorched; heartwood burned

Table 3.2: Significant indicator species for each stand treatment (GRN = green/control; HAR = harvested; BRN = burned; SAL = salvaged). Indicator values are presented as percent of perfect indication and significance ($p < 0.05$) was determined using Monte Carlo randomization (1000 permutations). Trophic role abbreviations are Fg = fungivore, Po = opportunistic predator of live or dead saproxylic insects, and Wb = wood/bark borer.

				Indicator	Indicator value	
		Trophic	Stand	value	from randomization	
Family	Species	Role	Treatment	(obs.)	Mean (± SE)	*P*
Curculionidae	*Polygraphus rufipennis* (Kirby)	Wb	GRN	74.5	46.3 (0.40)	0.019
Curculionidae	*Xylechinus montanus* Blackman	Wb	GRN	66.7	18.6 (0.30)	0.006
Anobiidae	*Microbregma emarginatum* (Duftschmid)	Wb	GRN	63.2	28.4 (0.38)	0.013
Carabidae	*Platynus decentis* (Say)	Po	GRN	60.2	28.6 (0.24)	0.001
Elateridae	*Ctenicera propola* (LeConte)	Po	GRN	55.7	19.3 (0.30)	0.004
Cantharidae	*Dichelotarsus piniphilus* (Eschscholtz)	Po	GRN	49.7	25.0 (0.27)	0.011
Curculionidae	*Trypodendron lineatum* (Olivier)	Wb	HAR	83.9	38.1 (0.35)	0.001
Clambidae	*Clambus pubescens* Redtenbacher	Fg	HAR	81.9	41.0 (0.30)	0.001
Cerambycidae	*Judolia instabilis* (Haldeman)	Wb	HAR	81.3	23.6 (0.30)	0.001
Staphylinidae	*Quedius rusticus* Smetana	Po	HAR	79.5	30.6 (0.29)	0.001
Nitidulidae	*Epuraea linearis* Mäklin	Fg	HAR	69.8	40.5 (0.28)	0.002
Latridiidae	*Latridius minutus* (Linné)	Fg	HAR	69.5	33.1 (0.29)	0.001
Staphylinidae	*Megarthrus angulicollis* Mäklin	Fg	HAR	67.5	29.5 (0.33)	0.002
Ptiliidae	*Acrotrichis* spp.	Fg	HAR	59.8	39.8 (0.29)	0.049
Cerambycidae	*Rhagium inquisitor* (Linné)	Wb	HAR	56.5	24.2 (0.28)	0.004
Corylophidae	*Clypastraea obesa* (Casey)	Fg	HAR	55.3	36.6 (0.18)	0.001
Leiodidae	*Anisotoma globososa* Hatch	Fg	HAR	52.7	28.7 (0.27)	0.017
Latridiidae	*Cartodere constricta* (Gyllenhal)	Fg	HAR	52.5	36.2 (0.17)	0.002
Elateridae	*Ampedus apicatus* (Say)	Po	HAR	50.7	23.5 (0.32)	0.012
Buprestidae	*Dicerca tenebrosa* (Kirby)	Wb	HAR	47.9	24.7 (0.27)	0.005
Curculionidae	*Orthotomicus caelatus* (Eichhoff)	Wb	HAR	45.8	29.6 (0.24)	0.035
Latridiidae	*Corticaria serrata* (Paykull)	Fg	HAR	45.5	33.9 (0.13)	0.007
Cerambycidae	*Stictoleptura canadensis* (Olivier)	Wb	HAR	44.4	21.8 (0.29)	0.013
Colydiidae	*Lasconotus complex* LeConte	Fg	HAR	44.1	18.5 (0.32)	0.039
Staphylinidae	*Phloeostiba lapponicus* (Zetterstedt)	Po	HAR	41.9	30.7 (0.18)	0.041
Cryptophagidae	*Atomaria ephippiata* Zimmermann	Fg	HAR	41.5	32.5 (0.14)	0.032
Cerambycidae	*Monochamus scutellatus* (Say)	Wb	BRN	68.0	27.8 (0.28)	0.001
Buprestidae	*Melanophila accuminata* (DeGeer)	Wb	BRN	63.2	21.7 (0.28)	0.003
Elateridae	*Ctenicera triundulata* (Randall)	Po	BRN	59.9	34.8 (0.26)	0.007
Carabidae	*Sericoda bembidioides* Kirby	Po	BRN	49.5	19.3 (0.31)	0.028
Curculionidae	*Cossonus pacificus* Van Dyke	Wb	BRN	43.8	20.1 (0.3)	0.041
Latridiidae	*Melanophthalma villosa* (Zimmermann)	Fg	BRN	38.6	31.4 (0.10)	0.021
Salpingidae	*Sphaeriestes virescens* (LeConte)	Po	SAL	83.2	33.5 (0.30)	0.001
Carabidae	*Bembidion grapii* Gyllenhal	Po	SAL	80.0	23.4 (0.29)	0.001
Carabidae	*Sericoda quadripunctata* (DeGeer)	Po	SAL	72.2	28.3 (0.27)	0.001
Cryptophagidae	*Caenoscelis antonnalis* (Casey)	Fg	SAL	69.8	38.5 (0.24)	0.001
Leiodidae	*Anisotoma* sp.	Fg	SAL	66.7	20.1 (0.35)	0.007
Carabidae	*Pterostichus adstrictus* Eschscholtz	Po	SAL	61.5	30.4 (0.25)	0.004
Leiodidae	*Hydnobius substriatus* LeConte	Fg	SAL	58.3	20.1 (0.30)	0.008
Carabidae	*Amara obesa* (Say)	Po	SAL	56.7	19.5 (0.30)	0.010
Carabidae	*Harpalus laevipes* Zetterstedt	Po	SAL	56.7	19.5 (0.30)	0.010
Staphylinidae	*Micropeplus tesserula* Curtis	Fg	SAL	55.3	28.5 (0.25)	0.004
Cryptophagidae	*Henoticus serratus* (Gyllenhal)	Fg	SAL	49.6	31.6 (0.14)	0.001
Staphylinidae	*Tachyporus maculicollis* LeConte	Po	SAL	42.5	30.2 (0.16)	0.010

Table 3.3: Summary of coarse woody debris characteristics for each stand treatment (GRN = green/control; HAR = harvested; BRN = burned; SAL = salvaged). Values are means (±SE) for six sites. Descriptions of decay stages and burn severity classes are provided in Table 3.1.

Characteristics	GRN	HAR	BRN	SAL
Volume (m^{3}ha^{-1})	94.98 (± 21.58)	90.76 (± 14.98)	329.56 (± 47.57)	90.75 (± 18.59)
Piece volume (m^3)	0.11 (± 0.02)	0.04 (± 0.01)	0.24 (± 0.03)	0.06 (± 0.01)
Piece density (No.ha^{-1})	896.58 (± 209.60)	2302.45 (± 482.93)	1411.18 (± 159.08)	1602.16 (± 212.52)
Type (m^{3}ha^{-1})				
Log	66.00 (± 14.88)	77.13 (± 14.01)	62.95 (± 21.20)	66.28 (± 19.72)
Snag	25.56 (± 11.47)	0.96 (± 0.96)	263.87 (± 34.33)	8.09 (± 7.25)
Stump	3.43 (± 1.93)	12.67 (± 3.40)	2.75 (± 1.59)	16.38 (± 6.58)
Decay stage (m^{3}ha^{-1})				
1	2.39 (± 1.02)	30.52 (± 9.43)	147.47 (± 70.42)	57.63 (± 16.33)
2	13.71 (± 8.36)	9.84 (± 3.72)	70.55 (± 29.82)	17.79 (± 5.61)
3	7.79 (± 3.48)	6.1 (± 2.75)	40.68 (± 24.52)	0.71 (± 0.39)
4	4.9 (± 2.40)	8.33 (± 3.31)	37.17 (± 28.15)	4.38 (± 3.34)
5	11.43 (± 3.86)	7.35 (± 2.36)	23.51 (± 16.17)	2.47 (± 1.76)
6	22.54 (± 7.79)	15.35 (± 2.19)	8.97 (± 3.98)	2.52 (± 1.75)
7	32.22 (± 9.80)	13.27 (± 6.71)	1.22 (± 0.64)	5.26 (± 4.31)
Burn severity (m^{3}ha^{-1})				
0	94.98 (± 21.58)	90.76 (± 14.98)	0.04 (± 0.04)	-
1	-	-	5.84 (± 5.84)	5.84 (± 5.84)
2	-	-	20.63 (± 20.23)	-
3	-	-	50.99 (± 40.46)	21.54 (± 4.83)
4	-	-	252.07 (± 64.37)	63.37 (± 15.26)
Species (m^{3}ha^{-1})				
Picea glauca (Moench) Voss	17.8 (± 4.77)	35.91 (± 10.14)	224.70 (± 40.19)	45.37 (± 14.11)
Picea mariana (Mill.) B.S.P.	8.89 (± 8.89)	-	4.20 (± 4.20)	0.06 (± 0.06)
Populus sp.*	24.61 (± 8.62)	19.69 (± 8.47)	91.00 (± 31.13)	33.69 (± 13.36)
Betula papyrifera Marsh.	7.27 (± 3.83)	5.10 (± 3.18)	0.20 (± 0.20)	0.08 (± 0.08)
Abies balsamea (L.) Mill.	3.06 (± 3.06)	6.05 (± 3.55)	-	0.07 (± 0.07)
Unknown	33.35 (± 11.99)	24.00 (± 9.89)	9.46 (± 2.71)	11.47 (± 7.35)

* includes both *Populus tremuloides* Michx. and *P. balsamifera* L.

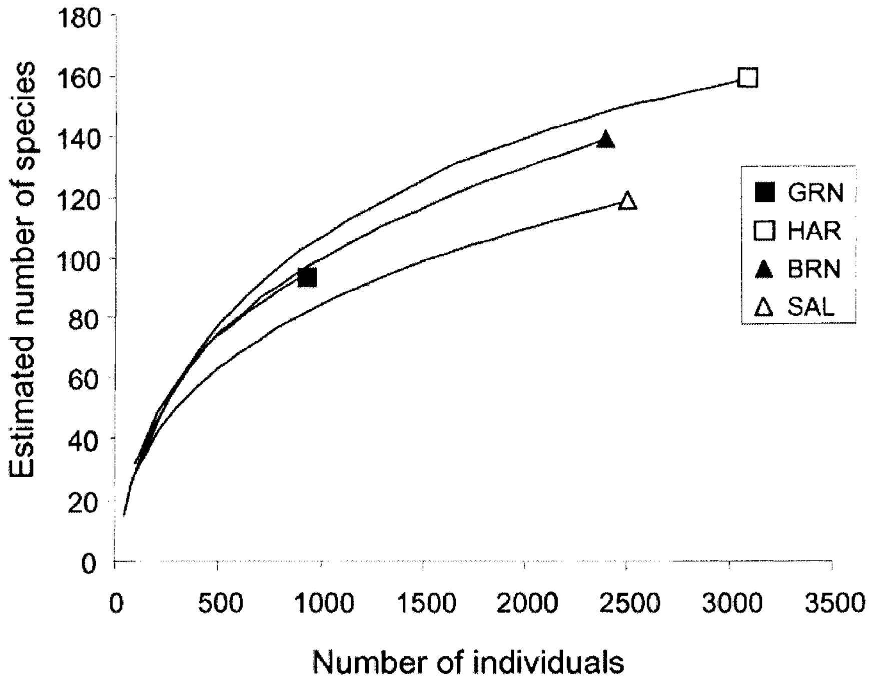

Figure 3.1: Rarefaction estimates of saproxylic beetle species richness for each stand treatment (GRN = green/control; HAR = harvested; BRN = burned; SAL = salvaged).

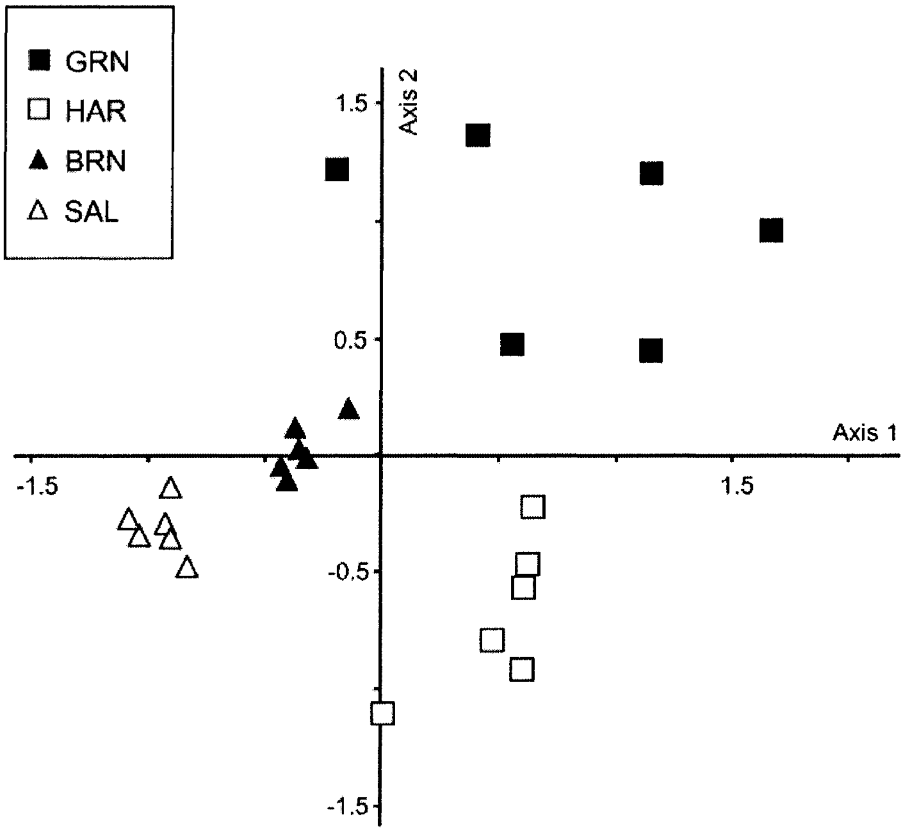

Figure 3.2: Nonmetric multidimensional scaling (NMS) ordination of saproxylic beetle catch rates (234 taxa) from 24 sites. Data are coded to show the effect of stand treatment (GRN = green/control; HAR = harvested; BRN = burned; SAL = salvaged) on saproxylic beetle assemblages from six sites within each treatment.

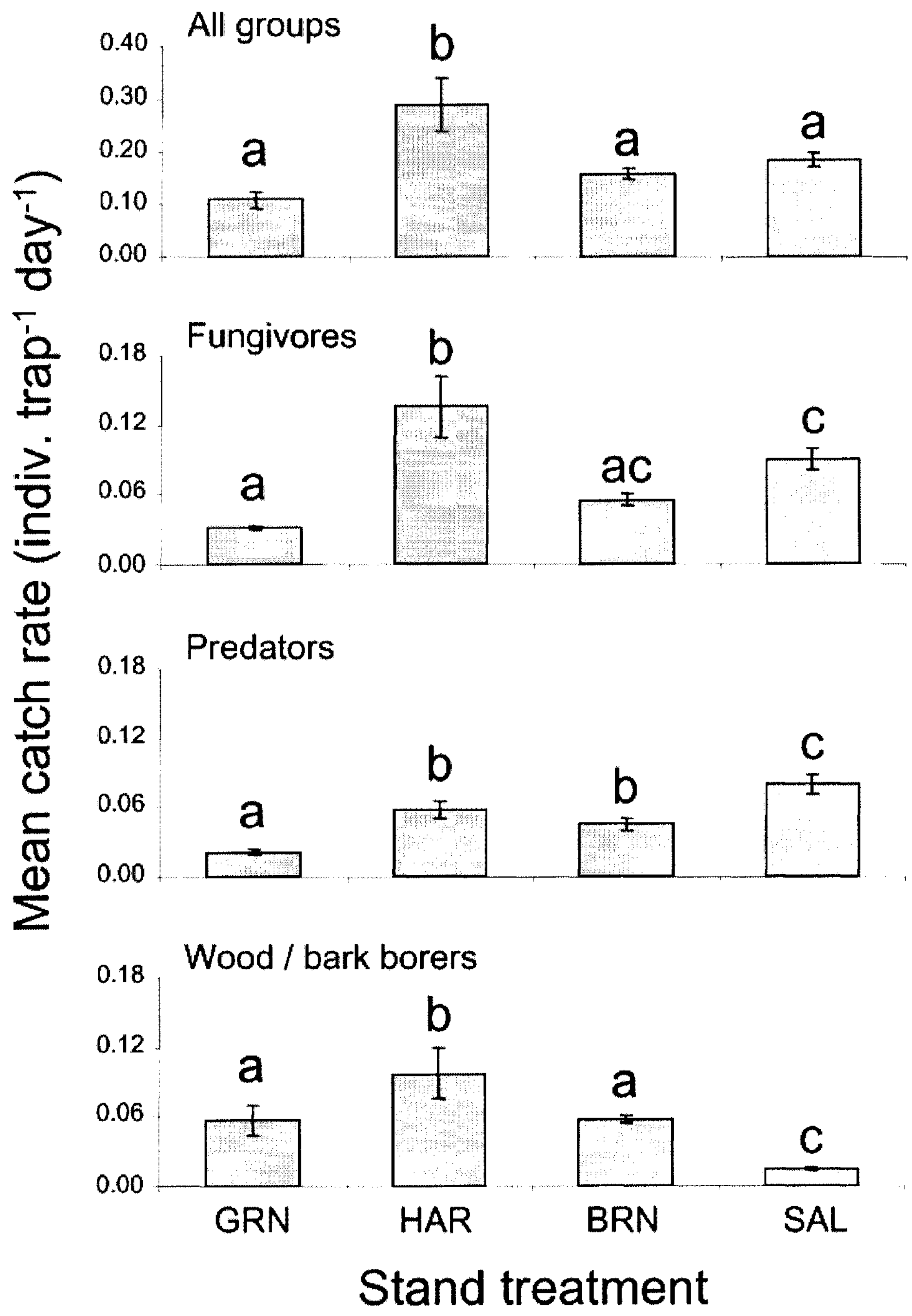

Figure 3.3: Comparison of mean catch rates among stand treatments (GRN = green/control; HAR = harvested; BRN = burned; SAL = salvaged) for all saproxylic beetle species (top) as well as three different trophic groups (Fungivores, Predators, Wood / bark borers). Different lower case letters indicate significant differences between treatments for each species group (Tukey's HSD; $p < 0.05$). Error bars show ± 1 SE for six sites in each stand treatment.

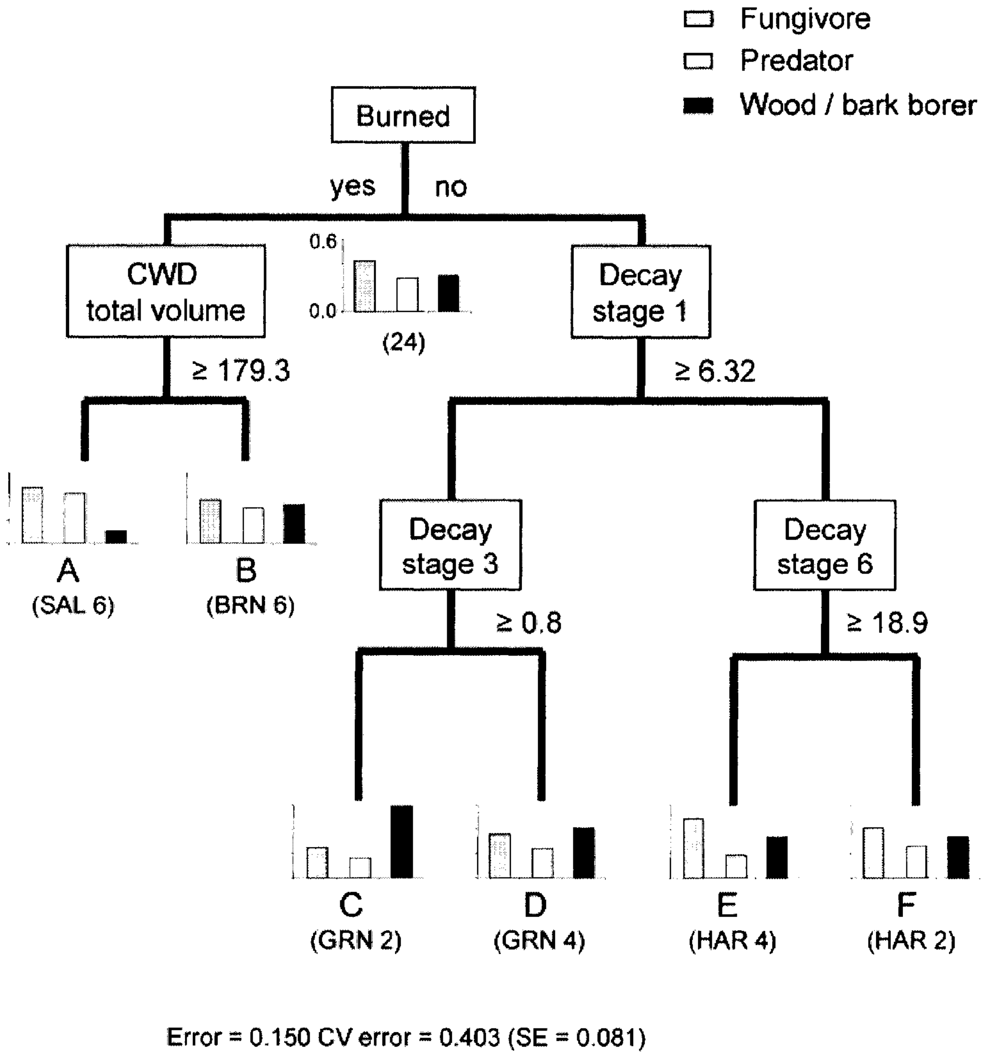

Figure 3.4: Multivariate regression tree showing the effect of coarse woody debris (CWD) characteristics on standardized catches of saproxylic beetles (234 taxa) belonging to three different trophic groups. Sørensen (Bray-Curtis) distance was used for splitting and cutoff values are presented as m^3ha^{-1}. Stand treatments (GRN = green/control; HAR = harvested; BRN = burned; SAL = salvaged) and total number of sites defined by each split are shown in parentheses. Barplots show relative roportion of the total catch of a particular set of sites (A-F) represented by each trophic group.

Appendix 3-A: Distribution of saproxylic beetles (total catch) across all stand treatments (GRN = green, HAR = harvested, BRN = burned, SAL = salvaged). Trophic roles (Wb = wood/bark borer, Po = predator or opportunistic feeder of living or dead saproxylic insects, Fg = fungivore, Sd = saprovore or detritivore, ? = unknown or uncertain of the stage(s) found in dead wood) based on information from various sources (Stehr 1991; Hammond 1997; Arnett & Thomas 2001; Arnett *et al.* 2002; Jacobs *et al.* 2006).

		Trophic	Stand treatment				
Family	Species	role	GRN	BRN	HAR	SAL	**Total**
Anobiidae	*Dorcatoma moderata* R.E.White	Fg	4	1			**5**
	Ernobius pallitarsus Fall	Wb		1			**1**
	Hemicoelus carinatus (Say)	Wb	2	2	4		**8**
	Microbregma emarginatum (Duftschmid)	Wb	52	3	2	1	**58**
	Ptilinus lobatus Casey	Wb		6			**6**
	Utobium elegans (Horn)	Wb	3		2		**5**
	Xestobium sp.	Wb		1			**1**
	Xyletinus lugubris LeConte	Wb		1			**1**
Anthicidae	*Anthicus coracinus* LeConte	Fg		1			**1**
	Anthicus floralis (Linné)	Fg			1		**1**
Anthribidae	*Allandrus populi* Pierce	Fg			2	1	**3**
	Tropideres dorsalis (Thunberg)	Fg				1	**1**
Buprestidae	*Anthaxia inornata* (Randall)	Wb			1		**1**
	Buprestis maculativentris Say	Wb		1	1		**2**
	Buprestis nuttalli Kirby	Wb				2	**2**
	Chrysobothris trinervia (Kirby)	Wb				1	**1**
	Dicerca tenebrica (Kirby)	Wb		26	5	26	**57**
	Dicerca tenebrosa (Kirby)	Wb		3	5	4	**12**
	Melanophila acuminata (DeGeer)	Wb		24		2	**26**
	Melanophila fulvoguttata (Harris)	Wb		1	1	1	**3**
Cantharidae	*Dichelotarsus piniphilus* (Eschscholtz)	Po	7		7		**14**
Carabidae	*Agonum placidum* (Say)	Po		1		4	**5**
	Agonum retractum LeConte	Po		1			**1**
	Agonum sordens Kirby	Po			2		**2**
	Amara apricaria (Paykull)	Po				1	**1**
	Amara latior (Kirby)	Po		1			**1**
	Amara littoralis Mannerheim	Po		2			**2**
	Amara lunicollis Schiødte	Po		2	2	4	**8**
	Amara obesa (Say)	Po		1		5	**6**
	Amara quenseli (Schönherr)	Po		1	1		**2**
	Amara torrida (Panzer)	Po		1	1	1	**3**
	Bembidion grapii Gyllenhal	Po		3		10	**13**
	Bembidion mutatum Gemminger&Harold	Po			2	1	**3**
	Bembidion nigripes (Kirby)	Po				1	**1**
	Bembidion rupicola (Kirby)	Po		1			**1**
	Bembidion timidum (LeConte)	Po		1		1	**2**
	Bradycellus lecontei Csiki	Po		1			**1**
	Bradycellus nigrinus (Dejean)	Po		1		3	**4**
	Calathus advena (LeConte)	Po			3	2	**5**
	Calathus ingratus Dejean	Po			4	6	**10**
	Cymindis cribricollis Dejean	Po				2	**2**

Appendix 3-A
(cont.)

		Trophic		Stand treatment			
Family	Species	role	GRN	BRN	HAR	SAL	**Total**
Carabidae	*Harpalus fulvilabris* Mannerheim	Po		1			**1**
	Harpalus laevipes Zetterstedt	Po		1		6	**7**
	Platynus decentis (Say)	Po	45	2	6	4	**57**
	Poecilus lucublandus (Say)	Po				2	**2**
	Pterostichus adstrictus Eschscholtz	Po	4	14	6	44	**68**
	Sericoda bembidioides Kirby	Po		17		3	**20**
	Sericoda obsoleta (Say)	Po	1	1		1	**3**
	Sericoda quadripunctata (DeGeer)	Po	1	46		70	**117**
	Stenolophus conjunctus Say	Po		1			**1**
	Stereocerus haematopus (Dejean)	Po		1	2	1	**4**
	Syntomus americanus (Dejean)	Po				1	**1**
	Trichocellus cognatus (Gyllenhal)	Po		2	3	3	**8**
Cerambycidae	*Acmaeops proteus* (Kirby)	Wb	3	99	32	38	**172**
	Arhopalus foveicollis (Haldeman)	Wb		2		1	**3**
	Asemeum striatum (Linné)	Wb			3		**3**
	Bellamira scalaris (Say)	Wb				1	**1**
	Grammoptera subargentata (Kirby)	Wb			4		**4**
	Judolia instabilis (Haideman)	Wb		1	8	3	**12**
	Meriellum proteus (Kirby)	Wb	1				**1**
	Monochamus scutellatus (Say)	Wb		134	23		**157**
	Neacanthocinus pusillus (Kirby)	Wb			3		**3**
	Neoclytus muricatulus (Kirby)	Wb		1			**1**
	Pachyta lamed liturata Kirby	Wb		10	8	1	**19**
	Pogonocherus parvulus LeConte	Wb		8	1	6	**15**
	Pogonocherus pencillatus LeConte	Wb	3		1		**4**
	Pygoleptura nigrella (Say)	Wb		3	1		**4**
	Pymatodes dimidiatus (Kirby)	Wb	1	1	4		**6**
	Rhagium inquisitor (Linné)	Wb	2	2	13	1	**18**
	Spondylis upiformes Mannerheim	Wb	4	13	6		**23**
	Stictoleptura canadensis (Olivier)	Wb		2	5	1	**8**
	Tetropium cinnamopterum Kirby	Wb		2	5		**7**
	Tetropium nanum Laplante	Wb	4	1			**5**
	Tetropium parvulum Casey	Wb	5				**5**
	Trachysida aspera (LeConte)	Wb		1			**1**
	Trachysida mutabilis (Newman)	Wb		5	4		**9**
	Xylotrechus undulatus (Say)	Wb	2	1	12	3	**18**
Cerylonidae	*Cerylon castaneum* Say	Fg		7	2	2	**11**
	Cis fuscipes Mellié	Fg		1	1		**2**
	Cis sp.	Fg				1	**1**
	Dolichocis manitoba Dury	Fg	1	1			**2**
	Octotemnus laevis Casey	Fg			1		**1**
Clambidae	*Clambus gibbulus* (LeConte)	Fg			3		**3**
	Clambus pubescens Redtenbacher	Fg	4	23	409	64	**500**
Cleridae	*Thanasimus dubius* (Fabricius)	Po			1	1	**2**
	Thanasimus undatulus (Say)	Po	11	72	31	36	**150**
Colydiidae	*Lasconotus complex* LeConte	Fg	1		5		**6**
Corylophidae	*Clypastraea obesa* (Casey)	Fg	13	124	180	46	**363**

Appendix 3-A (cont.)

		Trophic		Stand treatment			
Family	Species	role	GRN	BRN	HAR	SAL	**Total**
Corylophidae	*Orthoperus scutellaris* LeConte	Fg			1		**1**
Cryptophagidae	*Atomaria ephippiata* Zimmermann	Fg	7	54	83	75	**219**
	Atomaria nubipennis Casey	Fg		16	4	8	**28**
	Caenoscelis antennalis (Casey)	Fg	11	175	45	419	**650**
	Cryptophagus distinguendus Sturm	Fg			2		**2**
	Cryptophagus pilosus Gyllenhal	Fg	4	17	17	11	**49**
	Cryptophagus quadrihamatus Mäklin	Fg		1	2	3	**6**
	Cryptophagus sp.	Fg	1	1	1	1	**4**
	Cryptophagus tuberculosus Mäklin	Fg	27	9	24	16	**76**
	Henoticus serratus (Gyllenhal)	Fg	10	24	4	53	**91**
	Pteryngium crenatum (Gyllenhal)	Fg	1				**1**
Cucujidae	*Cucujus clavipes* Fabricius	Po	1	6	2	1	**10**
	Pediacus fuscus Erichson	Po	1	37	33	39	**110**
Curculionidae	*Cossonus pacificus* Van Dyke	Wb	1	10	1		**12**
	Cryphalus ruficollis Hopkins	Wb		1			**1**
	Crypturgus borealis Swaine	Wb	17	3	18		**38**
	Dendroctonus rufipennis (Kirby)	Wb	26	23	47	2	**98**
	Dryocetes affaber (Mannerheim)	Wb	138	77	155	10	**380**
	Dryocetes autographus (Ratzeburg)	Wb	12	277	129	82	**500**
	Ips borealis Swaine	Wb	1	2			**3**
	Ips pini (Say)	Wb	3	10	8		**21**
	Magdalis subtincta LeConte	Wb	1	1	3		**5**
	Orthotomicus caelatus (Eichhoff)	Wb	4	18	38	3	**63**
	Pityogenes plagiatus plagiatus (LeConte)	Wb		2			**2**
	Pityophthorus spp.	Wb	25	16	17	1	**59**
	Polygraphus rufipennis (Kirby)	Wb	67	10	25		**102**
	Rhyncolus brunneus Mannerheim	Wb	2	1	3	1	**7**
	Scierus annectans LeConte	Wb	9		36		**45**
	Scierus pubescens Swaine	Wb	37	5	24	1	**67**
	Scolytus piceae (Swaine)	Wb	1	6	2	1	**10**
	Trypodendron lineatum (Olivier)	Wb	34	5	275		**314**
	Trypodendron retusum (LeConte)	Wb			2		**2**
	Xylechinus montanus Blackman	Wb	11				**11**
Elateridae	*Ampedus apicatus* (Say)	Po		3	5		**8**
	Ampedus deletus (LeConte)	Po	17	5	14	14	**50**
	Ampedus luctuosus (LeConte)	Po		6	2		**8**
	Ampedus nigrinus (Herbst)	Po		2			**2**
	Ctenicera lutescens (Fall)	Po	4			1	**5**
	Ctenicera nigricollis (Bland)	Po	2				**2**
	Ctenicera nitidula (LeConte)	Po	5	5	1	7	**18**
	Ctenicera propola (LeConte)	Po	6	1			**7**
	Ctenicera resplendens (Escscholtz)	Po	1	8	4		**13**
	Ctenicera stricklandi (W.J. Brown)	Po		3			**3**
	Ctenicera triundulata (Randall)	Po	8	244	4	64	**320**
	Denticollis denticornis (Kirby)	Po	4	1	1		**6**
	Drasterius debilis LeConte	Po	1	1	2	1	**5**
	Eanus estriatus (LeConte)	?			1		**1**

Appendix 3-A (cont.)

Family	Species	Trophic role	Stand treatment GRN	BRN	HAR	SAL	**Total**
Elateridae	*Eanus* sp.	?		1	2		**3**
	Limonius pectoralis LeConte	Po		1			**1**
Erotylidae	*Triplax californica* LeConte	Fg	1	3			**4**
Eucnemidae	*Epiphanis cornutus* Escscholtz	Fg			5		**5**
	Hylis terminalis (LeConte)	Fg			1		**1**
Histeridae	*Hister* sp.	Po		1	1		**2**
	Hololepta aequalis Say	Po			1		**1**
	Platysoma lecontei Marseul	Po		1	4		**5**
Laemophloeidae	*Laemophloeus biguttatus* (Say)	Fg		2			**2**
Lampyridae	*Pyractomena angulata* (Say)	Po	1	1		1	**3**
Latridiidae	*Cartodere constricta* (Gyllenhal)	Fg	9	27	55	21	**112**
	Corticaria serrata (Paykull)	Fg	45	175	191	150	**561**
	Corticaria spp.	Fg	9	50	14	45	**118**
	Enicmus mimus Fall	Fg	11	144	13	88	**256**
	Enicmus tenuicornis LeConte	Fg	6	1	4	2	**13**
	Latridius hirtus Gyllenhal	Fg	1	3			**4**
	Latridius minutus (Linné)	Fg	6	9	49	2	**66**
	Melanophthalma villosa (Zimmermann)	Fg	240	419	37	99	**795**
Leiodldae	*Agathidium californicum* Horn	Fg			1		**1**
	Agathidium depressum Fall	Fg	4	2	3	2	**11**
	Agathidium jasperanum Fall	Fg		1			**1**
	Agathidium maculosum W.J.Brown	Fg		1		2	**3**
	Agathidium sp. A	Fg			1		**1**
	Agathidium sp. B	Fg		3	2		**5**
	Anisotoma discolor (Melsheimer)	Fg				1	**1**
	Anisotoma globososa Hatch	Fg	1	3	23	11	**38**
	Anisotoma sp.	Fg				8	**8**
	Anogdus superans (Fall)	Fg	1				**1**
	Catops americanus Hatch	Sd	1		1		**2**
	Hydnobius substriatus LeConte	Fg		1		6	**7**
	Leiodes assimilis (LeConte)	Fg			1		**1**
	Leiodes sp.	Fg		1		5	**6**
Lycidae	*Dictyopterus aurora* (Herbst)	Fg			5		**5**
Melandryidae	*Dircaea liturata* (LeConte)	Fg		3			**3**
	Enchodes sericea (Haldeman)	Fg	2		4	1	**7**
	Melandrya striata Say	Fg	1				**1**
	Orchesia castanea (Melsheimer)	Fg	1		1		**2**
	Serropalpus substriatus Haldeman	Fg	3	7	3		**13**
	Xylita laevigata (Helenius)	Fg	3	8	5		**16**
	Xylita livida (C.R.Sahlberg)	Fg			1		**1**
	Zilora hispida LeConte	Fg	2				**2**
Monotomidae	*Rhizophagus brunneus* Horn	Po	4	25	8	2	**39**
	Rhizophagus dimidiatus Mannerheim	Po	3	2	4		**9**
	Rhizophagus remotus LeConte	Po	1	1	10		**12**
Mycetophagidae	*Mycetophagus distinctus* Hatch	Fg			2		**2**
	Mycetophagus pluriguttatus LeConte	Fg			1		**1**
	Mycetophagus pluripunctatus LeConte	Fg			1		**1**

Appendix 3-A (cont.)

		Trophic		Stand treatment			
Family	Species	role	GRN	BRN	HAR	SAL	**Total**
Mycetophagidae	*Mycetophagus serrulatus* (Casey)	Fg		1			**1**
Nitidulidae	*Epuraea linearis* Mäklin	Fg	3	37	220	58	**318**
	Glischrochilus moratus W.J.Brown	Fg			1		**1**
	Glischrochilus sanguinolentus (Olivier)	Po			2		**2**
	Glischrochilus siepmanni W.J. Brown	Fg		3	6	10	**19**
	Glischrochilus vittatus (Say)	Po			2		**2**
	Nitidula sp.	?		2	11	3	**16**
Ptiliidae	*Acrotrichis* spp.	Fg	5	26	147	22	**200**
Pyrochroidae	*Schizotus cervicalis* Newman	Fg			1		**1**
Salpingidae	*Sphaeriestes virescens* (LeConte)	Po		145	5	510	**660**
Scraptiidae	*Anaspis nigrina* Csiki	?			2		**2**
Sphindidae	*Odontosphindus clavicornis* Casey	Fg			1		**1**
Staphylinidae	*Acidota crenata* (Fabricius)	Po		3	2		**5**
	Acidota quadrata (Zetterstedt)	Po	1	1	4	3	**9**
	Anotylus sobrinus (LeConte)	Sd	1	5	16	8	**30**
	Baeocera congenera Casey	Fg			3		**3**
	Bisnius tereus Smetana	Po	3	6	22	6	**37**
	Carphacis nepigonensis (Bernhauer)	Po		6	3	1	**10**
	Cilea silphoides (Linné)	?			3	1	**4**
	Deinopteroloma subcostatum (Mäklin)	Po			1		**1**
	Gabrius picipennis (Mäklin)	Po		2			**2**
	Heterothops minor Smetana	Po	1	13	18	35	**67**
	Ischnosoma fimbriatum Campbell	Po			1		**1**
	Ischnosoma splendidum (Gravenhorst)	Po	2		2	5	**9**
	Lathrobium nigrum LeConte	Po		1	1		**2**
	Lordithon fungicola Campbell	Po	2	13	6	5	**26**
	Megarthrus angulicollis Mäklin	Fg	2	3	54	1	**60**
	Micropeplus laticollis Mäklin	Fg		1	2	1	**4**
	Micropeplus tesserula Curtis	Fg	2	25		18	**45**
	Mycetoporus americanus Erichson	Po	1		4	1	**6**
	Mycetoporus lucidulus LeConte	Po		1	4		**5**
	Nanobius serricollis (LeConte)	?				1	**1**
	Nudobius cephalus (Say)	Po		6	7	3	**16**
	Olisthaerus megacephalus Zetterstedt	Po	1	2	2	1	**6**
	Olisthaerus substriatus (Gyllenhal)	Po	2	2	4		**8**
	Philonthus cyanipennis (Fabricius)	Po	1				**1**
	Philonthus leechensis Hatch	Po		1			**1**
	Phloeostiba lapponicus (Zetterstedt)	Po		68	45	33	**146**
	Pseudopsis sagitta Herman	Po			1	1	**2**
	Quedius brunnipennis Mannerheim	Po	1	1	1		**3**
	Quedius criddlei (Casey)	Po	1		1	2	**4**
	Quedius labradorensis Smetana	Po			1		**1**
	Quedius plagiatus Mannerheim	Po	5	3	26	6	**40**
	Quedius rusticus Smetana	Po	1	6	72	2	**81**
	Quedius simulator Smetana	Po	1		2		**3**
	Quedius transparens Motschulsky	Po			1		**1**
	Quedius velox Smetana	Po	7		5	1	**13**

Appendix 3-A (cont.)

Family	Species	Trophic role	GRN	BRN	HAR	SAL	**Total**
				Stand treatment			
Staphylinidae	*Scaphium castanipes* Kirby	Fg				1	**1**
	Sepedophilus littoreus (Linné)	Fg			3	2	**5**
	Siagonium punctatum LeConte	Sd			5	3	**8**
	Stenus austini Casey	Po			1	1	**2**
	Stenus spp.	Po		3	6	3	**12**
	Tachinus elongates Gyllenhal	Po		1			**1**
	Tachinus frigidus Erichson	Fg			1		**1**
	Tachinus fumipennis (Say)	Po	1	1	1		**3**
	Tachyporus borealis Campbell	Po	1			2	**3**
	Tachyporus maculicollis LeConte	Po	4	20	8	36	**68**
	Tachyporus sp.	?		1		1	**2**
Subfamily Aleocharinae		?	15	199	258	224	**696**
Stenotrachelidae	*Cephaloon tenuicorne* LeConte	Wb	3	29	24	6	**62**
Sylvanidae	*Dendrophagus cygnaei* Mannerheim	Fg		3	1	1	**5**
Tenebrionidae	*Upis ceramboides* (Linné)	Fg	1	1	4	4	**10**
Trogositidae	*Ostoma ferruginea* (Linné)	Po				1	**1**
	Total individuals		**1098**	**3311**	**3342**	**2703**	**10454**
	*** Total species**		**106**	**160**	**168**	**125**	**244**

* Excluding Staphylinidae: Aleocharinae

CHAPTER 4

Effects of postfire salvage logging on *Monochamus s. scutellatus* (Coleoptera: Cerambycidae): implications for wood decomposition, nutrient cycling and forest succession

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4.1 Summary

In this chapter, I investigated the effects of postfire salvage logging on populations of the white-spotted sawyer, *Monochamus scutellatus scutellatus* (Say) (Coleoptera: Cerambycidae) and its ecological function in boreal forest using a series of both field and laboratory studies. *M. s. scutellatus* adults were relatively abundant in both burned and clear-cut logged sites, but were absent from salvage logged sites. An *in situ* mesocosm experiment showed that abundance of *M. s. scutellatus* larvae in burned white spruce bolts was linked to changes in total organic N and C in mineral soil. Organic nutrient inputs in the form of *M. s. scutellatus* frass more than tripled mineral soil microbial respiration rates and altered N availability. Changes in N availability decreased germination and growth of *Epilobium angustifolium* and *Populus* spp., but had no significant effect on *Calamagrostis canadensis*. Collectively, my findings suggest that continued economic emphasis on postfire salvage logging

may not only negatively impact biodiversity but, through its effects on biodiversity, may also alter decomposition processes, nutrient cycling, and successional trajectories in forest ecosystems recovering from wildfire.

4.2 Introduction

Concern over the ecological consequences of human influences on natural ecosystems continues to drive issues regarding biodiversity conservation and the persistence of ecosystem function to the forefront of ecological research (Chapin III *et al.*, 2000; Ehrlich & Wilson, 1991; Hooper *et al.*, 2005; Naeem, 2002; Naeem *et al.*, 1999; Pimm *et al.*, 1995; Vitousek *et al.*, 1997). Modern ecosystems are increasingly stressed by demands for natural resources and the compounding effects of global environmental change (Sala *et al.*, 2000; Vitousek *et al.*, 1997). Climate models, for example, predict dramatic increases (*c.* 30-50%) in the occurrence of wildfires in many forest ecosystems over the next century (Flannigan *et al.*, 1998; Li *et al.*, 2000; Overpeck *et al.*, 1990; Stocks *et al.*, 1998), while global economic demands for both timber and non-timber resources continue to rise. As a result, there may be increased economic pressure to salvage logs from burned forests, a trend that is already apparent in many North American forests (Lindenmayer *et al.*, 2004; Sessions *et al.*, 2004).

At present, the ecological consequences of postfire salvage logging are insufficiently understood to develop effective management guidelines (Lindenmayer, 2006; Lindenmayer *et al.*, 2004; Schmiegelow *et al.*, 2006). Despite the lack of scientific data, however, such policies must be developed (Lindenmayer *et al.*, 2004; Nappi *et al.*, 2004; Schmiegelow *et al.*, 2006; Sutherland *et al.*, 2006). Recent work suggests that large-scale salvage operations may alter postfire bird (Morissette *et al.*, 2002; Nappi *et al.*, 2004) and ground beetle assemblages (Koivula *et al.*, 2006; Phillips *et al.*, 2006) and affect plant regeneration (Donato *et al.*, 2006; Fraser *et al.*, 2004; Greene *et al.*, 2006). In addition, wildfires increase the amount of dead wood across forested landscapes, and research from Australia (Grove, 2002; Grove *et al.*, 2002), Europe (Ehnström, 2001; Jonsell *et al.*, 1998; Martikainen, 2001; Martikainen & Kaila, 2004; Martikainen *et al.*, 1998; Siitonen, 2001; Siitonen & Martikainen, 1994), and North America (Hammond, 1997; Hammond *et al.*, 2001, 2004) suggests that this resource is critical for maintaining biodiversity in forest ecosystems. In fact, the loss of dead wood from intensely managed Fennoscandian forests has already resulted in the extirpation of several saproxylic insect species (Siitonen and Martikainen 1994). Although most saproxylic insects are thought to be involved in wood decomposition (Speight *et al.*, 1999), few direct tests of this relationship have been conducted (*c.f.* Edmonds & Eglitis, 1989) and the precise functional roles of most species are inadequately understood (Grove, 2002). Thus, the ecological consequences of losing saproxylic species are difficult to predict.

The white-spotted sawyer, *Monochamus s. scutellatus* (Say) (Coleoptera: Cerambycidae), is a pyrophilous ("fire-loving"), saproxylic beetle found throughout most of North America, with the exception of the central United States (Yanega, 1996). It is common in coniferous forests with an abundance of recently killed, weakened or dying trees, especially following fire (Rose, 1957; Wilson, 1962). The primary host tree species appears to be eastern white pine (*Pinus strobus* L.), but females readily oviposit in and larvae feed on freshly cut or otherwise weakened jack pine (*P. banksiana* Lamb.), red pine (*P. resinosa* Ait.), balsam fir (*Abies balsamea* [L.] P.Mill.), white spruce (*Picea glauca* [Moench] Voss), black spruce (*P. mariana* [P.Mill.] B.S.P.) and red spruce (*P. rubens* Sarg.) (Wilson, 1962). Adults eat needles and twig bark causing minor damage to the tips of branches (Wilson, 1962). After mating (Hughes, 1979, 1981; Hughes & Hughes, 1985), eggs are deposited singly in scars in the bark made by the female's mandibles and larvae hatch within 9-14 days (Peddle *et al.*, 2002; Rose, 1957). Larvae feed primarily in the phloem and sapwood, but burrow into the heartwood to pupate, thereby causing significant economic degradation in standing dead trees and log decks (Richmond & Lejeune, 1945; Rose, 1957; Ross, 1960). Larval development generally requires 2 years, but may be shorter in the southern extremes of the species' range (Wilson, 1962; Yanega, 1996). In addition to the galleries under the bark, evidence of larval feeding activity is visible on the ground as wood chips and frass (faecal material) frequently build up around the base of the tree.

I investigated the effects of postfire salvage logging on *M. s. scutellatus* and the role of this beetle in recycling nutrients from burned coniferous trees. Using a series of field and laboratory studies, I determined: (1) the effect of postfire salvage logging on populations of adult *M. s. scutellatus*; (2) the relationship between larval abundance and soil nutrients at the base of burned white spruce trees; (3) the effect of organic nutrient inputs in the form of larval frass on soil microbial activity and nitrogen availability; and (4) the effect of such frass on germination and growth of plant species that colonize recently burned forests.

4.3 Methods

4.3.1 Field studies

4.3.1.1 Beetle survey

Populations of adult *M. s. scutellatus* were surveyed in and around a severe, large-scale wildfire (*c.* 120,000 ha) that occurred May 23 – June 4, 2001 near the hamlet of Chisholm, Alberta, Canada (N54°55′, W114°10′). Before the fire, the area was dominated by pure and mixed stands of white spruce (*Picea glauca* [Moench] Voss), black spruce (*P. mariana* [P.Mill.] B. S. P.), trembling aspen, (*Populus tremuloides* Michx.), balsam poplar (*P. balsamifera* L.), and jack pine (*Pinus banksiana* Lamb.), with minor elements of balsam fir (*Abies balsamea* [L.] P.Mill.), larch (*Larix laricina* [Du Roi] K. Koch), and paper birch (*Betula papyrifera* Marsh.). For this survey, I focused on mixed stands of white spruce (*c.* 60% of canopy composition) and trembling aspen (*c.* 40%). Specifically, I selected sites in one of the four following categories: (1) GRN – "green", reference sites that had not been burned or harvested in >100 yrs; (2) BRN – sites that were "burned" by the Chisholm fire; (3) HAR – unburned, "harvested" sites that were clear-cut logged in 2001; and (4) SAL – sites that were burned by the Chisholm fire and then "salvaged" during the winter of 2001/2002. Sites were individual stands of trees (3-30 ha) selected on the basis of pre-disturbance stand characteristics (age, tree species composition, stem density, soil characteristics) and accessibility, determined initially from forest inventory maps (Alberta Vegetation Inventory, Alberta Sustainable Resource Development, 2000) and then verified on the ground. Six sites were selected for each stand category (total = 24 sites). The minimum distance between any two sites was 1 km.

Adult beetles were sampled using flight-intercept traps (Hammond, 1997; Kaila, 1993) attached to white spruce trees and stumps. Although previous work has shown that other trap designs tend to yield larger catches of large cerambycids, like *Monochamus* sp. (McIntosh *et al.* 2001), the traps used here formed part of a larger study of the overall saproxylic beetle assemblage (Chapter 3). The traps deployed in this study consisted of a thin (0.3 cm) piece of clear plastic (20 cm x 30 cm) connected below to a heavy cloth funnel and a plastic sample cup (100 ml) that was charged with *c.* 30 ml of silicate-free ethylene glycol. A total of 120 traps were deployed in this study. In GRN and BRN sites, 4 traps/site were attached to standing white spruce trees at approximately 1.5 m above the ground, whereas in HAR and SAL sites, the traps (4/site) were attached to stumps due to the scarcity of available trees. To account for the possible confounding effect of trap height, an additional 2 traps/site were placed at the base of the standing trees in the GRN and BRN sites. All traps were serviced biweekly during the frost-free months (Apr. to Sept.) of 2002 and 2003 to remove all collected beetles and replace the ethylene glycol.

4.3.1.2 Mesocosm experiment

I conducted an *in situ* mesocosm experiment to examine the relationship between the abundance of larval *M. s. scutellatus* feeding on burned white spruce stems and changes in soil nutrients. This experiment was designed as a 1-factor (larval abundance) analysis of variance (ANOVA) with 5 levels (0, 2, 5, 8, 10 larvae) and 4 replicates. Larval abundance levels were selected to span the natural range of densities observed in the surrounding area. Twenty enclosures (0.22 m^3) were placed on the ground at one of the burned (BRN) sites (N54°54.3', W114°6.8') described above. Enclosures were open-bottomed, but screened on the top and sides to prevent colonization by additional beetles or predation by woodpeckers and parasitoid wasps. In the center of each enclosure, I placed a single bolt of wood vertically so that one end remained in contact with the ground. Bolts were obtained by falling 3 healthy (unburned) white spruce trees and then cutting the stems into 50-cm lengths. Each bolt was scorched to simulate the action of wildfire and to kill any existing fauna. The top end of each bolt was sealed with paraffin wax to reduce the rate of moisture loss. Bolts were randomly assigned to a particular enclosure position and larval abundance treatment.

Monochamus s. scutellatus larvae (2nd instar) were collected from nearby burned white spruce trees and placed in notches in the experimental bolts that were made with an ethanol-sterilized chisel. Second-instar larvae were used exclusively because this stage was most readily available at the start of the experiment. Larvae that did not immediately burrow under the bark and begin feeding in the experimental bolts were discarded and replaced. In accordance with the rate of development expected in the northern portion of the beetle's range, larvae were allowed to feed for 2 consecutive years. Enclosures were monitored biweekly and any germinating plants were removed. At the end of July 2003 and 2004 (1 and 2 years post-treatment), I determined the mass (± 0.1 kg) of each log using a digital bathroom scale (Siltec™ GS-1) and collected mineral soil samples (2 cm corer; 0-3 cm depth) from each enclosure. For each soil sample, I determined pH, total C, N, and P using standard methods described in Kalra and Maynard (1991). Specifically, pH was determined on a 1:2 soil: 0.01 *M* $CaCl_2$ suspension, total C by combustion, total N by the Kjeldahl method, and total extractable P by the Bray 1 method.

4.3.2 Laboratory studies

4.3.2.1 Frass collection

For all laboratory experiments, *M. s. scutellatus* frass was obtained from individuals reared in captivity on scorched white spruce logs. Rearing cages were maintained at 20°C, 30 – 60% relative humidity, and a constant photoperiod (16 hrs light: 8 hrs dark) for two years. Frass that accumulated in the bottom of each cage was periodically collected, manually sorted into its two components (chewing dust and faecal pellets), and air-dried at 20°C.

4.3.2.2 Microbial activity and N-availability

The effect of *M. s. scutellatus* larvae frass on soil microbial activity was examined in a laboratory experiment that compared CO_2 evolution and changes in N availability in mineral soil samples with and without the addition of frass. Ten flat-bottomed, glass test tubes (150 ml) were filled with 50 g of air-dried (20°C) mineral soil and 15 ml of de-ionized water. Mineral soil (0-3 cm depth) for this experiment was collected from 3 available, recently burned (< 30 days) mixed-wood sites (white spruce and trembling aspen) in northern Saskatchewan, Canada (site 1 N56°16.0', W108°54.1'; site 2 N55°29.1', W104°51.1'; site 3 N53°13.2' W105°58.3'). Soil from all three sites was combined, sieved (0.5 cm mesh size) to remove as much of the debris and vegetative propagules as possible, and air-dried for several weeks at 20°C.

The frass augmentation treatment consisted of both faecal pellets (1.2 mg/g-soil) and chewing dust (20.8 mg/g-soil). Concentrations of frass components were derived from 10 field-collected samples, which averaged a 1:17 ratio (faecal pellets:chewing dust) by mass. The contents of all test tubes were thoroughly mixed, covered with gas-permeable film and allowed to settle for 6 days at 20°C. Microbial activity was assessed by monitoring CO_2 evolution after the test tubes were covered with rubber stoppers for one hour. Head-space CO_2 concentrations were determined using a Hewlett-Packard 5890 Series II gas chromatograph equipped with a 1m Poropak Q column, HP3396 Series II integrator, and He as the carrier gas.

I examined changes in N availability by incubating all the test tubes described above for an additional 13 days at 20°C. Following this incubation, water extracts (45 ml) of the soil (3.0 g fresh mass) were analyzed for concentrations of total soluble C and N (Shimadzu Carbon and Nitrogen Analyzer, Mandel Scientific Co. Inc. ON, Canada), NH_4^+ and NO_3^- (Technician Auto Analyzer II, Technician Industrial Systems, Tarrytown, NY), and organic-N (by difference).

4.3.2.3 Plant germination and growth

Effects of *M. s. scutellatus* larvae frass on plant germination and growth were examined experimentally in a culture chamber (22°C, 60-70% R.H., 16hrs light: 8hrs dark). This experiment was designed as a 1-factor ANOVA with 3 levels ("+ Frass", "- Frass", and "germination control") and ten replicates. A total of thirty plastic pots (10-cm diameter, closed-bottom) were filled with 240 g of soil collected and prepared as described for the microbial activity study above. The "+Frass" treatment (n=10 pots) was established, as above, by adding 4.992 g of chewing dust (20.8 mg/g-soil) and 0.288g of faecal pellets (1.2 mg/g-soil), whereas the "- Frass" treatment (n=10 pots) contained only unamended soil. These twenty pots were each seeded with twenty field-collected seeds of each of the following species: trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*P. balsamifera* L.), fireweed (*Epilobium angustifolium* L.), and bluejoint grass (*Calamagrostis canadensis* [Michx.]). Plant species were chosen to represent common early colonizers in the region and final selection was based on seed availability. An additional ten pots were established as a "germination control" to examine natural germination levels. All pots were watered with de-ionized water at a rate of 65 ml/week during the 180-day duration of the experiment. At each watering, the number of germinants was recorded and, at the end of the experiment, shoot and root biomass for each germinant was determined. Biomass values for all plant tissues were assessed after washing thoroughly with de-ionized water and drying to a constant mass (70°C). At the end of the experiment, water extracts of the soil were analyzed for concentrations of total soluble C and N, organic-N, NH_4^+, and NO_3^- by the same methods as described for the microbial study above.

4.3.3 Statistical analyses

To account for variability in sampling effort arising from trap disturbance, catches of adult *M. s. scutellatus* were standardized (number of individuals / trap-day) prior to analysis. Differences in mean catch rates across stand treatments were evaluated using 1-factor ANOVA followed by Tukey's HSD *post-hoc* tests when the overall analysis was significant. Repeated measures analysis of variance (RM-ANOVA) was used to examine year-to-year changes in the mass of the wood bolts used in the mesocosm experiment. Linear regression was used to examine relationships between larval abundance and soil nutrient parameters in the mesocosm experiment. Student *t*-tests were used to compare the effect of frass addition on mean microbial CO_2 evolution as well as post-incubation nutrient parameters. Finally, to evaluate the effects of frass on plant germination, growth and post-plant growth soil nutrient parameters, we again used 1-factor ANOVA. For all tests, data were transformed ($log_{10(x+1)}$) prior to analysis when necessary to meet the assumptions of normality (Kolmogorov-Smirnov) and homoscedasticity (Levene's test) (Zar, 1996). These analyses were performed using SPSS for Windows 11.5 (SPSS 2002, LEAD Technologies Inc. 2002) and employed a rejection coefficient of 0.05.

4.4 Results

4.4.1 Field studies

4.4.1.1 Beetle survey

Sampling effort (traps x days) for the field survey was 28,207 trap-days and resulted in a total collection of 157 adult *M. s. scutellatus*. The effect of stand treatment on standardized mean catch rates (individuals / trap-day) was significant (ANOVA; $F_{3,20} = 19.695, p < 0.001$) (Fig. 4.1) as catch rates were higher in BRN sites than in HAR sites and no specimens were collected in either GRN or SAL sites (Tukey's HSD; $p < 0.05$). Trap height (high vs. low) had no statistically significant effect on *M. s. scutellatus* catch rates (Student t-test: $t = 1.630, p = 0.106$).

4.4.1.2 Mesocosm experiment

In the mesocosm experiment, frass production was visible in individual enclosures within 2 days of larval introduction. Based on a visual inspection of emergence holes and larval galleries in each bolt at the end of the experiment, larval mortality was estimated at approximately 5-10% across all replicates. However, it was not possible to accurately determine when mortality occurred, so nutrient values were averaged across years to reduce the effect of year-to-year variation within replicates. Soil chemistry analyses revealed that increasing larval density significantly increased total C, total N, N:P and C:P, but did not significantly affect total P or C:N (Fig. 4.2). Soil pH levels ranged from 4.9-6.2 in all samples, but did not vary significantly with changing larval densities (linear regression: $r^2 = 0.010, p = 0.6712$). Bolt masses declined gradually during this study (RM-ANOVA, effect of year: $F_{1,15} = 25.42, p < 0.001$), but did not vary across treatments (RM-ANOVA, effect of larval abundance: $F_{4,15} = 1.80, p = 0.1819$).

4.4.2 Laboratory studies

4.4.2.1 Microbial activity and N-availability

Monochamus s. scutellatus frass that accumulates at the base of burned trees is comprised of both faecal pellets and chewing dust that can be readily separated under a dissecting microscope. Chemical analysis of composite samples of both faecal pellets and chewing dust from individuals reared in captivity on burned white spruce bolts indicated similar C:N values in both types of material (Table 4.1). Further analysis revealed that soluble forms of C and N in both faecal pellets and chewing dust were largely organic. However, the faecal pellets also contained a small amount of soluble inorganic-N as NO_3^- and the chewing dust contained a small amount of both NO_3^- and NH_4^+ (Table 4.1).

The addition of *M. s. scutellatus* frass (faecal pellets and chewing dust) to mineral soil samples significantly increased microbial respiration rates (Fig. 4.3). Compared to controls, head-space CO_2 evolution was more than 3 times greater in frass-augmented samples. Following a 13-day incubation of these samples, we found that water extracts of frass-augmented soil contained significantly greater concentrations of organic-C, organic-N, and NH_4^+, but significantly lower total N and NO_3^- concentrations than that of the frass-free soil (Table 4.2).

4.4.2.2 Plant germination and growth

In the culture chamber, germination began in all pots 21 days after the initial seeding. The addition of *M. s. scutellatus* frass significantly altered the germination and growth of 2 of the 3 plant taxa investigated (Table 4.3). Seeded pots contained more germinants than the un-seeded control ("germination control") pots, and the mean number of germinants was significantly lower in frass-augmented pots than in those without frass. Germinants of the two *Populus* spp. were combined as they could not be readily distinguished at this early stage of development. Analysis of final biomass values indicated that the addition of frass reduced the above-ground biomass accumulation (shoot growth) of *Epilobium angustifolium* and *Populus* spp., but had no significant effect on *Calamagrostis canadensis*. Composite values (all plant taxa combined) for total shoot mass, root mass, and root:shoot ratios were not significantly affected by the addition of frass. Chemical analysis of water extracts of the soil from each pot at the end of the 180-day plant growth period (Table 4.4) showed that total C and NH_4^+ did not vary significantly between treatments, but that frass-augmented pots contained significantly greater amounts of organic-N and significantly lower amounts of total N and NO_3^-.

4.5 Discussion

Broadly, my results showed that removal of dead wood from burned forests by postfire salvage logging has the potential to alter naturally occurring links between wood-feeding insects and nutrient dynamics in forests recovering from wildfire (Fig. 4.4). Pyrophilous, wood-boring beetles are among the first organisms to colonize recently burned forests (Evans, 1962, 1971; Gardiner, 1957b; Hart, 1998; Schmitz & Bleckmann, 1998; Whitehouse, 2000; Wikars, 1997, 2002) and my data illustrates that the abundance of at least one of these species is clearly linked to nutrient cycling. By feeding on burned dead wood, *M. s. scutellatus* larvae help to begin the process of gradually returning organic materials from standing burned coniferous trees to the soil. My data show that this feeding activity is linked to changes in soil microbial activity, N availability, and the germination and growth of colonizing plants in early postfire ecosystems.

Previous studies have demonstrated that populations of *M. s. scutellatus* increase sharply in the first 1-2 years after a wildfire (Richmond & Lejeune, 1945; Rose, 1957; Ross, 1960; Saint-Germain *et al.*, 2004), leading to the recommendation that salvage operations be conducted as soon as possible after a fire to minimize damage to timber and maximize economic recovery (Richmond & Lejeune, 1945; Ross, 1960; Sessions *et al.*, 2004). The abundance of *M. s. scutellatus* in stands with a profusion of fire-killed or freshly cut coniferous trees and stumps, like the BRN and HAR sites in my study, has been attributed to attraction of adults to volatile compounds such as ethanol and terpenes in conifer oleoresin and smoke (Allison *et al.*, 2001; Chénier & Philogène, 1989a, 1989b; Gardiner, 1957a, 1957b). Several studies have noted increased catches of this and related cerambycid taxa in traps baited with ethanol and blends of monoterpenes including (±)-α-pinene, (-)-β-pinene, (±)-camphene and myrcene (Chénier & Philogène, 1989b; de Groot & Nott, 2001, 2004; Peddle, 2000). However, I collected no specimens in salvage logged sites, despite an abundance of burned and freshly cut stumps, suggesting that postfire salvage logging negatively affects colonization by this species. Data from studies conducted at mill sites (Allison *et al.*, 2001; Morewood *et al.*, 2002; Richmond & Lejeune, 1945) and our own observations of salvaged logs on trucks and at the mill suggest that postfire salvage logging does not hinder oviposition, but rather that the larvae were simply being removed from my field sites in salvaged stems.

Results from the mesocosm experiment showed that decreasing *M. s. scutellatus* larval abundance may impact soil chemistry, at least at a local scale. I found weak, but significant, positive relationships between larval abundance and both total C and total N of mineral soil samples taken from around the base of burned white spruce bolts (Fig. 4.2). In addition, because of relatively constant total P levels across all enclosures, N:P and C:P ratios increased with increasing larval abundance (Fig.

4.2). Together with relatively constant pH values across all enclosures, these findings show that decreasing larval densities by salvage logging burned trees could alter plant growth by altering relative P availability (Giesler *et al.*, 2002; McGroddy *et al.*, 2004; Tessier & Raynal, 2003). However, it is not clear from my results whether modified larval densities can affect soil chemistry at the stand-level. Although I observed that the accumulation of frass around the base of burned trees may be transported by wind throughout the stand, the extent to which this affects soil chemistry beyond the local scale remains to be studied.

Published estimates of N content in conifer phloem tissue (Mattson, 1980) along with my data on N content in larval *M. s. scutellatus* frass (Table 1), suggest that nutrient absorption by these beetles is inefficient, requiring individuals to process a relatively large volume of plant material during their development. Despite a small amount of NO_3^- (0.56% of total N) in the beetle's faeces (Table 4.1), most of the N being returned to the soil does not appear to be readily available to plants. However, I found that the addition of organic nutrients in *M. s. scutellatus* frass led to a significant increase in microbial activity which, in turn, led to a significant increase in NH_4^+ concentrations and a decrease in NO_3^- concentrations in the soil. While the elevated NH_4^+ concentrations may increase N available for plant uptake, the decrease in the more soluble NO_3^- suggests that this form of N is immobilized by the increased microbial activity (Fig. 4.4 and Table 4.2). Immobilization of both NO_3^- and NH_4^+ by microbes may reduce leaching of N in early postfire forests (Schimel & Bennett, 2004). Moreover, the fact that the development time for *M. s. scutellatus* is 1 or 2 years (Rose, 1957; Wilson, 1962) suggests that organic nutrient inputs in the frass of this species are somewhat gradual, which may also reduce leaching of N from burned stands.

In N-limited boreal forests, competition for different forms of N (*i.e.,* NO_3^- and NH_4^+) between plants and microbes and among plant species is one of many factors that influences primary productivity and plant species composition (Kronzucker *et al.*, 1997; Smithwick *et al.*, 2005). Plant species differ in their capacity to assimilate particular forms of N and this plays a role in determining their natural distributions (Bledsoe & Rygiewicz, 1986; Kielland, 1994). For example, many coniferous species (*e.g.*, white spruce, western hemlock and lodgepole pine) perform better when NH_4^+ is available as a N source instead of NO_3^-, whereas for others (*e.g.,* Douglas fir, western red cedar), the reverse may be true (Krajina *et al.*, 1973; Min *et al.*, 1998; van den Driessche, 1971). Kronzucker *et al.* (1997) suggested that adaptations to these various N sources may help to explain plant successional patterns following disturbance.

In the plant growth experiment, I found that the addition of *M. s. scutellatus* frass to mineral soil reduced the germination and growth of *Populus* spp. and *Epilobium angustifolium,* which are common colonizers of early postfire boreal forests. Immobilization of NO_3^- by the elevated microbial activity in frass-augmented soils may partially explain this result because I found that these soils contained significantly lower soluble NO_3^- concentrations at the end of our plant growth study (Table 4.4). However, *Calamagrostis canadensis* was not significantly affected by NO_3^- immobilization in my experiment, suggesting that this species may remain unaffected by these conditions in the field. Although I did not directly examine the effects of *M. s. scutellatus* frass on any conifer species, the changes in soil chemistry that I found may offer additional insight into recent findings of reduced natural regeneration of conifers following postfire salvage logging, which have been largely attributed to mechanical disturbance (Donato *et al.*, 2006; Greene *et al.*, 2006). Therefore, reduced densities of *M. s. scutellatus* larvae resulting from postfire salvage logging may not only alter soil nutrient dynamics, but may also influence growth of colonizing plant species and postfire successional trajectories.

While *M. s. scutellatus* and other wood-feeding beetle species may be considered "pests" that rapidly reduce the economic value of salvaged timber (Ross, 1960; Sessions *et al.*, 2004), their role in nutrient cycling and food web dynamics (Hoyt & Hannon, 2002) in burned forests should not be overlooked in the development of guidelines for postfire management. By removing fire-killed trees, postfire salvage logging in boreal ecosystems may be as damaging to saproxylic insect diversity as have intensive forestry and fire suppression in Europe (Grove, 2002; Siitonen, 2001). In addition to biodiversity consequences, the results of this study indicate that postfire salvage logging may also influence nutrient dynamics and succession in regenerating burned forests. Therefore, the long-term persistence of boreal ecosystem function may require the retention of some burned timber. Questions about the quantity and quality of burned timber needed to sustain populations of *M. s. scutellatus* and other saproxylic species require further study. However, given projected increases in the occurrence of wildfire, especially in parts of North American forests (Flannigan *et al.*, 1998; Li *et al.*, 2000; Overpeck *et al.*, 1990; Stocks *et al.*, 1998), wise policy and effective guidelines for the management of postfire salvage logging in the future will be required to balance ecological and economic considerations.

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Table 4.1: Summary of C and N content of *M. s. scutellatus* frass components (faecal pellets and chewing dust) obtained from laboratory cultures (250 individuals) reared on burned white spruce bolts. Values are from a composite sample of both materials.

Parameter	Faecal Pellets	Chewing Dust
Total C (%d.w.)	49.56	48.36
Total N (%d.w.)	0.59	0.58
C:N	84.71	83.81
Soluble		
Total C (mg/g)	60.0364	11.2146
Total N (mg/g)	0.4257	0.0951
organic - N (mg/g)	0.4233	0.0886
inorganic - N (mg/g)	0.0024	0.0065
NH_4^+ (mg/g)	0.0000	0.0003
NO_3^- (mg/g)	0.0024	0.0062

Table 4.2: Effect of *M. s. scutellatus* frass on post-incubation soluble C and N. Values are means (± 1SE) for n = 5 samples. Incubation was 13 days at 20°C.

Parameter	- Frass	+ Frass	*d.f.*	*t*	*p*
Total C (µg/g-soil)	147.88 (± 8.59)	234.73 (± 9.73)	8	- 6.732	<0.001
Total N (µg/g-soil)	34.21 (± 2.40)	10.95 (± 0.48)	8	9.573	<0.001
Organic - N (µg/g-soil)	1.26 (± 0.43)	9.17 (± 0.68)	8	- 9.851	<0.001
NH_4^+ (µg/g-soil)	0.02 (± 0.01)	1.68 (± 0.71)	8	-2.464	0.039
NO_3^- (µg/g-soil)	33.61 (± 2.95)	0.18 (± 0.11)	8	11.486	<0.001

Table 4.3: Summary of laboratory plant study results showing the effects of beetle frass on germination and growth of three plant taxa, *Calamagrostis canadensis*, *Epilobium angustifolium*, and *Populus* spp.. Biomass values are for oven-dried (70°C) tissues standardized by the number of plants. Values are presented as means (± 1SE) for n = 10 replicates. Different lower case letters indicate significant differences (Tukey's HSD; $p < 0.05$) within each parameter.

Parameter	Germination Control	- Frass	+ Frass	$F_{2,27}$	p
no. of germinants	0.7 (± 0.7) ^{a}	10.3 (± 1.3) ^{b}	6.3 (± 1.7) ^{c}	75.510	< 0.001
All shoots (µg/plant)	118.4 (± 34.6)	27.4 (± 2.6)	18.3 (± 2.7)	0.180	0.837
Calamagrostis (µg/plant)	118.4 (± 34.6)	44.6 (± 19.2)	29.3 (± 12.8)	1.040	0.367
Epilobium (µg/plant)	0.0 (± 0.0) ^{a}	20.6 (± 2.4) ^{b}	11.2 (± 3.1) ^{c}	20.860	< 0.001
Populus (µg/plant)	0.0 (± 0.0) ^{a}	37.9 (± 9.4) ^{b}	15.3 (± 3.6) ^{c}	10.743	< 0.001
All roots (µg/plant)	450.6 (± 171.1)	34.9 (± 14.0)	29.2 (± 12.8)	0.993	0.384
root : shoot	2.4 (± 0.9)	1.2 (± 0.3)	1.4 (± 0.5)	1.159	0.329

Table 4.4: Summary of soluble C and N values of mineral soil showing the effect of *M. s. scutellatus* frass after 180 days of plant growth. Values are means (± 1 SE) for n = 10 replicates. Different lower case letters indicate significant differences (Tukey's HSD; $p < 0.05$) for each parameter.

Parameter	Germination Control	- Frass	+ Frass	$F_{2,27}$	p
Total C (µg/g-soil)	1.12 (± 0.17)	1.03 (± 0.14)	1.43 (± 0.27)	1.064	0.359
Total N (µg/g-soil)	0.24 (± 0.03) ^{ab}	0.30 (± 0.02) ^{a}	0.15 (± 0.08) ^{b}	7.258	0.003
Organic - N (µg/g-soil)	0.07 (± 0.02) ^{ab}	0.04 (± 0.01) ^{a}	0.11 (± 0.02) ^{b}	4.366	0.023
NH_4^+ (µg/g-soil)	0.04 (± 0.01)	0.05 (± 0.01)	0.03 (± 0.01)	0.999	0.381
NO_3^- (µg/g-soil)	0.13 (± 0.04) ^{a}	0.21 (± 0.03) ^{a}	0.01 (± 0.01) ^{b}	15.138	< 0.001

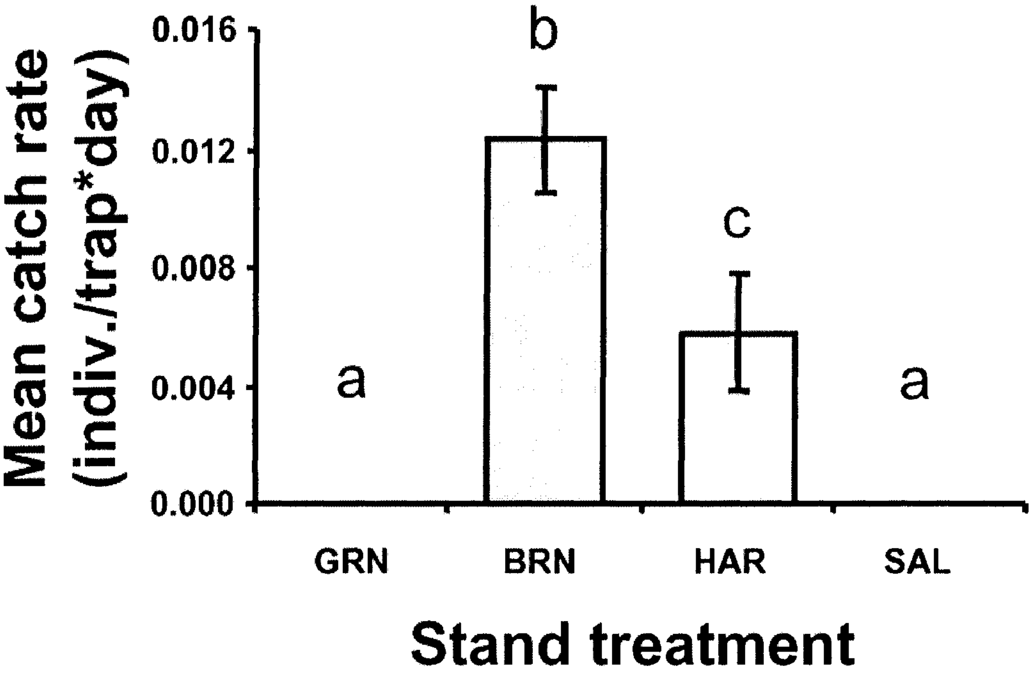

Figure 4.1: Standardized mean catch rate of adult *Monochamus s. scutellatus* (Say) across the four stand treatments (GRN = green, control; BRN = burned; HAR = harvested; SAL = salvage logged). Different lower case letters indicate significant differences between stand treatments (Tukey's HSD, $p < 0.05$). Bars represent ± 1SE for $n = 6$ sites.

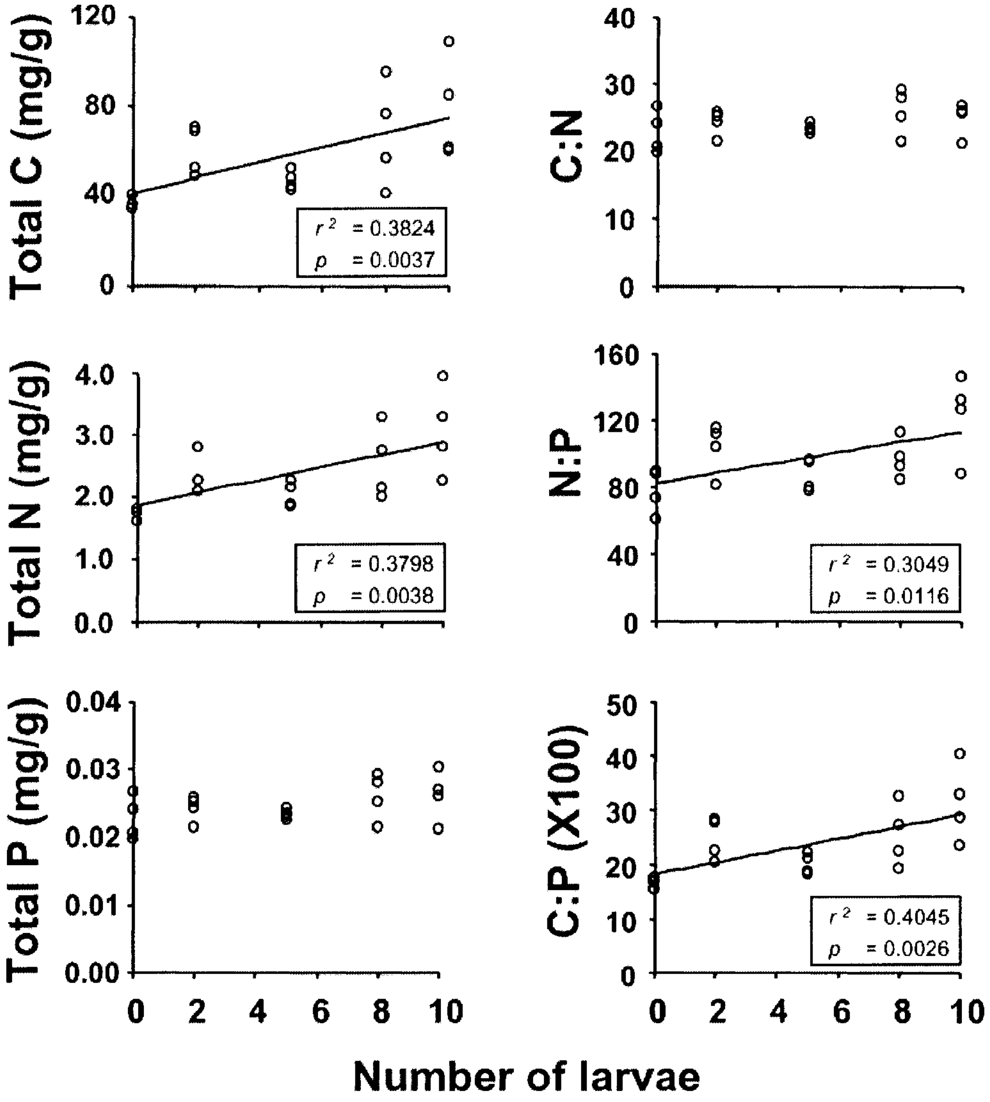

Figure 4.2: Summary of mesocosm experiment results showing the effect of varying larval *M. s. scutellatus* abundance on nutrient parameters in the top 0-3 cm of mineral soil. Trend lines indicate significant relationships (linear regression).

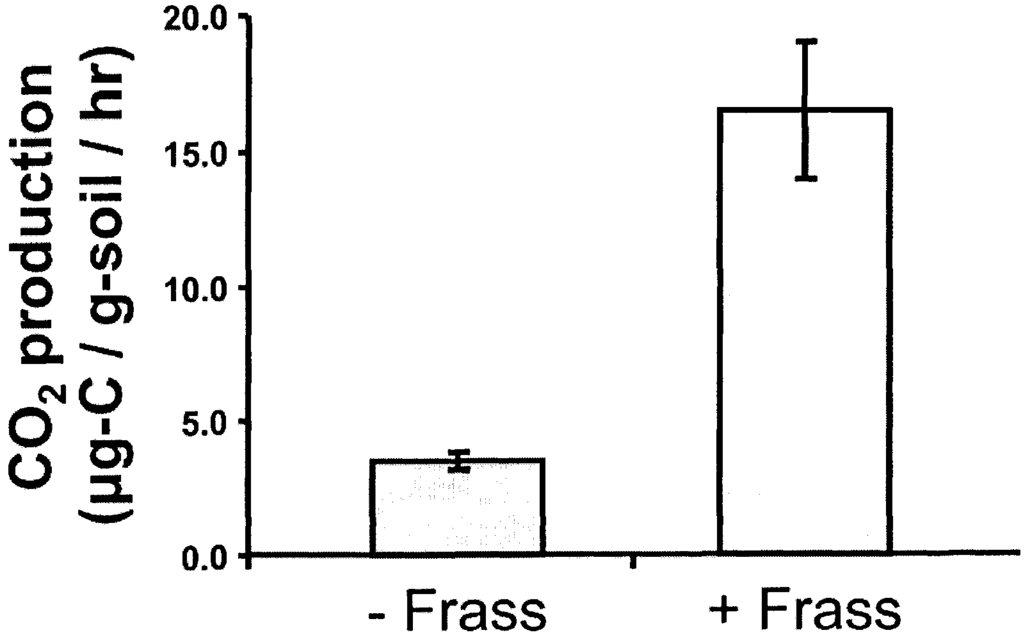

Figure 4.3: Microbial activity, as measured by microbial CO_2 production, in samples with and without the addition of *M.* s. *scutellatus* frass. Bars are means ± 1 SE for *n* = 5 samples of mineral soil.

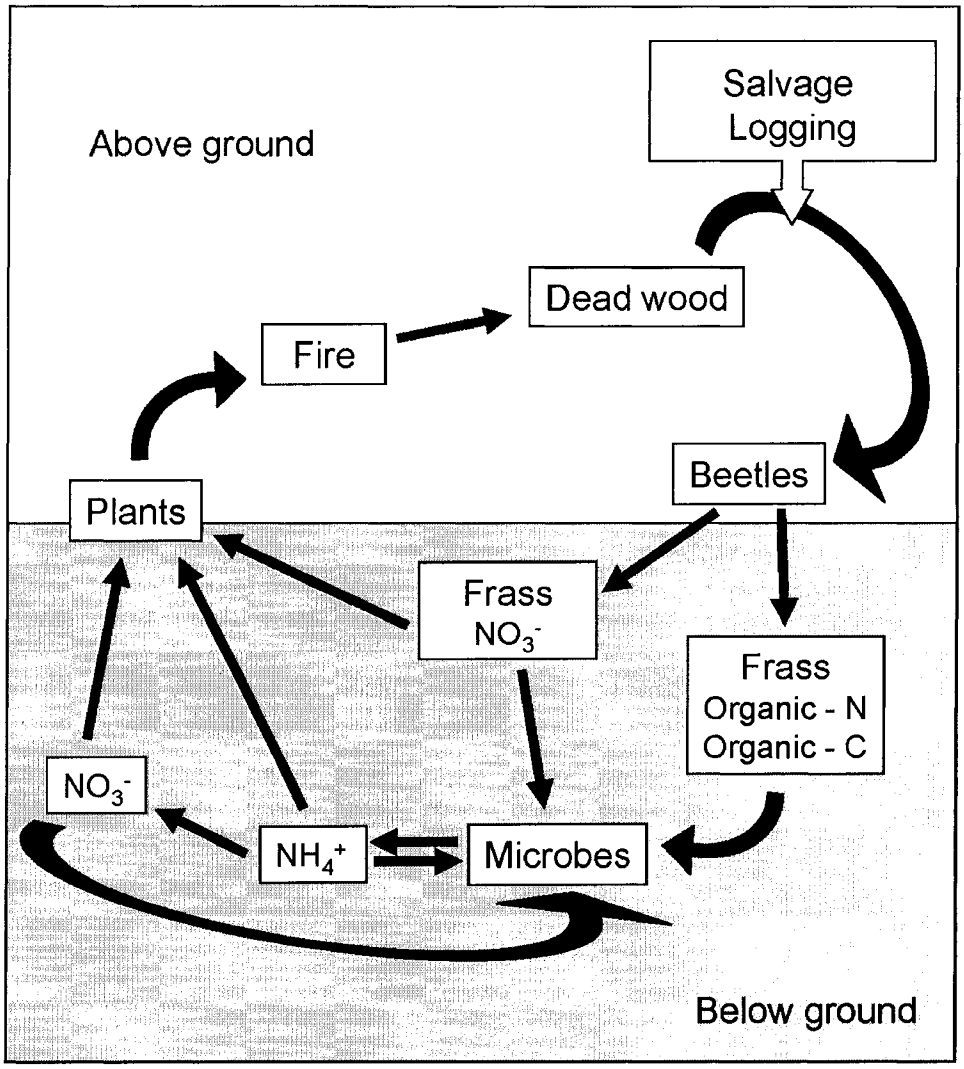

Figure 4.4: A conceptual model illustrating the ecological linkages between saproxylic beetles and nutrient cycling in forest ecosystems. Postfire salvage logging (top right) may upset this pathway by severing the link between dead wood and saproxylic beetles in forests recovering from wildfire.

CHAPTER 5

General Discussion

5.1 Synthesis

Evidence presented in each chapter of this dissertation supports the thesis that boreal mixed-wood beetle assemblages can be used effectively to illustrate impacts of multiple ecosystem disturbances on biodiversity and ecological function. Chapter 2 examined responses of a single beetle family (Carabidae) to the individual and combined effects of wildfire, forest harvesting and herbicide use. The scope was broadened in chapter 3 to include responses of 39 saproxylic beetle families belonging to various trophic groups and compared the effects of postfire salvage logging with those of either wildfire or harvesting alone. The link to ecological function was made in chapter 4, which examined the response of a single wood-boring species to postfire salvage logging and provided a detailed examination of its ecological role in the process of woody debris decomposition in burned forests. Here, I briefly synthesize the key findings and conclusions of each of these chapters and place them in the context of sustainable boreal forest management.

In chapter 2, ground beetle responses to wildfire, forest harvesting, and herbicide use, either alone or in combination, were species-specific and highly variable. Individual species responses to these disturbances were positive, negative or neutral, but were linked to changes in several habitat parameters such as the amount of exposed bare ground associated with each disturbance. Of all of the disturbances investigated, wildfire had the strongest effect on the ground beetle assemblage. However, when forestry-related disturbances were combined with wildfire, ground beetle compositional diversity was reduced to a greater extent than by single disturbances. This finding led to the prediction that increasing industrial forestry in the boreal forest has significant potential to simplify ground beetle assemblages when placed on a backdrop of natural disturbances like wildfire.

In chapter 3, saproxylic beetle responses to the combined effects of wildfire and forest harvesting were even more pronounced. Postfire salvage logging reduced saproxylic beetle species richness and altered species composition to a greater extent than either wildfire or harvesting alone. A more detailed examination of the responses of several different trophic groups showed that changes in the quantity and quality of woody debris associated with each disturbance impacted the overall trophic structure of the saproxylic beetle assemblage. In particular, wood- and bark-boring species were found to be especially sensitive to the effects of postfire salvage logging, suggesting that this trophic group may be of particular conservation concern under scenarios of continued economic emphasis on postfire salvage logging.

Detailed experimental work presented in chapter 4 examined the relationship between the abundance of one common wood-boring, saproxylic species, *Monochamus s. scutellatus* (Say) and soil nutrient dynamics. A combination of field and laboratory experiments demonstrated that feeding activity of *M. s. scutellatus* larvae on burned white spruce trees was linked to changes in soil microbial activity and nutrient concentrations. A follow-up experiment illustrated that such changes in nutrient concentrations affected the growth rate of common, early post-fire successional plants. In addition, survey data indicated that populations of this species could be severely impacted by postfire salvage logging due to the removal of larvae from burned sites in salvaged stems. Thus, by negatively affecting populations of *M. s. scutellatus* in burned forests, postfire salvage logging may impact nutrient cycling and successional trajectories in stands recovering from wildfire.

5.2 Recommendations for sustainable forest managment

Taken together, the results of all of these studies have several important implications for biodiversity conservation and sustainable forest management. While many studies have examined the effects of single disturbances on biodiversity (*e.g.*, Hunter 1999; Stelfox 1995), there is a growing awareness that independent consideration of disturbances may be insufficient from a sustainable forest management perspective (Lindenmayer and Noss, 2006). Today, forest ecosystems face multiple, often simultaneous, natural and anthropogenic environmental stressors. Disturbance regimes in most forest ecosystems now include environmental stress associated with increasing natural resource extraction (*e.g.*, timber, natural gas, oil, minerals, *etc.*) (Kennedy 2002; Schneider 2002), pollution (Perry 1994) and global climate change (Flannigan *et al.*, 1998; Li *et al.* 2000; Overpeck *et al.*, 1990). Thus, forest management models based on emulating natural disturbances like wildfire (Attiwill 1994; Hunter 1993) may be overly simplistic and fail dramatically in application on many landscapes.

Increasingly, guidelines for sustainable forest management aimed at biodiversity conservation may well be directed toward initiatives that avoid compounding disturbances whenever possible. However, for some practices like postfire salvage logging, the effects of combining multiple disturbances on the same sites are unavoidable. In such cases, increased understanding of the cumulative ecological consequences is needed to inform forest management decisions and policy. At present, there is considerable debate over the ecological consequences of postfire salvage logging (*e.g.,* see Stokstad 2006), suggesting that studies like the one presented here may provide useful results that can assist policy development.

Current postfire forest management policies in Canada (and elsewhere) appear to favour economic interests over ecological forest values (Schmeigelow *et al.* 2006; Lindenmayer *et al.* 2004). In Alberta, for example, unburned residual areas within the perimeter of a wildfire ("fire-skips") are treated as burned if they are < 4 ha in size (Alberta Sustainable Resource Development, 2007) and can be harvested at a reduced fee (Alberta Forests Act R.S.A. 2000 AR 182/95, s. 6). From an economic perspective, such "fire-skips" may be extremely valuable because they contain very large trees, commonly reflecting a history of being skipped (*e.g.*, old-growth areas) or increased moisture conditions (*e.g.*, riparian zones). However, such "fire-skips" may also be ecologically valuable as refuges for biodiversity (Ghandi *et al.* 2004), which may help to repopulate burned areas. My data and those of many other studies (*e.g.*, Buddle *et al.* 2000; Hobson and Schieck 1999) show that the biota of burned and unburned areas are distinct at least initially. Thus, management prescriptions that fail to account for these intial differences will probably fail to meet biodiversity conservation targets, especially in relation to species characteristic of early succession.

Perhaps even more disconcerting is that fact that land tenure holders in Alberta and elsewhere face a threat of timber quota reductions if they do not comply with special management plans to salvage forests after a natural disturbance (Alberta Forests Act R.S.A. 2000 AR 60/73, s. 153). Such a policy will most likely favour increased salvage logging in Alberta, a situation already apparent in Québec (Nappi *et al.* 2004). Data presented here for beetles, as well as data for birds (*e.g.*, Hutto 1995; Morissette *et al.* 2001) and plants (Donato *et al.* 2006; Fraser *et al.* 2004; Greene *et al.* 2006) suggest that regulations involving compliance penalties for not salvaging should be abolished. Moreover, data presented here and elsewhere suggest that leaving portions of burned, merchantable stands unsalvaged (Macdonald 2007) or even delaying salvage operations for a few years (Nappi *et al.* 2004) may offer reasonable, ecologically sensitive, alternatives to rapid, clear-cut salvage logging. As of January 11th, 2007, guidelines in Alberta recommend retention of 10-25% of merchantable burned timber (Alberta Sustainable Resource Development, 2007). While this is a step in the right direction, many questions remain unanswered about whether this level of retention will be sufficient to sustain biodiversity and ecological integrity of forests recovering from wildfire. Clearly, if long-term goals for sustainable forest management and biodiversity conservation are to be attained in the boreal forest, a non-trivial balance must be struck between economic and ecological considerations.

As a group, beetles are arguably one of the most significant elements of biodiversity (Chapter 1) and cumulative effects of disturbances I have reported for beetles may be indicative of the response of boreal forest biodiversity as a whole. The ecological consequences of biodiversity loss are difficult to predict, but there is a growing consensus that such losses may impact ecosystem-level processes (Naeem *et al.* 1999; Naeem *et al.* 1994). Research presented here suggests that combining wildfire and forestry-related disturbances in boreal ecosystems may not only impact beetle diversity, but has significant potential to also impact decomposition and nutrient cycling processes. These effects, in turn, may well affect successional pathways and have broad effects on regeneration Thus, the ecological integrity of these ecosystems may depend, at least in part, on organisms we consider to be either economic "pests" or of no economic significance (Chapter 4).

5.3 Recommendations for future research

Aside from a reasonable desire to probe the generality of my ideas by increasing the spatial and temporal scope of the studies presented here, several other avenues for future research may prove promising. From a sustainable forest management perspective, more work needs to be done to adequately assess the ecological value of dead wood in boreal forest stands. In burned forests, more work is also required to determine whether or not to delay salvage operations as well as to develop clear guidelines about the quality and quantity of dead wood residuals (and spatial arrangement) required to sustain beetle diversity.

I have focused my work entirely on beetle assemblages inhabiting the forest floor (Chapter 2) and those associated with dead wood (Chapters 3 and 4). While this taxonomic focus has provided some insight into the cumulative effects of multiple disturbances on biodiversity, additional insight would no doubt be gained by broadening this scope to include a greater portion of the biota. Chapter 2, for example focused entirely on ground beetles (Carabidae) in order to provide a detailed analysis of both community and species-level responses. A follow up study that included a larger portion of the epigaeic fauna (*e.g.*, Staphylinidae and Araneae) may provide valuable additional insight about the impacts of disturbance on the forest floor biota. Unfortunately, although such a study would be more complete, it is unlikely that it would support single prescriptions with universal application (*e.g.*, see Buddle *et al.* 2006).

Even within the beetle groups I studied, many species were necessarily excluded due to taxonomic "impediments" (Chapter 1) and logistic constraints. For example, the staphylinid subfamily Aleocharinae (696 specimens) had to be excluded from further analysis of the saproxylic fauna (Chapter 3) because the specimens could not be reliably identified to species. Such impediments no-doubt hinder understanding of saproxylic beetle assemblages and are at least partially attributable to the fact that saproxylic beetle research in Canada is still in its infancy (Langor *et al.* 2005). However, my research builds on earlier Canadian work (*e.g.*, Jacobs *et al.* 2006; Hammond *et al.* 2004; Saint-Germain *et al.* 2004) and each new study offers the promise of increased taxonomic resolution and a more complete understanding of the Canadian saproxylic beetle fauna.

In addition to taxonomic advances, more work is needed to better understand the life history and ecology of beetles and other components of boreal forest biodiversity. Chapter 4 demonstrated a link between *Monochamus s. scutellatus* and decomposition in burned forests, which raises a wide range of questions about other ecological relationships and other species. For example, how might other pyrophilous, wood-boring beetle species (*e.g.*, *Melanophila acuminata*, Buprestidae) (Evans, 1971), which were also negatively affected by postfire salvage logging (Chapter 3), be involved in woody debris decomposition process in burned forests? Similarly, what interactions exist between pyrophilous beetles and cellulolytic fungi associated with burned woody debris (Lumley *et al.* 2000)? More importantly, how might such interactions be impacted by practices like postfire salvage logging? Despite many unanswered questions, the work presented here illustrates that burned trees are ecologically valuable resources that provide the basic requirements for many natural ecosystem processes involving specific biotic elements. However, in terms of understanding the depth of ecological relationships of the boreal mixed-wood beetle fauna and decomposition processes in burned forests, I have barely scratched the surface.

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