Influence of variable retention and deadwood characteristics on saproxylic beetles in boreal white spruce stands

by

Seung-Il Lee

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University of Alberta

Abstract

Retention forestry aims to maintain a significant level of continuity in forest structure, composition and complexity so as to support conservation and recovery of biodiversity and ecological function on managed landscapes; however, the amount and distribution of retention that best meets conservation goals remains unclear. The problem of biodiversity loss through direct effects of forestry seems most demonstrably acute for the saproxylic biota (i.e., species associated with deadwood). In this dissertation, I sought to understand how deadwood characteristics and variable retention harvest influence the composition and diversity of saproxylic beetle assemblages in boreal white spruce (*Picea glauca*) stands on the western boreal plain of Canada. I worked in both the EMEND (Ecosystem Management Emulating Natural Disturbance) experiment and in nearby industrial harvest blocks, located in northwestern Alberta, Canada. My general thesis is that forest management can be adjusted to be more sensitive to saproxylic biodiversity, and particularly, that mixing dispersed and aggregated retention on cut-blocks leads to better outcomes than traditional clear-cutting.

Overall, 75 719 saproxylic beetles representing 377 species in 44 families were collected using window traps, emergence traps and rearing drums. Most were identified to species and these records constitute the database for this dissertation. I have demonstrated that saproxylic beetle assemblage structure changes progressively over the decompositional stages of white spruce deadwood, emphasizing that retention of the entire range of decay classes is necessary to conserve the associated saproxylic beetle fauna on post-harvest landscapes. Beetle assemblages also responded to retention patch size and to different levels of dispersed retention surrounding retention patches. Although small retention patches maintained or attracted representative populations of ‘initial colonizers’ 10 years post-harvest, beetle assemblages in patches ≤ 2.93 ha were strongly influenced by edge effects and less similar to those in intact forests than in larger patches. I also showed that relatively small retention patches (0.20 ha and 0.46 ha) surrounded by higher levels of dispersed retention (i.e., 20% and 50%) provided conditions sufficient to retain assemblages of early colonizing species that are broadly similar to those in intact forests. Thus, my work underscores that using a combination of aggregated and dispersed retention on harvested blocks will better conserve saproxylic beetle species than leaving patches alone. This dissertation contributes to a more complete understanding of how retaining living green trees at harvest can be strategically adjusted to achieve better results for saproxylic beetles, a bio-diverse functional group that has been negatively affected by traditional forestry.

Preface

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CHAPTER 1

Introduction

1.1. Retention forestry

1.1.1. Definition and goals of retention forestry

Retention forestry was initially proposed and applied on a commercial scale in the Pacific Northwest of the USA and Canada, and has been subsequently developed as a new approach to conserve biodiversity on managed forest landscapes in North and South America, Australia and Fennoscandian countries (Franklin et al., 1997; Lindenmayer and Franklin, 2002; Aubry et al., 2009; Work et al., 2010; Baker, 2011; Baker and Read, 2011; Lencinas et al., 2011; Gustafsson et al., 2012). What I will refer to as 'retention forestry' in this dissertation has been variously termed 'variable retention', 'green tree retention', 'tree retention', 'retention harvesting', and 'the retention approach' (Franklin et al., 1997; Spence, 2001; Aubry et al., 2009; Gustafsson et al., 2012; Lindenmayer et al., 2012; Pinzon et al., 2012; Simonsson et al., 2015). Although there may be subtle differences in emphasis, these terms all belong under the common umbrella of retention forestry.

According to Gustafsson et al. (2012), 'retention forestry' is defined as "an approach to forest management based on the long-term retention of structures and organisms, such as live and dead trees and small areas of intact forest, at the time of harvest". Retention forestry aims strategically to achieve a significant level of continuity in forest structure, composition, and complexity that maintains both biodiversity and ecological functions in a landscape context (Gustafsson et al., 2012; Lindenmayer et al., 2012). Inspired by natural disturbances such as wild fire, those practicing retention forestry also frequently attempt to emulate natural disturbance patterns in harvest designs, hoping to conserve natural processes in shaping spatio-temporally heterogeneous forests (Lindenmayer et al., 2012; Gustafsson et al., 2012).

The most important thing that distinguishes retention forestry from harvesting approaches, such as uneven-aged selection management or even-aged shelterwood and seed tree systems, is that retained forest structures are not removed in future harvesting operations, contributing to long-term continuity of structures and forest organisms (Spence, 2001; Lindenmayer et al., 2012). Unlike conventional forestry that has focused on timber production and rapid regeneration, retention forestry attempts to strike a balance between timber production and biodiversity conservation (Lindenmayer et al., 2012; Fedrowitz et al., 2014; Simonsson et al., 2015).

1.1.2. Forest management emulating natural disturbance regimes

Although using natural disturbance regimes as models was proposed for forest management more than a century ago (Lindenmayer et al., 2012), application of the modern natural disturbance-based approach really began with Hunter's (1993) seminal paper. This paper provided clear motivation for change centered on biodiversity conservation and using emulation of natural disturbance patterns as the principal guidance for improving forest management over conventional clear-cutting.

The natural disturbance emulation (NDE) approach to forest management is based on an understanding that forest organisms have evolved with natural disturbances, and thus posits that the forest biota and important ecosystem functions can be maintained by emulating natural disturbance regimes (Hunter, 1993; Lindenmayer et al., 2012). Under this approach, patches of living trees including microhabitats such as standing and downed deadwood are retained on harvested landscapes specifically to leave legacy structures similar to those left by natural disturbance (e.g., unburned fire-skips) and that promote recovery of biodiversity (Lindenmayer and Franklin, 2002; Lindenmayer et al., 2012; Pinzon et al., 2012). The amounts and spatial patterns of residual trees may vary according to management goals (Gustafsson et al., 2012; Fedrowitz et al., 2014). In the absence of data about spatial effects some advocate matching these spatial patterns rather blindly to natural patterns (Baldwin et al., 2004).

Despite the advantages of the NDE model, there are significant differences between natural disturbance and forest management based on NDE. Natural disturbances leave: 1) various sizes and shapes of unburned fire-skips (Andison, 2004); 2) huge amounts of deadwood around unburned tree patches (Hunter, 1993; Schneider, 2002); 3) trees with various characteristics ranging from damaged to dying and dead, depending on intensities of fire or insect outbreak (Hunter, 1999); and 4) various sizes and shapes of disturbed areas, contributing to the structure of complex forest landscapes (Bergeron et al., 2002). Under the NDE approach, however, harvest planners leave only relatively small numbers of live and dead trees in the harvested matrix surrounding retention patches (Hunter, 1993; Schneider, 2002). Therefore, in addition to other questions (e.g., the reliability of history in forecasting aspects of a changing world), the NDE model may not include all important processes intrinsic to natural disturbances, and additional tests of the natural disturbance hypothesis are required (Pinzon et al., 2012).

1.1.3. Different roles of aggregated and dispersed retention

Residual trees may be retained in aggregations or as more-or-less singularly dispersed elements in large harvested areas, and both retention patterns have different advantages and disadvantages. Aggregated retention, also known as clumped retention and group retention, refers to groups of live trees preserved at the time of harvest (Franklin et al., 1997; Lindenmayer and Franklin, 2002) (Fig. 1.1a). Aggregated retention contributes to long-term persistence of live trees, interior forest species, and preservation in pockets of microhabitats such as undisturbed soils and understory plants (Franklin et al., 1997; Baker, 2011; Pinzon et al., 2012). In contrast, dispersed retention leaves individual trees distributed randomly or more-or-less uniformly throughout a harvested area (Franklin et al., 1997) (Fig. 1.1b). It better conserves connectivity of belowground biota such as ectomycorrhizal fungi and distribution of deadwood over a cut block, and furthermore contributes to maintenance of edge-preferring species, and forest aesthetics that appeal to public perception (Lindenmayer and Franklin, 2002; Baker and Read, 2011). However, dispersed retention generally fails to conserve interior forest species (Pinzon et al., 2012). For instance, Halaj et al. (2008) concluded that even 40% dispersed retention does not conserve forest-dependent invertebrate predators, and clearly high levels of retention (i.e., > 50% dispersed retention) are required to preserve beetle assemblages that represent late-successional stages (Work et al. 2010).

Relationships between sizes of aggregated retention and biodiversity have shown that relatively small patches (≤ 1 ha) are generally insufficient to conserve whole assemblages of epigaeic invertebrates (Matveinen-Huju et al., 2006; Aubry et al., 2009). Several studies have concluded that even 3 ha patches were ineffective to conserve carabid beetles and spiders in coniferous forests (Halme and Niemelä, 1993; Pearce et al., 2005).

Structural persistence of aggregated retention is also a matter of significant interest for determining how benefits vary with patch size. It is known, for example, that small aggregated retention patches (≤ 1 ha) are susceptible to windthrow (Jönsson et al., 2007; Aubry et al., 2009; Urgenson et al., 2013). In Sweden, for example, a single 1 ha Norway spruce (*Picea abies* (L.) Karst.) retention patch surrounded by 41 ha clear-cut harvest block has lost about a half of trees within 18 years (Jönsson et al., 2007). Patches that are too small to persist until the regenerating forests provide habitats for harvest-sensitive species hold little long-term conservation value.

In an effort to maximize positive effects of both aggregated and dispersed retention on biodiversity in the face of uncertainty, some forestry companies are implementing a combination of both aggregated and dispersed retention practices in an adaptive management framework (Fig. 1.1c). In Alberta, Canada, for example Daishowa-Marubeni International applies such a mix on all harvested areas of its Forest Management Agreement (FMA) area. In fact, balancing these tactics in an overall strategy appears to be the main approach to delivering so-called new or ‘green’ forestry in western Canada (Work et al. 2003).

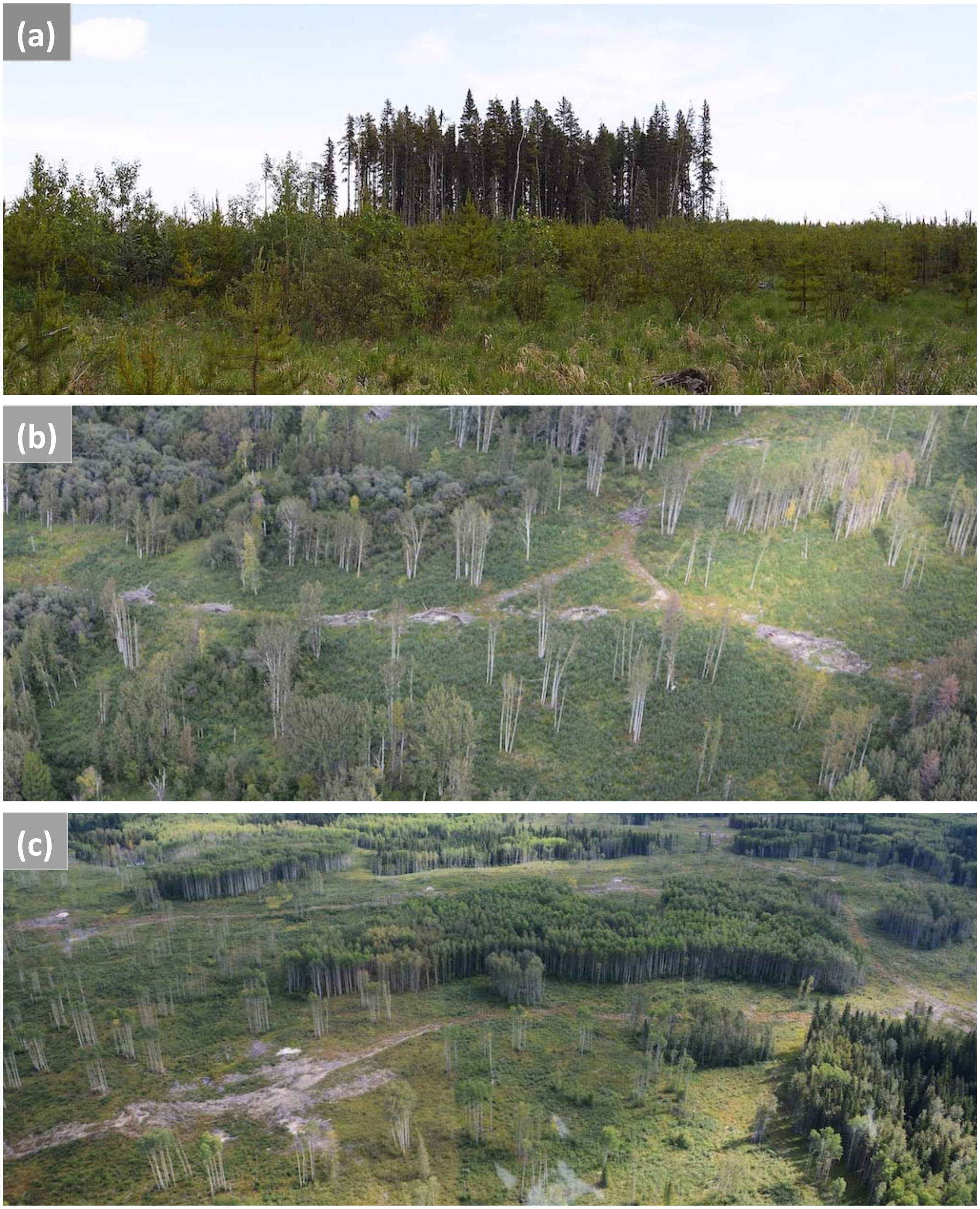


Fig. 1.1. Different types of retention: (a) Aggregated retention, (b) Dispersed retention, and (c) Combination of aggregated and dispersed retention. Courtesy of ground and aerial photos: Seung-Il Lee.

1.2. Ecosystem Management Emulating Natural Disturbance (EMEND) experiment

The field work in this dissertation was conducted on the site of the Ecosystem Management Emulating Natural Disturbance (EMEND) experiment (Fig. 1.2), or on a nearby landscape harvested to retention prescriptions. The EMEND experiment is among the earliest and most extensive attempts to explore multiple effects of stand cover type, disturbance type and tree retention level on a wide variety of forest response variables using a rigorous experimental design [see Spence et al. (1999), Work et al. (2010) and www.emendproject.org for details].

The EMEND design is factorial, crossing cover type with disturbance treatments involving either harvest or prescribed burns and uncut 'control' compartments. A range of retention treatments were applied to c. 10 ha compartments in each of four different stand types (i.e., deciduous dominated, deciduous with spruce understory, mixed, and conifer dominated stands) during the winter of 1998-1999 on the EMEND landscape. Disturbance treatments included clear-cuts (2% retention), retention prescriptions (10%, 20%, 50%, 75% dispersed retention) and two burn treatments (whole compartment burns, slash burn on 10% retention), and unharvested controls. The design was fully factorial with three replications planned for each treatment combination. Unexpected difficulty in delivering the whole compartment burns has delayed full establishment of the experiment, and to adjust for this, the 'slash burns' were developed and applied several years after the harvest treatments to provide some sort of commonly delivered fire treatment. Given time, differences in initiation date will become less important to interpretation of data, but mainly because of such difficulties at present, this work was restricted to the harvest treatments, using un-cut ‘control’ compartments as targets for forest recovery after harvest. EMEND response variables include biodiversity, soil structure, nutrient cycling, forest productivity, ecosystem function, economic viability and public perceptions.

An interesting and unique aspect of the EMEND design is that two sizes of aggregated retention ellipses (0.20 ha and 0.46 ha) were embedded inside each 10 ha compartment. Thus, retention patches of both sizes are surrounded by different dispersed retention prescriptions, including the 2% retention typical of standard Canadian ‘clear-cuts’. During project development it was thought that these retention patches would provide a continuous supply of coarse woody debris that will influence recovery in the regenerating stands that surround them. To date Pinzon et al. (2012) is the only study in the 17-year history of EMEND that has attempted to understand responses of biota (spiders) in retention patches surrounded by varying levels of dispersed retention prescriptions. In this dissertation, especially in Chapters 4 and 5, I focused on the response of saproxylic beetles to aggregated retention patches surrounded by clear-cuts, and 20% and 50% dispersed retention in both white spruce and mixedwood stands.

The EMEND research site is located in northwestern Alberta, Canada (56°46′N, 118°22′W). The landscape is a rolling catena with elevations ranging from 677 m to 880 m above sea level. Climate in this region is characterized by cold winters and moderately warm summers. Mean temperatures in 2010 were -14.9 °C for January and 17.1 °C for July, and the total annual precipitation was 232.0 mm (Environment Canada 2010). Soils at the EMEND site are fine-textured, formed predominantly on glacio-lacustrine deposits.

The majority of soils are Luvisolic, followed in order of abundance by Brunisoles, Gleysoles, and Solonetzic soils (Kishchuk, 2004).

The EMEND forests are dominated by two deciduous tree species, trembling aspen (*Populus tremuloides* Michaux) and balsam poplar (*Populus balsamifera* L.) and one coniferous species, white spruce (*Picea glauca* (Moench) Voss), but also include in lesser abundance, lodgepole pine (*Pinus contorta* Dougl. ex Loud.), black spruce (*Picea mariana* (Mill.) B.S.P.), balsam fir (*Abies balsamea* (L.) Mill.), tamarack (*Larix laricina* (Du Roi) K. Koch) and paper birch (*Betula papyrifera* Marsh.). The forest understories at EMEND are dominated by *Viburnum edule* (Michx.) Raf., *Rosa acicularis* Lindl., *Sherpherdia canadensis* (L.) Nutt., *Alnus crispa* (Ait.) Purch, *A. tenufolia* Nutt., and *Ledum groenlandicum* Oeder. *Salix* spp. and *Alnus* spp. are also common in wet areas of the EMEND landscape (Bergeron et al., 2011). The origin of the present forest stands is in a mosaic of wildfires (Bergeron 2012).

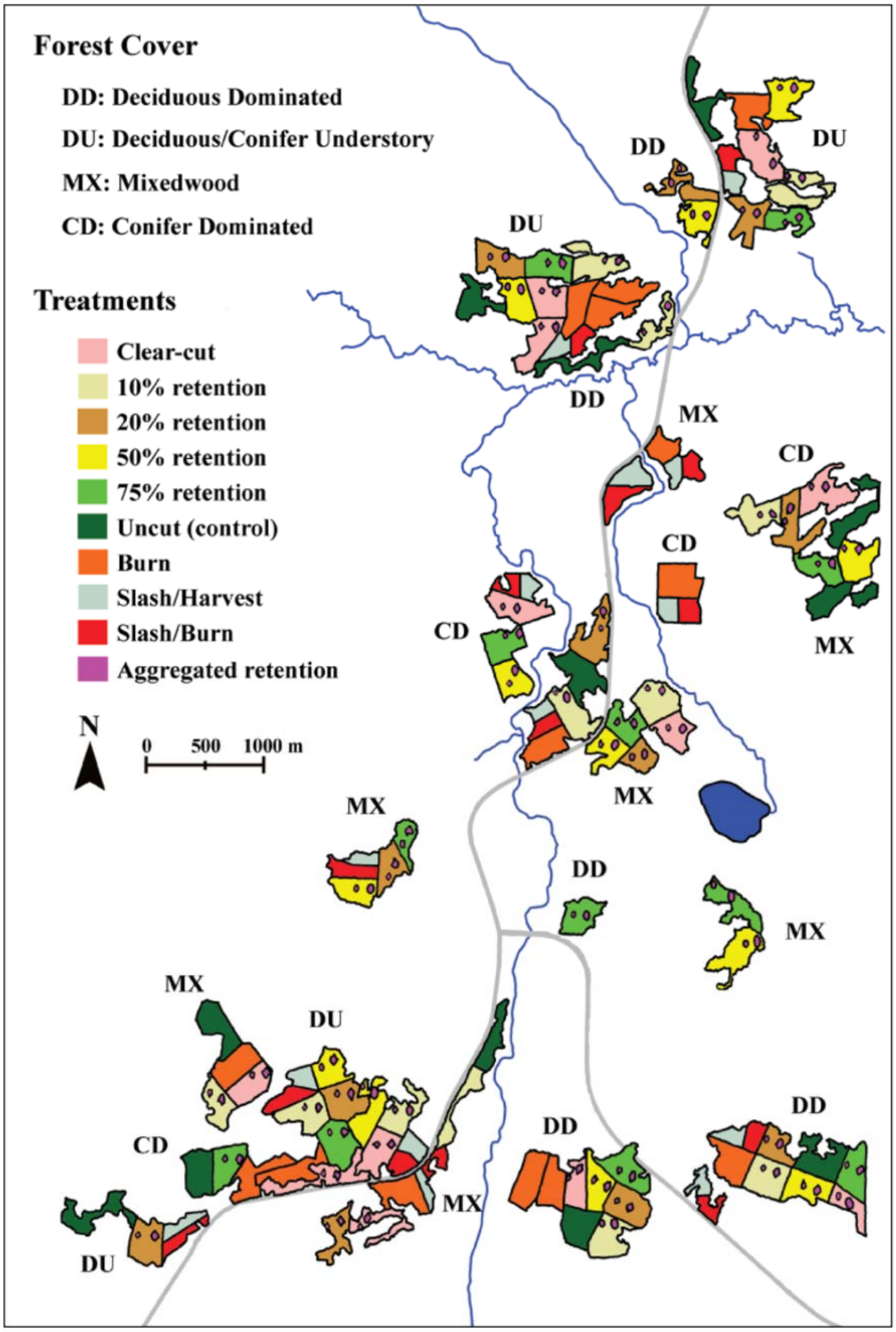


Fig. 1.2. The EMEND map showing different forest cover types and treatments. Note that each 10-ha harvesting treatment has two sizes (0.20 and 0.46 ha) of aggregated retention patches. The map is adapted from Pinzon (2011).

1.3. Coarse woody debris and decay classification system

Deadwood, especially in the form of coarse woody debris (CWD), is an important functional component of forest ecosystems, and also provides substrate and habitat for the deadwood-dependent biota (Siitonen, 2001; Grove, 2002; Stokland et al., 2012). CWD, for example, holds moistures, provides a seedbed for plant germination, slowly releases nutrients, reduces soil erosion, and serves as food, habitat and shelter for many forest organisms (Harmon et al. 1986; Stevens 1997). Furthermore, the different decomposition stages of CWD promote biodiversity by providing a variety of microhabitats required for many forest arthropods (Esseen et al., 1997). Therefore, deadwood management is now widely accepted as an essential component for sustainable forest management (Franklin et al., 1987; Hagan and Grove, 1999; Lindenmayer and Franklin, 2002; Jacobs et al., 2007a; Hjältén et al., 2012).

It is known that the two main structurally different types of CWD (i.e., logs and snags) harbor quite different assemblages of saproxylic biota, although relationships among species richness, composition and CWD types vary with study organism, tree species and decomposition stage of deadwood (Franc, 2007; Langor et al. 2008; Bouget et al., 2012; Wood, 2012). For example, Franc (2007) concluded that downed deadwood of European oaks (*Quercus* spp.) supports more species of saproxylic beetles than do standing snags. Similarly, Ulyshen and Hanula (2009) concluded that logs have generally higher species richness of saproxylic beetles in the mixedwood forests of South Carolina, USA. However, in contrast, the work of Bouget et al. (2012) suggests that saproxylic beetles in European oak snags have higher species richness and abundance than in logs.

We have come to understand that forest CWD of either type is not a uniform entity, and to facilitate study, various CWD decay classification systems have been proposed to accommodate different research objectives (Maser et al., 1979; Sollins, 1982; Hofgaard, 1993; Enrong at al., 2006; Wood, 2012). For instance, Hammond et al. (2004) used a three-class system to understand saproxylic beetle succession in trembling aspen CWD. Hale and Pastor (1998) used a four-class system to study nitrogen dynamics in red oak (*Quercus rubra* L.) and sugar maple (*Acer saccharum* Marsh.) logs. A five-class system was used to study fungal populations (Fogel et al., 1973) and to understand decomposition and productivity (Sollins, 1982). Wood (2012) proposed six- and four-class systems for aspen logs and snags, respectively, to understand relationships between saproxylic beetles and substrate qualities. Also, Lee et al. (2014) suggested a six-class system for white spruce logs to characterize saproxylic beetle assemblages using different decompositional stages. Cobb et al. (2011) used a seven-class system to assess relationships among post-fire stand treatments, CWD characteristics, and beetle species composition in white spruce deadwood. Even eight-class systems have been used to describe plant succession (McCullough, 1948; Hofgaard, 1993) and to measure the quantity and quality of deadwood (Zielonka, 2006). Thus, decay classification systems vary to accommodate different research objectives as well as differences in decompositional characteristics of different tree species and types (Harmon et al., 2006). I use a simplified CWD classification system to facilitate pursuit of research objectives in each of the following data-based chapters.

1.4. Ecosystem roles of saproxylic beetles in deadwood

Saproxylic organisms are defined as those that depend on wounded or dying woody plants, or on deadwood, during some parts of their life cycle (Speight, 1989; Alexander, 2008; Langor et al., 2008; Stokland et al., 2012; Lee et al., 2014). The Greek words ‘sapros’ and ‘xylon’ means ‘decayed’ and ‘wood’, respectively. The term ‘saproxylic’ was first used by Dajoz (1966) to describe insects that live in decaying wood, although Silvestri (1913) had used the term ‘saproxylophiles’ earlier to describe deadwood-dependent invertebrates (Stokland et al., 2012).

In this dissertation, I have used the broad definition of ‘saproxylic’, suggested by Stokland et al. (2012): “any species that depends, during some part of its life cycle, upon wounded or decaying woody material from living, weakened, or dead trees”. Therefore, I have analyzed data about both obligatory and facultative saproxylic species, including many predatory species, such as ground beetles (Coleoptera: Carabidae) and rove beetles (Coleoptera: Staphylinidae), which feed on prey inhabiting deadwood. In fact, the difference between saproxylic and non-saproxylic species is somewhat vague and often arbitrary. Because decayed wood eventually becomes forest floor, many species that inhabit well-decayed deadwood also use forest floor as a habitat (Wood, 2012). For instance, Ferro et al. (2012b) showed that 30% of beetle species, including many that would undoubtedly be classified as saproxylic, occurred in both well-decayed angiosperm CWD and leaf litter.

Saproxylic organisms have received much attention because they are important components of functional and biological diversity, and provide important ecosystem services, food and medicine that are much appreciated by human beings (Siitonen, 2001;

Langor et al., 2008; Stokland et al., 2012; Bouget et al., 2014). Some polypore fungi, for example, display strong antimicrobial activity and humans have used them to control and prevent carcinogenesis and tumor metastasis (Zjawiony, 2004). Saproxylic organisms also serve as significant indicators of habitat loss and fragmentation in forest ecosystems (Siitonen, 2001; Langor et al., 2008; Hjältén et al., 2012). As study organisms, saproxylic beetles (order Coleoptera) have great advantages over other saproxylic groups because they are hyper-diverse, and relatively well-known taxonomy and ecology, making detailed species level analyses both interesting and possible (Jacobs et al., 2007a; Wood, 2012; Lee et al., 2014) (Fig. 1.3). Despite the importance and diversity of saproxylic beetles in forest ecosystems, little research has addressed associations of saproxylic beetles with deadwood succession, especially in North America. Moreover, even though negative impacts of intensive conventional forestry on saproxylic beetle diversity have been well established (Siitonen and Martikainen, 1994; Stokland et al., 2012), the long-term impacts of modern retention forestry are largely unknown.

In my work, each species was assigned to one of the eight following feeding guilds based on information in the literature (e.g., Klimaszewski et al., 2007; Dollin et al., 2008; Bishop et al., 2009; Wood, 2012; Lee et al., 2015): detritivores (DET, feeding on decomposing plant and animal tissues), mycetophages (MYC, feeding on fungi), myxomycophages (MYX, feeding on slime molds), omnivores (OMN, feeding on a variety of materials), phloeophages (PHL, feeding in phloem tissues), predators (PRE, feeding on live invertebrates), rhizophages (RHI, feeding on plant roots), and xylophages (XYL, feeding in xylem tissues). Species that I could not confidently place in one of the above guilds were assigned to the unknown (UNK) category of feeding guilds.

I followed the nomenclature, ‘Checklist of Beetles (Coleoptera) of Canada and Alaska’, using the most current genus and species names (Bousquet et al., 2013).

Fig. 1.3. Diverse saproxylic beetles found in the study areas: (a) Tenebrionidae: *Upis ceramboides* (Linnaeus), (b) Cerambycidae: *Xylotrechus undulatus* (Say), (c) Cerambycidae: *Rhagium inquisitor* (Linnaeus), (d) Lycidae: *Dictyoptera aurora* (Herbst), (e) Trogossitidae: *Peltis fraterna* (Randall), and (f) Pythidae: *Pytho seidlitzi* Blair. Courtesy of beetle photos: Seung-Il Lee.

1.5. Sampling methods

I used three sampling methods (i.e., window traps, emergence traps, and rearing drums) to collect saproxylic beetles in my studies, because a combination of sampling methods yields considerable understanding of a saproxylic fauna (Hammond, 1997; Alinvi et al., 2007; Wood, 2012). Below, I describe advantages and disadvantages of each method and give specific descriptions of trap installation procedures that I used.

Window traps or flight-intercept traps have been widely used for collecting saproxylic beetles because they yield large numbers of beetle species and individuals, and thus provide standardized and mostly non-zero samples that may be reliably replicated for statistical analysis. However, window traps do not give exact information about microhabitat selection because they do not specifically collect beetles that use CWD as a habitat (Siitonen, 1994; Hammond, 1997; Langor et al., 2008; Sverdrup-Thygeson and Birkemoe, 2009). Chapters 3 and 4 of this dissertation are based on data from window traps installed on both girdled trees and snags of white spruce. Window traps were transparent plexiglass panels (20 × 30 cm) with a cloth funnel attached along the bottom edge (Hammond, 1997). A 100 mL plastic cup was attached to the bottom of each funnel, containing approximately 30 mL of propylene glycol as preservative. The traps were placed perpendicularly on the boles of trees at breast height (ca. 130 cm) (Fig. 1.4a).

Emergence traps are a relatively new and non-destructive method for sampling saproxylic invertebrates that provides sound information about the habitats of species that emerge from the inside of the wood (Langor et al., 2008). However, this method frequently yields relatively low numbers of individuals (Alinvi et al., 2007; Wood, 2012), making statistical comparisons challenging. I used emergence traps to sample saproxylic beetles in Chapter 4, to overcome some shortcomings of window traps that were particularly relevant to that work. To install the kind of emergence trap that I used in the field, the selected piece of CWD was covered by 1.2 m high no-see-um mesh (0.6 mm × 0.6 mm), tied with wires 100 mm from the both end of mesh. I then applied glue on the wires to fill the space between the wire and bark to prevent beetle escape. A 300 mL plastic bottle (diameter of spout 25 mm) containing approximately 50 mL of propylene glycol was attached to the bottom of the mesh to sample beetles emerging from the bolt (Fig. 1.4b).

Rearing drums are another kind of emergence traps used when bolts can be removed from field sites and the study objectives and timing allow one to wait for beetles to complete larval development. I used rearing drums to study beetle colonization because this method provides exact information about saproxylic invertebrates that were actually living in a particular species of deadwood at the time that the piece of CWD was put into the drum (Langor et al., 2008; Wood, 2012; Lee et al., 2014). I cut bolts from field sites and transported them to the field laboratory to allow beetles to emerge over time inside the rearing drums. Some vagile species may escape during transport and preparation of bolts for rearing and so samples still may be somewhat incomplete, but this is among the best and most efficient techniques to sample the beetles in a piece of deadwood at a single point in time (Wood, 2012; Lee et al., 2014).

Rearing drums were used to sample obligatory saproxylic beetles for work reported in Chapters 2 and 5. Rearing drums used in this study were constructed from 121-L bins (diameter 60cm, height 91 cm) (Rubbermaid, Wooster, Ohio) by cutting ventilation holes (10 × 10 cm) into both sides of each drum, and covering them with fine (0.8 × 0.8 mm) mesh (Wood, 2012; Lee, 2014) (Fig. 1.4c). A hole (diameter 9cm) was cut in the bottom of each drum, and a canning jar (250 mL) was attached over the hole to sample reared beetles. Each jar contained approximately 50 mL of propylene glycol as a killing agent and preservative. Each rearing drum was tightly sealed with tape except for the screened ventilation holes, and was placed on a plywood table in a forest patch near the EMEND camp (Fig. 1.4c).

Fig. 1.4. Three sampling methods: (a) Window trap, (b) Emergence trap, and (c) Rearing drums. Courtesy of photos: Seung-Il Lee.

1.6. Overall objectives of this dissertation

The overall goal of my work is to examine influences of aggregated retention patches on saproxylic beetle assemblages using dead and dying white spruce. In the dissertation, I give particular attention to exploring edge and matrix effects (i.e., different levels of surrounding dispersed retention), and to characterizing the saproxylic beetle assemblages associated with a full range of white spruce downed CWD in boreal forest ecosystems. The specific objectives for each chapter of the dissertation are described below.

In the introductory chapter, I establish the context for my work by clarifying the essential background of my research relative to the data-based chapters that follow in the dissertation. I introduce the basic context of retention forestry, the natural disturbance model, the EMEND experiment, CWD and decay classification systems, and the ecological role of saproxylic beetles in deadwood ecosystems.

In Chapter 2, I examine saproxylic beetle assemblages, including both adults and larvae, in white spruce downed CWD across a ‘decomposition’ gradient ranging from freshly dead to well-decayed wood. Then, I show how species assemblages and functional guilds change along this decomposition trajectory. This work was published in *Agricultural and Forest Entomology* (Lee et al., 2014).

In Chapter 3, I explore relationships between white spruce patch size and early-colonizing beetle assemblages on an operational forest landscape that is being broadly managed under the natural disturbance management paradigm. Most importantly, I explore edge effects, and to link variation in deadwood quality to differences in species composition. Lastly, I suggest a minimum patch size that should maintain local saproxylic beetle assemblages using spruce that are similar to those of intact mixedwood forests in the western boreal zone of Canada. This work was published in *Forest Ecology and Management* (Lee et al., 2015).

In Chapter 4, I examine the combined effects of aggregated retention and different levels of dispersed retention on saproxylic beetle assemblages in white spruce stands. Specifically, I assess, using both window and emergence traps, how different functional guilds respond to combinations of both retention types. The results underscore the importance of physical structures associated with aggregated retention, CWD quality, and matrix quality (i.e., the surrounding dispersed retention) for maintenance and recovery of saproxylic beetle assemblages.

In Chapter 5, I identify saproxylic beetle species that initially colonize white spruce logs and snags exposed in a mixed wood setting, and assess the combined influence of aggregated and dispersed retention on early colonization of fresh CWD by saproxylic beetle assemblages. I discuss the importance of different types of CWD, patch size and matrix quality in relation to conservation of the spruce-associated saproxylic beetle fauna found in the Canadian boreal mixedwood.

In the general discussion of the thesis (Chapter 6), I first synthesize the findings presented in the dissertation, and relate them to relevant work that has been previously published. Finally, I suggest important questions for future research about implications of retention forestry for conservation of saproxylic beetles in boreal mixedwood forests and provide a framework for integrating such research into forest management.

In summary, this dissertation focuses on understanding the implications of *in situ* wood decay and dispersed and aggregated retention for saproxylic beetle species using white spruce in the boreal mixedwood forests of western Canada. I use this new information to improve understanding of the composition and dynamics of saproxylic beetle assemblages, and to suggest improvements in forest management practices.

CHAPTER 2

Succession of saproxylic beetles associated with decomposition of boreal white spruce logs

2.1. Introduction

Saproxylic organisms are defined as those that depend upon wounded or dying woody plants, or on deadwood, during some parts of their life cycle (Alexander, 2008; Stokland *et al*., 2012). Many features of deadwood and its environment influence composition of saproxylic assemblages. These include tree species, stages of decomposition, position of tree (i.e., snag vs. log), size of tree, fungi associated with the material, cause of tree death, land-use history, etc. (Siitonen, 2001; Boulanger & Sirois, 2007; Ferro *et al*., 2012b). Saproxylic organisms, particularly those in the order Coleoptera, are critical to forest ecosystem function, because they play important roles in nutrient cycling and food web dynamics (Speight *et al*., 1999; Cobb *et al*., 2011). Furthermore, saproxylic beetle assemblages account for much invertebrate diversity in forests, and are also highly sensitive to environmental changes associated with forestry operations (Speight, 1989; Hammond *et al*., 2004; Gibb *et al*., 2006; Langor *et al*., 2008; Ulyshen & Hanula, 2010).

Deadwood (also called coarse woody debris or ‘CWD’) is a key functional ecosystem attribute and a vital component for conservation of deadwood dependent species (Siitonen, 2001; Grove, 2002). In Sweden, for instance, where distribution and abundance of CWD has been profoundly affected by forestry practices, 85% of red-listed forest-inhabiting beetle species are considered as deadwood dependent (Jonsell *et al*., 1998). CWD provides a range of structural characteristics uniquely associated with the specific habitats used by various species, ranging from microorganisms to vertebrates (Franklin *et al*., 1987; Langor *et al*., 2008). Different stages of CWD decomposition promote biodiversity by offering a wide range of microhabitats especially for insects (Esseen *et al*., 1997). Furthermore, CWD influences the ecological character of stands by holding moisture, providing substrates for growth of many organisms, releasing nutrients slowly, and reducing soil erosion (Harmon *et al*., 1986; Stevens, 1997). Thus, deadwood management is increasingly included as a central aspect of forest ecosystem management (Franklin *et al*., 1987; Hagan & Grove, 1999; Lindenmayer & Franklin, 2002; Jacobs *et* al., 2007b; Hjältén *et al*., 2012).

A first step in understanding relationships between saproxylic organisms and CWD is to develop a sensible classification system for deadwood in forest settings, and one vital aspect of such a classification system is degree of decay. Toward this end various CWD decay classification systems have been proposed and developed (Maser *et al*., 1979; Sollins, 1982; Hofgaard, 1993; Enrong *at al*., 2006; Wood, 2012). For CWD in the boreal mixed-wood forest of Alberta, Canada, for instance, Hammond *et al*. (2004) used 3-class system to characterize saproxylic beetle succession in trembling aspen, *Populus tremuloides* Michaux, deadwood and Wood (2012) proposed 6- and 4-class systems for trembling aspen logs and snags, respectively, to facilitate understanding of relationships between saproxylic beetles and substrate qualities. Also, Cobb *et al*. (2011) used a 7-class system to assess relationships among post-fire stand treatments, coarse woody debris characteristics, and beetle species composition in white spruce, *Picea glauca* (Moench)

Voss. Decay classification systems vary to accommodate differences in characteristics and time-course of decomposition between tree species, especially between deciduous and coniferous CWD (Harmon *et al*., 1986). In addition, various systems are developed to meet different objectives.

Studies about decomposition of deadwood have focused largely on changes over time in its physical nature, nutrient dynamics, and decay rate (Sollins, 1982; Daniels *et al*., 1997; Krankina *et* al., 1999; Campbell & Laroque, 2007). Although some researchers have studied succession of saproxylic organisms on this template, only a few quantitative studies have examined relationships between progression of decay and succession of hyperdiverse assemblages of deadwood-associated organisms (Vanderwel *et al*., 2006; Saint-Germain *et al*., 2007; Ulyshen & Hanula, 2010; Wood, 2012). Moreover, there is no published information about saproxylic beetle succession in white spruce logs that covers the full range of decay classes, despite the large importance and extensive harvesting of this species as a source of forest fibre in Canada.

The overall goals of the study were to: 1) compare saproxylic beetle assemblages in white spruce downed CWD across a 'decomposition' gradient ranging from freshly dead to well-decayed; and 2) understand how species assemblages and functional guilds change along this decomposition trajectory.

2.2. Materials and methods

2.2.1. Study area

The study was conducted using material collected from a 10-ha uncut stand of white spruce (56°79'N, 118°36'W, 758 MASL) at the Ecosystem Management Emulating

Natural Disturbance (EMEND) research site. This is the uncut ‘control’ compartment for ‘G block’ of the EMEND experiment, set out during 1998–99 to investigate impacts of variable retention harvesting, and it represents the pre-harvest condition of a much larger (c. 80 ha) stand. Because the distribution of saproxylic insects is locally patchy among logs (Work & Hibbert, 2011) and the capacity of the rearing facility was limited, we chose to maximize replication of decay classes from this single forest stand to better understand variation of CWD at the local scale.

The site is located in the Clear Hills Upland, in the Lower Foothills eco-region of northwestern Alberta, approximately 90 km northwest of Peace River (Work *et al.*, 2004). Mean daily temperatures of the coldest and hottest month (i.e., January and July) in this region are –16.6 °C and 16.0 °C, respectively, and mean monthly precipitation is 21.3 mm and 66.6 mm, respectively, for those same months (Environment Canada, 2013). The compartment is characterized by a structurally simple understory composed mainly of mosses and lichens. The limited shrub layer is dominated by *Rosa acicularis* Lindl. and *Viburnum edule* (Michx.) Raf., and the most common vascular plants include *Cornus canadensis* L., *Linnaea borealis* L., *Rubus pubescens* Raf., and *Epilobium angustifolium* (L.) Holub.

2.2.2. Downed CWD sampling and decay classification

During the summers of 2009 and 2010, respectively, 24 and 30 naturally downed white spruce were chosen to comprise nine replicates of each of six pre-determined decay classes (DCs). Our decay classification system is similar to the 8-class system proposed by Hofgaard (1993) for Norway spruce (*Picea abies* (L.) Karst) CWD. Both systems distinguish between DC 1 and 2 based on the presence of needles. The main difference between our system and Hofgaard's is that we merged her DCs 6–7 as DC 6. Hofgaard's DC 6 and DC 7 differ in the extent of lichen cover, but in our study there were few lichens but much moss (Table 2.1). We did not use DC 8, because white spruce logs meeting these criteria are essentially part of the duff layer in the forests of northern Alberta and thus could not be effectively sampled using the approach used for other decay classes (Fig. 2.1 and Table 2.1).

Every bolt chosen for rearing was cut to 60 cm in length between 3–6 m from the base of a different log. Once cut, bolts were moved to rearing drums located in a forest patch near the EMEND camp where they could be protected from disturbance. Bolts were not precisely standardized for volume, because logs in the most advanced decay stage (especially, DC 6) were entirely covered by thick mosses and highly variable in shape; thus it was impossible to reliably determine the diameter of all bolts at the time of collection. However, variation in diameter of bolts among all measurable decay classes (i.e., DCs 1–5) was small (Table 2.1), and we assume logs from DC 6 were similar in volume.

2.2.3. Saproxylic beetle sampling and identification

We used rearing drums for this work because this method provides exact information about saproxylic invertebrates that are actually living in wood bolts at the time of sampling, even though individuals of some vagile species may be lost during transport and preparation of samples for rearing. Rearing drums were constructed from 121 L Rubbermaid™ garbage bins (60 cm diameter X 91 cm height) by cutting ventilation holes (10 cm X 10 cm) into the sides of each drum and covering them with fine (0.8 mm X 0.8 mm) mesh (Wood, 2012). A 9 cm diameter hole was cut in the bottom of each drum, and a canning jar (250 ml) was attached over the hole to collect saproxylic beetles. Each collection jar contained ~50 ml of propylene glycol as preservative. Rearing drums were held on plywood tables in the forest and monitored for beetle emergence.

The first set of 24 bolts (6 different decay classes X 4 replicates of each) were placed in the drums in mid-summer 2009, emerging beetles were collected three times between late summer 2009 and early summer 2010. A second set of 30 (6 different decay classes X 5 replicates of each) were placed in the drums in early summer 2010, and emerging beetles were collected five times until early summer 2011. All bolts were discarded after the final collection. All beetles collected were transferred into 70% ethanol for storage and identification. As emerged beetles were largely associated with deadwood, most specimens collected can be considered to represent either obligate or facultative saproxylic species.

Adult beetles were identified to species using relevant literature (Arnett & Thomas, 2001; Arnett *et al*., 2002), and through comparison with the reference collection in the Arthropod Museum at the Northern Forestry Centre and support from taxonomic specialists (see Acknowledgements). Overall 86% of taxa were identified to described species. The remaining 10%, 2%, 1%, and 1%, respectively, could be reliably identified to the level of genus, tribe, subfamily, and family, but were sufficiently distinct to be treated as morphospecies. Beetle larvae were identified mostly to genus and family levels using relevant literature (Lawrence, 1991) and treated as morphospecies. Each species was assigned to one of the five following feeding guilds, based on information from the literature: mycetophagous (feeding on fungi); myxomycophagous (feeding on slime molds); phloeophagous (feeding in phloem tissues); predaceous (feeding on live invertebrates); and xylophagous (feeding in xylem tissues) (Klimaszewski *et al*., 2007; Dollin *et al*., 2008; Bishop *et al*., 2009; Wood, 2012). When adequate biological information was not available at the species level, feeding guild was assigned based on information available for the most closely related species or genus for which there was information. Voucher specimens are held in the beetle reference collection of the Invertebrate Ecology Laboratory (Department of Renewable Resources at the University of Alberta, Edmonton, Alberta, Canada) and in the Arthropod Museum of the Northern Forestry Centre, Canadian Forest Service, Edmonton, Alberta.

2.2.4. Statistical analysis

Differences in species richness of saproxylic beetles across decay classes were tested using a Generalized Linear Model (GLM) using a Poisson distribution to model variance. Differences in abundance were tested using a GLM based on the Negative Binomial distribution since data were overdispersed. Multiple comparisons among all decay classes were tested using a Tukey's H.S.D. test for abundance. The tests were carried out in R (R Development Core Team, 2012, version 3.0.1).

Non-metric multidimensional scaling (NMS) ordination was used to compare species composition among decay classes using PC-ORD for Windows (version 5.10; McCune & Mefford, 2006). NMS avoids the assumption of linear relationships among variables and reduces the zero-truncation problem by using ranked distances (McCune & Grace, 2002).

Singletons were excluded, the data were log (x+1) transformed, and the analysis was based on the Sørensen (Bray-Curtis) distance measure.

Multi response permutation procedures (MRPP) were used to determine the significance of ordination groupings based on decay class, again using the Sørensen distance measure in PC-ORD software. MRPP provides the test statistic (*T*) that describes the separation between the groups (more negative value = stronger separation), the chance-corrected within-group agreement (*A*) that represents within-group homogeneity (0 = all members different, 1 = all members identical), and a *p*-value to evaluate differences between groups (McCune & Grace, 2002).

Indicator species analysis (ISA) (Dufrêne & Legendre, 1997) was used to describe associations between species and each decay class, using PC-ORD software. This analysis considers both relative abundance and relative frequency, providing an indicator value (IV). Significant indicator values were identified using a Monte Carlo test with 4999 permutations ($\alpha = 0.05$).

Welch's two sample t-test was used to compare abundance of mycetophages between DC 2 and DC 3, and a chi-square goodness-of-fit test was used to evaluate differences in total species richness of adults among decay classes. Both tests were conducted using R, version 3.0.1 (R Development Core Team, 2012).

Morisita's index (MI) was calculated to determine dispersion patterns of saproxylic beetles in each decay class as follows:

$$\mathrm{MI} = \frac{S(\sum n^2 - N)}{N(N-1)}$$

where n = total number of individuals in a CWD sample of each decay class, N = total number of individuals in all CWD samples of each decay class, and S = total number of

CWD samples of each decay class (*S* = 9 in our study). A ratio > 1 indicates an aggregated dispersion of individuals, a ratio ≈ 1 indicates a random dispersion, and a ratio < 1 indicates a uniform dispersion (Bakus, 2007).

2.3. Results

A total of 1764 adults and 275 larvae of saproxylic beetles, representing 94 and 31 species, respectively, were collected from the 54 CWD bolts during 2009–2011. The phloeophagous bark beetle, *Dryocoetes affaber* (Mannerheim) (Curculionidae: Scolytinae), was the most common species with 872 individuals, accounting for 49.4% of the total abundance of adults. Two other scolytines, the phloeophagous *Polygraphus rufipennis* (Kirby) and the mycetophagous and xylem-inhabiting *Trypodendron lineatum* (Olivier), were the second and third most abundant species with 215 and 201 individuals, respectively (See Appendix 2-A).

2.3.1. Species richness and abundance

Although mean species richness of adults differed significantly among decay classes (Deviance = 118.6, $p = 0.009$), *post hoc* comparisons did not reveal significant differences between any pair of decay classes. Nonetheless, species richness tended to be highest in DCs 1 and 5, and lowest in DC 4 (Fig. 2.2A). Overall species richness of adults pooled across replicate samples was highest in DCs 1 and 5 but this trend was not statistically significant ($X^2 = 3.05$, $p = 0.69$), and the data clearly show that richness did not vary much over decay classes (Fig. 2.2A). Instead high variation in species composition among replicate bolts reflects the existence of a rich fauna across the entire sequence of decay. In contrast, mean adult abundance differed hugely among decay classes (Deviance = 124.6, $p < 0.001$) and abundance was significantly lower in DCs 3–6 according to *post hoc* comparison of means (Fig. 2.2B). Furthermore, beetle abundance was significantly highest in DCs 1–2 and declined rapidly to DC 3 and remained low for DCs 4–6 (Fig. 2.2B).

In contrast mean species richness of larvae differed marginally among decay classes, even given the sample sizes obtained from rearing (Deviance = 101.5, $p = 0.041$) (Fig. 2.3A), although *post hoc* pairwise comparisons did not identify significant differences between particular decay classes. Although average larval species richness tended to be highest in DC 5 and lowest in DC 3, overall larval species richness from the pooled sample was higher in the two earliest decay classes than in DC 5, and differences among decay classes are amplified in comparison to the data about means. This suggests relatively low variation in species composition of larvae among bolts from late decay classes, as compared to the situation in DCs 1–2 (Fig. 2.3A). Although mean abundance of larvae differed significantly among decay classes (Deviance = 70.1, $p = 0.023$), significant differences between pairs of decay classes were not identified by *post-hoc* comparisons. Nonetheless, captures of larvae from rearing drums were conspicuously lowest in DCs 3–4 (Fig. 2.3B).

2.3.2. Species composition

NMS ordination was performed using data about only adults because these data should best represent the entire saproxylic beetle assemblage in each bolt. The ordination explained 46.3% of the variation in assemblage structure across decay classes and MRPP revealed that variation among decay classes was significant ($T = –6.44$, $A = 0.06$, $p << 0.001$). NMS axes 1, 2, and 3 explained 11.7%, 10.5%, and 24.1%, respectively, of the variation in assemblage composition (Fig. 2.4); because axis 2 could not be related to decay class, and it is not shown here. Assemblages associated with each decay class were not perfectly distinct, but rather overlapped with those of adjacent decay classes along the decomposition gradient (i.e., from DC 1 to 6). This pattern is also demonstrated by pairwise comparisons through MRPP, which demonstrate the highest similarity amongst adjacent decay class pairs (Table 2.2). Overall, the NMS reflects a continuous change in beetle assemblages as decay class increases along axis 3 (Fig. 2.4). Beetle assemblages from the earliest decay stage were associated with bark cover and height from the ground, whereas assemblages from advanced decay stages were associated more strongly with plant and moss cover of CWD (Fig. 2.4).

MRPP analysis based on three broad decay class categories (i.e., DCs 1–2 combined as early decay stage; DCs 3–4 combined as intermediate decay stage; DCs 5–6 combined as advanced decay stage) gave a more clear separation of beetle assemblages ($T = –8.84$, $A = 0.05$, $p << 0.001$). Separation of assemblages by species composition was highest between the early and advanced decay stages (MRPP; $T = –11.35$, $A = 0.08$, $p << 0.001$). Degree of separation of species composition between early and intermediate decay stages (MRPP; $T = –4.13$, $A = 0.03$, $p = 0.003$) was similar to the separation between the intermediate and advanced decay stage (MRPP; $T = –4.18$, $A = 0.02$, $p = 0.019$), suggesting that these three broad categories are reasonable proxies for species composition, and that understanding of the species assemblages is reasonably represented in terms of three broad decay stages.

2.3.3. Indicator species analysis

Overall, sixteen species were identified as significant decay class indicators (Table 2.3). Half of the eight indicators of DC 1 were bark or ambrosia beetles (Curculionidae: Scolytinae). The other indicators of DC 1 were species commonly associated with bark beetle galleries and included predaceous groups such as the staphylinid beetle (*Phloeostiba lapponicus* (Zetterstedt)), the nitidulid (*Epuraea terminalis* Mannerheim), the nitidulid larva (*Epuraea* larva sp.1, likely *E. terminalis*), and the colydiid (*Lasconotus complex* LeConte). Three species indicated DC 5 with a predaceous ground beetle larva (*Agonum* larva sp.1, likely *Agonum retractum* LeConte) being the strongest indicator followed by adults of the mycetophagous cryptophagid, *Cryptophagus acutangulus* Gyllenhal, and adults of the predaceous carabid, *A. retractum*. Five species, all predaceous beetles, were indicators of DC 6. Four of these were the members of Staphylinidae, followed in strength of indicator value by a soldier beetle larva (Cantharidae larva sp.1). The predaceous staphylinid, *Tachyporus borealis* Campbell was the strongest indicator of DC 6. Interestingly, no significant indicators were identified for DCs 2–4, suggesting that the faunas of early and advanced decay stages were most distinctive.

2.3.4. Changes in feeding guilds

Feeding guild structure changed profoundly as wood decayed (Fig. 2.5A). Phloeophagous beetles (mostly Curculionidae: Scolytinae) dominated the early decay stage, accounting for 64.7% of the beetles from DC 1 and 89.6% of those from DC 2, then decreased in DC

3, and were entirely absent from DCs 4–6. The proportion of xylophagous beetles was highest in DC 3 (6.0%). The relative abundance of mycetophagous beetles (mostly Cryptophagidae, Latridiidae, and Ptiliidae) across decay classes was highest in DC 3; however, these beetles made up a smaller proportion of those from DC 2 only because of the high abundance of phloeophagous beetles in that decay class. In absolute terms, the abundance of mycetophages did not differ significantly between DC 2 and DC 3 ($t = -0.98$, $df = 10.83$, $p = 0.35$). Myxomycophagous beetles accounted for a small proportion (1.4–6.3%) of beetles reared from DCs 3–5. Predators comprised a small proportion in DCs 1–3 (3.2–13.4%), but accounted for the largest proportion of total abundance in DCs 4–6 (59.4–88.1%) (Fig. 2.5A).

The pattern of variation in feeding guild structure across decay classes based on abundance of beetle larvae, as expected, gives a quite different picture from that provided by adults (Fig. 2.5B). For example, phloeophagous and xylophagous larvae did not emerge from any decay classes, except for a very low proportion (6.9%) from DC 2 in which depletion and degeneration of phloem habitat could well be expected. Clearly, most of these larvae stayed the course of development within the bolts and either emerged as adults or died in situ. The relative abundance of predaceous larvae was the highest through all decay classes (51.5–66.7%). The proportion of unknown feeding guild was high through all decay classes (33.3–48.5%).

2.3.5. Species distributions along the decay classes

There was high variation in diversity of adult beetles among log samples from a single 10-ha forest compartment. Clearly, beetles were aggregated in logs for all decay classes (Table 2.4); in fact, at least one CWD sample in each decay class gave rise to either no adult beetles, or to specimens of only a single species. Saproxylic beetle assemblages, as defined by adults, were characterized by associating each species with particular decay classes to determine the extent of specialization for different stages of decomposition (Fig. 2.6) (See Appendix 2-A). Adults of most species emerged from only a narrow range of decay classes. Thirty-four species represented by more than a single specimen were found exclusively in either one or two adjacent decay classes: 14 spp. in early decay stage (DCs 1–2), 2 spp. in intermediate decay stage (DCs 3–4), and 12 spp. in advanced decay stage (DCs 5–6). Adults of many species found in DCs 3–4 were also found in either the two earlier (11 spp.), or in the two more advanced decay classes (10 spp.). Four species (*Acrotrichis* sp.1, *Amischa* sp.1, *Corticaria rubripes* Mannerheim, and *Cryptophagus tuberculosus* Mäklin) were generalists, using a broad range of decay classes from early to advanced decay classes; however, only adults of *Amischa* sp.1 were discovered from all six decay classes.

High variation in abundance of beetle larvae among logs suggests strong aggregation in logs for most decay classes (Table 2.4). Species richness of beetle larvae that emerged from reared bolts also varied much among log samples, from a high of six species in four CWD samples (i.e., DCs 2, 5, and 6) to a low of zero in 33% of all CWD samples. However, the proportion of CWD samples that produced no beetle larvae decreased with advancing decay classes. Diversity of beetle larvae was no more strongly associated with the advanced decay classes than was adult diversity (Fig. 2.7). For larval species represented by more than a single specimen, 7, 2, and 2 spp., respectively, were found exclusively in the early, intermediate, and advanced decay stages, as defined above. As in adults, larvae of some species found in intermediate decay stages were also found in either early (2 spp.) or advanced decay stages (4 spp.). Three species represented by larvae were discovered from a broad range of decay classes, i.e., Staphylinidae larva sp.1, carabid larva sp.2, and elaterid larva sp.1 occupied 6, 5, and 4 different decay classes, respectively, and thus were decay class generalists in white spruce downed CWD.

2.4. Discussion

Study of saproxylic beetles through rearing from wood samples provides relatively low numbers of specimens compared to more widely employed sampling methods, such as window traps attached to deadwood. Nonetheless, rearing produces high proportions of saproxylic species that are rarely collected by other commonly used methods (Wood, 2012). It also samples saproxylic organisms in a way that is clearly specific to tree species and decay class of substrate because it captures individuals after habitat choice has been exercised (Ferro & Carlton, 2011; Wood, 2012). Finally, species with mobile larvae are collected from rearing drums, supporting useful interpretations about larval use of CWD substrates. To our knowledge, no other published studies have investigated both larval and adult beetle diversity across all decay classes of deadwood. Thus, our study helps to fill a large information gap about variation in assemblages of immature beetles using deadwood habitats. As resources for species-specific identification of larvae become more widely available, association of species-specific patterns for both adults and larvae will reveal more about the significance of CWD in the life history, especially of predatory species that use it. At this point, predatory beetles are frequently dismissed from lists of ‘true’ saproxylic species because the extent of their requirements of CWD as larval habitat is poorly appreciated.

2.4.1. Early decay stage (DCs 1–2)

The most conspicuous characteristic of the early decay stage identified in our study is the extremely high numbers of adult saproxylic beetles that emerged from the rearings. Among the adult beetles from DC 1, 84% of them belonged in the subfamily, Scolytinae. *Dryocoetes affaber* was the most abundant species, accounting for 48.9% of the beetles from DC 1, followed by *T. lineatum* (19.6%) and *P. rufipennis* (10.9%). The total abundance of bark beetles in DC 2 was lower than in DC 1, but the proportion of bark beetles was even higher (89.6%) than in DC 1 because we collected a lower proportion of fungus feeding species such as the mycetophagous rove beetle (*Placusa tachyporoides* (Waltl)) and the ambrosia beetle (*T. lineatum*) than in DC 1. *Dryocoetes affaber* (68.9%) remained the most abundant species in DC 2, followed by *P. rufipennis* (19.5%) and the cerambycid, *Tetropium cinnamopterum* (Kirby) (3.4%).

Overall, phloeophagous beetles dominanted the feeding guild of the early decay stage of white spruce downed CWD, reflecting the high activity of bark beetles. This activity is among the most important forces in the early decay of coniferous downed CWD, because it contributes to rapid physical breakdown of CWD (Vanderwel *et al.*, 2006; Ulyshen & Hanula, 2010) and opens up much surface area of xylem to the action of fungi and microbes (Esseen *et al.*, 1997). In many species of coniferous logs, bark beetles, which actively consume the nutrient-rich habitat of phloem and cambium, also introduce fungi into the wood, accelerating decay processes (Harmon *et al*., 1986; Esseen *et al.,* 1997; Ulyshen & Hanula, 2010).

Although bark beetles accounted for a huge proportion of beetles from the early decay stage and included four indicator species of DC 1, another four predaceous beetle species (*Epuraea* larva sp.1, *E. terminalis*, *L. complex*, and *P. lapponicus*) were also exclusively found in the initial decay stage. Interestingly, the omaliine rove beetle, *Phloeostiba lapponicus*, which is a subdominant species in freshly dead aspen CWD (Wood, 2012), was the second strongest indicator species of DC 1 in white spruce, suggesting that this beetle is catholic with respect to choice of tree species. This latter observation likely flows from our assignment of the species to the predator feeding. We note that there is not consensus about the feeding habits of *P. lapponicus*; although the species has been designated a predator (Toivanen & Kotiaho, 2010; Azeria *et al*., 2012) in line with our designation, others have classified it as a sap feeder (Jacobs *et al*., 2007a; Dollin *et al*., 2008), or both predator and sap feeder (Wood, 2012). Only natural history data, largely missing for the Nearctic fauna, will provide understanding of such ecological linkages. Nonetheless, our results clearly establish that this species uses both coniferous and broad-leaved trees, a fact more consistent with a predatory nutritional habit than with one that depends on chemical composition of wood.

Saproxylic beetles living in CWD are challenging to sample effectively. Even where beetles were reasonably abundant overall (five DC 1 samples yielded 97–353 individuals), three CWD samples of DC 1 produced 0–2 individual adult beetles. This may have been a function of exact sample age: the three least productive samples of CWD in terms of both species richness and abundance of beetles had green needles at the time of collection, while the five most productive samples had light green or brown needles, and had doubtlessly been down and exposed to colonization for a longer period. This result underlines the sensitivity of sampling time in the early stage of decomposition. If CWD is collected before the host colonization period of primary colonizers, the sample will return low numbers of beetles. Thus, we suggest that fading needles is associated with colonization of pioneer saproxylic species and thus indicates the onset of suitable sampling time for biodiversity studies.

Clearly, a large proportion of bark beetle larvae occur in the earliest decay stage where phloem is abundant; however, rearing drums catch none of them, because they die or complete their life cycle inside a single piece of CWD instead of moving in and out of logs in nature. Thus, the data about beetle larvae provided by this study was limited to species with mobile larvae that may leave particular pieces of CWD during their development. These appear to be disproportionally predaceous.

2.4.2. Intermediate decay stage (DCs 3–4)

Turnover in saproxylic beetle assemblages is correlated with a significant decrease of phloem and cambium tissues, as well as a reduction in the area covered by bark in DC 3 logs (Vanderwel *et al*., 2006; Jacobs *et al*., 2007a). Disappearance of phloem-feeding beetles (i.e., mostly bark beetles) was followed by a subsequent shift to mycetophagous and predaceous beetles. For example, total species richness and abundance of bark beetles recovered from DC 3 was markedly low (2 spp. and 26 individuals), compared to DC 1 (9 spp. and 865 individuals) and DC 2 (6 spp. and 472 individuals). The bark-gnawing beetle (Trogossitidae), *Peltis fraterna* (Randall), mostly found in DC 3, is adapted to exploit the subcortical environment, having a dorso-ventrally flattened body shape (Stokland *et al*., 2012). The intermediate decay stage thus appears to be characterized by an abrupt shift in dominant feeding guilds and increased abundance of species that exploit microhabitats that appear during DC 3, and as indicative of a truly successional process, this results from feeding activities of beetles in the earlier decay stages.

The intermediate decay stage is also characterized by relatively low species richness and abundance for both adult and larval beetles. Interestingly, no indicator species was found for the intermediate decay stage, as is in line with the results from pine-dominated stands (Vanderwel *et al*. 2006). Many species seem to use the intermediate decay stage mainly as a transient habitat, being most specialized for either early or advanced decay stages. Although intermediate decay stages may be used by beetles specialized for feeding on specific fungal species that sporadically emerge in deadwood, we collected logs only in early and mid-summer and thus our study may not completely reveal fungus-associated beetle diversity in this stage of decomposition.

The ground beetle, *Psydrus piceus* LeConte, is considered rare in North America despite its transcontinental distribution, having been mainly collected under bark of western larch and western hemlock (Lindroth, 1961). Our study provides records of this species from white spruce CWD; it was reared from two samples representing DC 4. During a period of three years in which extensive sampling was conducted in boreal white spruce stands with window traps, emergence traps and rearing drums, *P. piceus* was the only carabid species found exclusively in rearing drums. Furthermore, despite extensive sampling effort (see Work *et al*., 2010) it has not been collected in pitfall traps at EMEND. Thus, it appears to be a true saproxylic species, and serves as a caution against using unqualified inference based simply on family-level identity to disqualify particular species as having saproxylic habit.

2.4.3. Advanced decay stage (DCs 5–6)

Fungivorous insects are generally most abundant in the final stages of decomposition of coniferous trees, and along with an increase of predators and parasitoids, their presence is typical in assemblages of advanced decay stage (Vanderwel *et al*., 2006). In our beetle-specific study, predators were actually more abundant than fungivores. However, the latter decay classes also included a large proportion of larvae assigned to the 'unknown' feeding group (33.3% and 48.5% in DC 5 and 6, respectively), which was comprised mostly of rove beetle larvae (Staphylinidae). Deadwood-associated staphylinid larvae are thought to be either predaceous or mycetophagous (Lawrence, 1991), but cannot be placed with certainty in a particular trophic category. Nonetheless, it seems that more beetle predators than fungivores use the advanced decay stage of white spruce, even if all staphylinid larvae are fungivores.

Species richness and abundance of adult beetles did not differ notably between advanced and intermediate decay stages; however, species composition of the advanced decay stage was clearly distinct from both the early and intermediate decay stages. Overall, more beetle larvae were collected from the advanced decay stage than the intermediate decay stage, possibly because the higher moisture associated with high moss and plant cover on the surface of CWD makes these habitats more suitable for larvae (Wood, 2012). Also logs in these decay classes may include food highly appropriate for mobile predatory beetle larvae, as later stages of decomposition are mostly dominated by slow-moving saprophagous and fungivorous dipterans (Vanderwel *et al*. 2006).

Eight species were significant indicators of advanced decay stages (3 spp. in DC 5 and 5 spp. in DC 6). *Tachyporus borealis* Campbell, the dominant species in the advanced decay stage of aspen downed CWD (Wood, 2012), was also not only the most commonly reared species in DC 6 of white spruce logs, but also the strongest indicator species of DC 6 in our study. The predaceous rove beetle, *Lathrobium washingtoni* Casey, a dominant species of well-decayed aspen logs (Wood, 2012), was also an indicator species for DC 6 and subdominant in both DC 5 and 6 in white spruce logs. The carabid, *A. retractum*, an indicator species of DC 6 in aspen logs (Wood, 2012), was also indicator species of DC 5 in white spruce, although adults of this species are also commonly found in aspen leaf litter in Alberta (Niemelä *et al*., 1992). The extent of dependence of such taxa on CWD remains undefined, but present data suggest that CWD is a significant habitat factor for these species. Many other indicator species of the later stages of decomposition in aspen logs were also found in the advanced decay stage of white spruce logs (e.g., *Lathrobium fauveli* Quedenfeldt, *Gabrius brevipennis* (Horn), *Ischnosoma splendidum* (Gravenhorst), and *Pseudopsis sagitta* Herman) (Wood, 2012). The fact that many species of later decomposition stages are shared between aspen and white spruce CWD supports inference that invertebrate assemblages of different tree species become more similar with more advanced stages of decomposition (Jonsell *et al*., 1998), a reflection of the fact that many of these species are generalist predators.

2.4.4. Succession and structure of saproxylic beetle assemblages

Species composition of beetle assemblages changed progressively with decomposition stage in white spruce downed CWD. Similar patterns have been found in saproxylic assemblages of several pine species in eastern Canada (Vanderwel *et al*., 2006), trembling aspen near our study area of western Canada (Wood, 2012), and in hardwoods of cove forest in the southeastern United States (Ferro *et al*., 2012b). However, the extent to which these changes can be thought of as a formal succession of communities has not been explored thoroughly.

The Clementsian and Gleasonian concepts of succession are two important classical models that have been central to describing patterns of species distribution as communities age (Emery, 2012). Under the Clementsian concept, groups of species are closely linked and shift coincidentally as whole units over time, with groups changing progressively from early to more mature stages. This concept thus envisions sharp boundaries between successive communities and permits one to predict the course of succession (Clements, 1916; Presley *et al*., 2010; Emery, 2012). In contrast, the Gleasonian concept holds that species respond to environment independently, thus changes of communities are quite unpredictable (Gleason, 1926; Emery, 2012). Although there has been work to address the balance of competitive and facilitative effects among small subsets of saproxylic invertebrates (e.g., Weslien *et al*. 2011; Victorsson 2012), there has been little reasoned consideration of the overall succession of saproxylic beetles across the full decay cycle of CWD. In particular, no studies have addressed whether specific assemblages are linked to particular decay classes in more Clementsian fashion, or whether these changes involve independent variation in habitat associations of each species reflecting a sort of Gleasonian process in changes of saproxylic assemblages. We consider this latter matter in the following discussion.

Assemblages of saproxylic organisms do not change synchronously in blocks along the decomposition gradient of white spruce downed CWD, as suggested by the extreme Clementsian view of succession in plant communities. Clearly, decomposition of deadwood is a continuous process and the species composition of saproxylic beetles changes somewhat continuously along the decay gradient of deadwood. However, our results suggest some utility of the Clementsian view, in that groups of beetle species are more specialized for particular decay stages. Composition of saproxylic beetle assemblages overlaps among adjacent decay classes; however, in a general sense, groups of species defined by the most common species do shift somewhat coincidentally across early, intermediate, and advanced decay stages, and might be loosely interpreted to function as ecologically significant units supporting particular aspects of the decomposition process. To the limited extent that such patterns can be interpreted from our dataset, the shifts in distribution of less commonly collected species is more idiosyncratic and more suggestive of a Gleasonian process.

We found that adult saproxylic beetle assemblages in early decay stage (especially DC 1) form the most distinctly Clementsian beetle assemblage units in decomposition of white spruce CWD. A group of bark and ambrosia beetle species (i.e., *D. affaber*, *P. rufipennis*, *T. lineatum*, *I. pini*, and *Crypturgus borealis* Swaine) were frequently and coincidentally found in four same CWD samples of DC 1, and their phloeophagous feeding habits suggest that they collectively contribute to the processes transforming this stage of CWD to the next decay class. Interestingly, no species was dominant across all

CWD samples of DC 1. *Dryocoetes affaber* was perhaps the most common scolytine in DC 1; however, it was only the third most abundant species in one CWD sample of DC 1. Rank abundance of other species of scolytines shifted in apparent random pattern among CWD samples, suggesting considerable equivalence in ecological function among the species. Two bark beetle species (i.e., *D. affaber* and *P. rufipennis*) from DC 2 were found in three same CWD samples; however, the rest of species were distributed more or less independently among bolts.

In the intermediate decay stages (both DCs 3 and 4), no group of species was found in more than three CWD samples, suggesting that beetle assemblages in this stage follow a more strongly Gleasonian pattern. In the advanced decay stages, two predaceous rove beetles, *L. washingtoni* and *T. borealis*, were also found in three and four of the same CWD samples of DCs 5 and 6, respectively, while each of those species appeared independently in one CWD sample of DCs 5 and 6. This suggests a relatively strong pattern of coexistence of these two species in late decay stages. However, the rest of species in both DCs 5 and 6 showed more random distributions, supporting a more Gleasonian interpretation of changes in these saproxylic beetle assemblages.

2.4.5. Implications for conservation and management

As the first study to examine saproxylic beetles in white spruce downed CWD over a decomposition gradient, our work complements that of Jacobs *et al*. (2007a, b), which focused on the fauna of standing dead white spruce. Our 6-grade decay classification system revealed the existence of an overall succession of relatively discrete beetle assemblages along the decomposition gradient. The 6-class system used for white spruce logs provides greater separation of early decay stages and increased combination of later decay stages than is found in other classification systems (McCullough, 1948; Hofgaard, 1993). From the biodiversity point of view, our study emphasizes that finer separation of early decay stages is essential to effectively capture variation in the initial response of saproxylic beetles in the decomposition process. Phloem and cambium provide important food resources that are quickly consumed by beetle colonizers in the early stages of white spruce decay, and rapid depletion of this resource is associated with dramatic changes of the saproxylic beetle assemblages over a short period.

We argue that different decay stages of deadwood harbor different saproxylic beetle assemblages, because each stage provides unique habitats required by some species. Therefore, this is a succession of sorts and maintaining a full range of continuously recruiting decay classes is critical to conservation of various species of saproxylic beetles that use white spruce downed CWD. Careful logging to retain a considerable fraction of the advanced decay stages as forest legacy has important conservation value because it is likely to require a long time to reconstitute these later stages naturally. For example, it is estimated that it takes more than 50 years before Norway spruce downed CWD reaches the advanced decay stage (Storaunet & Rolstad, 2002). In order to minimize gaps in availability of these later decay classes, large trees ready to recruit into the CWD decay cycle must also be left on site. Deadwood in the early decay stage is relatively easy to provision after harvesting by simply leaving standing green trees that are likely to blow down over a few years in new harvest blocks. Saproxylic species adapted to use deadwood in this early decomposition stage will quickly recolonize these habitats after modern variable retention harvesting, just as they do after natural disturbances (Cobb *et* *al*., 2011; Gibb *et al*., 2006; Jacobs *et al*., 2007b). However, species adapted to the later stages of decomposition may disappear in local systems once the abundance of logs in advanced decay passes some lower threshold, especially because other decaying materials in the forest floor (e.g., leaf litter) do not provide suitable habitats for these species (Ferro *et al*., 2012a). And, in the case of species that can be found in both logs and litter (e.g., the carabid, *A. retractum*), there is no information about population performance in systems without log habitat, as is required for serious evaluation of the extent of their dependence on CWD. Fortunately, advanced decay stages appear to be relatively long-lived. Nonetheless, we suggest that forest managers should ensure protection of deadwood in advanced decay stages at harvest, in addition to retaining green trees to ensure recruitment of specialists in early and intermediate decay stages. In order to achieve this goal, design of retention patches must include sufficient representation of advanced decay stages of white spruce CWD to sustain the saproxylic species associated with them. Clearly, development of effective conservation strategies for saproxylic species in white spruce requires more information about the dynamics and longevity of advanced decay stages in blocks to be commercially harvested on large scales.

Table 2.1

White spruce downed coarse woody debris (CWD) classification across six decay classes (DCs).

	DC 1	DC 2	DC 3	DC 4	DC 5	DC 6
Diameter (cm) ± S.D.[a]	21.4±4.9	22.3±3.6	20.8±2.8	20.5±3.3	22.4±2.6	hard to measure
Bark remaining (%)	100	100	60–90	0–70 (mostly < 30 underneath)	0–20 (mostly 0 or < 10 underneath)	0
Bark tightness	tight	tight to loose	loose	no bark or loose	no bark or loose	no bark
Wood texture	hard	hard	hard	relatively soft, variable	mostly soft	soft
Shape of cross section	round	round	round	round	round to oval	oval
Presence of needles	present	absent	absent	absent	absent	absent
Branches remaining (%)[b]	mostly > 80	20–70	< 50	mostly no branches	mostly no branches	no branch
Ground contact	30–100 cm off the ground	0–120 cm off the ground	slightly off the ground or slightly sunken	slightly off the ground or slightly sunken	10–50 % sunken	mostly > 50 % sunken
Plants remaining (%)	0	0	mostly no plants	mostly no plants	5–30	10–60, mostly > 30
Mosses remaining (%)	0	0	0–5	0–70, variable	10–100, mostly > 70	80–100, mostly 100

[a] Similar diameter classes were selected to decrease the effect of CWD size that might affect species composition, however diameter in DC 6 was not precisely measured because of variable shapes with thick mosses covered on CWD.

[b] Measured along entire substrate.

Table 2.2

Pairwise comparisons in multi response permutation procedures (MRPP) for saproxylic beetle assemblages among decay classes (DCs) of white spruce downed coarse woody debris (*T* = test statistic; *A* = chance-corrected within-group agreement; *p* = *p*-value). Significant differences ($p < 0.05$) are highlighted in bold.

DC compared	*T*	*A*	*p*
DC1 VS DC2	-0.773	0.011	0.191
DC1 VS DC3	-2.625	0.040	**0.017**
DC1 VS DC4	-4.149	0.055	**0.003**
DC1 VS DC5	-5.983	0.088	**< 0.001**
DC1 VS DC6	-5.337	0.090	**< 0.001**
DC2 VS DC3	0.364	-0.006	0.593
DC2 VS DC4	-3.430	0.041	**0.004**
DC2 VS DC5	-5.702	0.074	**< 0.001**
DC2 VS DC6	-5.850	0.081	**< 0.001**
DC3 VS DC4	-0.877	0.012	0.178
DC3 VS DC5	-2.858	0.039	**0.007**
DC3 VS DC6	-3.488	0.048	**0.002**
DC4 VS DC5	0.221	-0.003	0.550
DC4 VS DC6	-0.744	0.010	0.214
DC5 VS DC6	-0.661	0.009	0.226

Table 2.3

Significant indicator species for saproxylic beetle assemblages in different decay classes (DCs) of white spruce downed coarse woody debris (after a Monte-Carlo test with 4999 permutations, α = 0.05). Indicator values (IV) are given for each species.

DC	Family	Species	Feeding Guild	IV	*p*	Freq
1	Curculionidae	*Dryocoetes affaber*	Phloeophagous	37.7	0.028	5
1	Curculionidae	*Dryocoetes autographus*	Phloeophagous	25.0	0.046	2
1	Curculionidae	*Ips pini*	Phloeophagous	37.5	0.006	3
1	Curculionidae	*Trypodendron lineatum*	Mycetophagous	37.5	0.006	3
1	Colydiidae	*Lasconotus complex*	Predaceous	25.0	0.047	2
1	Nitidulidae	*Epuraea terminalis*	Predaceous	35.8	0.010	3
1	Nitidulidae	*Epuraea* larva sp.1	Predaceous	28.1	0.032	3
1	Staphylinidae	*Phloeostiba lapponicus*	Predaceous	37.5	0.006	3
5	Carabidae	*Agonum retractum*	Predaceous	28.4	0.031	4
5	Carabidae	*Agonum* larva sp.1	Predaceous	32.2	0.017	5
5	Cryptophagidae	*Cryptophagus acutangulus*	Mycetophagous	29.6	0.018	4
6	Cantharidae	Cantharidae larva sp.1	Predaceous	34.6	0.006	5
6	Staphylinidae	*Acidota crenata*	Predaceous	25.0	0.042	2
6	Staphylinidae	*Lathrobium washingtoni*	Predaceous	22.9	0.043	4
6	Staphylinidae	*Stenus austini*	Predaceous	23.5	0.036	3
6	Staphylinidae	*Tachyporus borealis*	Predaceous	37.0	0.006	5

Freq = frequency (the number of occurrence of each species in a corresponding decay class where it has nine replicates).

Table 2.4

The Morisita's index (MI) for abundance of saproxylic beetles in different decay classes (DCs) of white spruce downed coarse woody debris. MI value > 1 indicates an aggregated dispersion of individuals among coarse woody debris samples in each decay class.

	DC 1	DC 2	DC 3	DC 4	DC 5	DC 6
MI for abundance of adults	2.17	6.63	3.94	1.09	1.54	1.35
MI for abundance of larvae	1.91	5.78	2.62	1.38	2.57	1.14

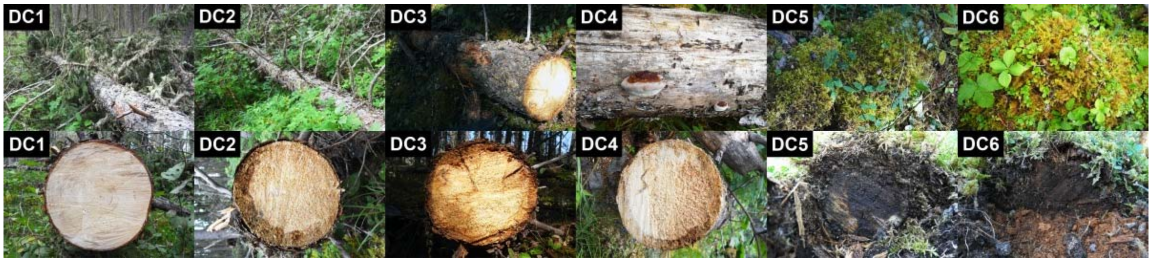


Fig. 2.1. White spruce downed coarse woody debris of each decay class (DC). Upper photos indicate outer surfaces, and lower photos indicate cross-sections of each DC.

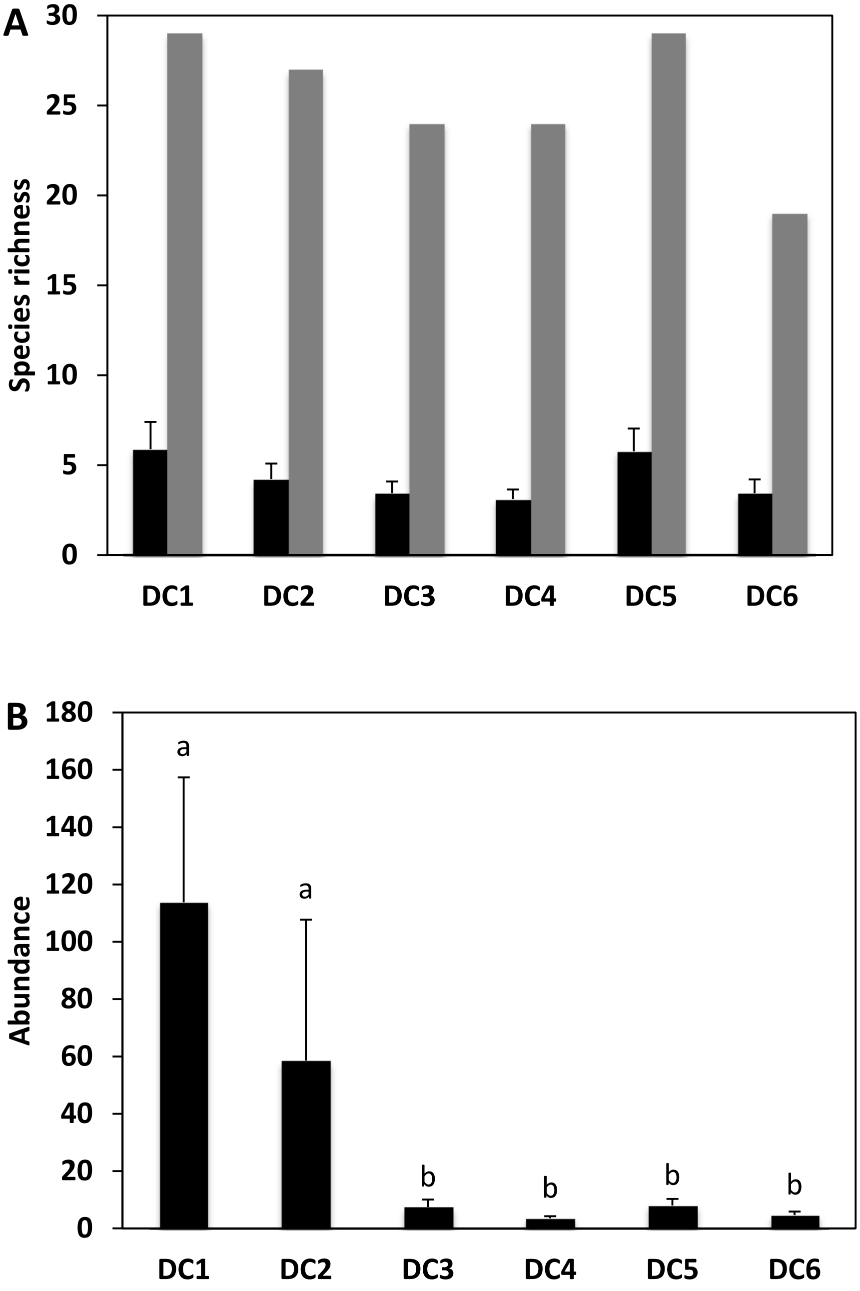


Fig. 2.2. Species richness (A) and abundance (B) of adult saproxylic beetles among decay classes (DCs). Black bars represent mean species richness and mean abundance per replicate. Grey bars represent total species richness for all replicates combined. Error bars represent +1 SE for nine substrates in each DC. Different small letters indicate significant *post hoc* results (Tukey's H.S.D. tests, $p < 0.05$).

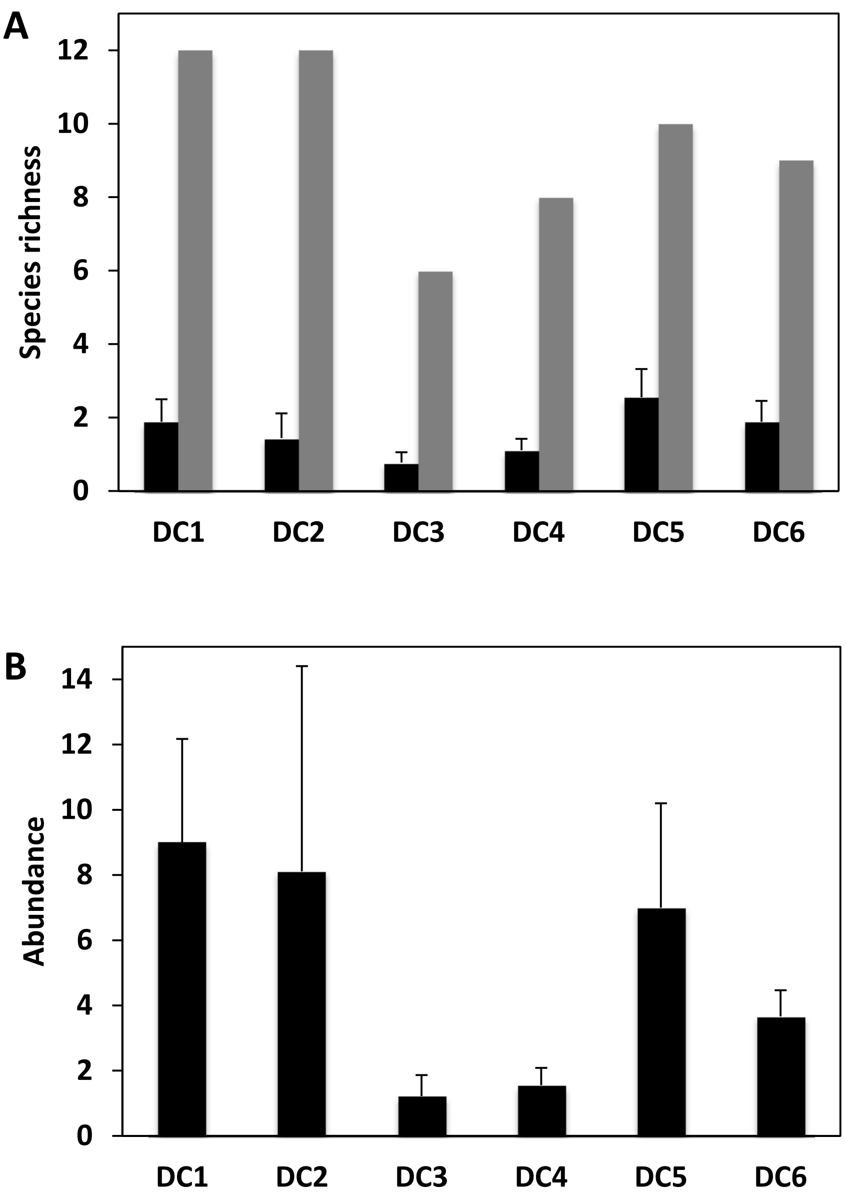


Fig. 2.3. Species richness (A) and abundance (B) of saproxylic beetle larvae among decay classes (DCs). Black bars represent mean species richness and mean abundance per replicate. Grey bars represent total species richness for all replicates combined. Error bars represent +1 SE for nine substrates in each DC.

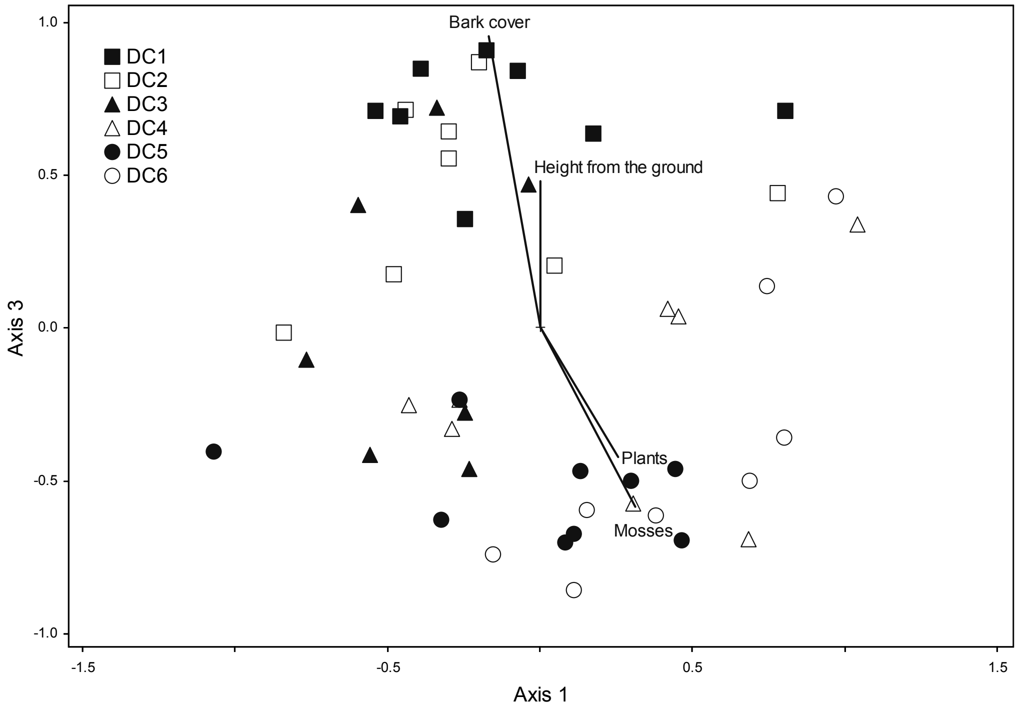


Fig. 2.4. Non-metric multidimensional scaling ordination of adult saproxylic beetles grouped by decay class (DC). Singletons were excluded, and the data were transformed to log (x + 1) prior to analysis. Final stress for a three-dimensional solution = 16.2.

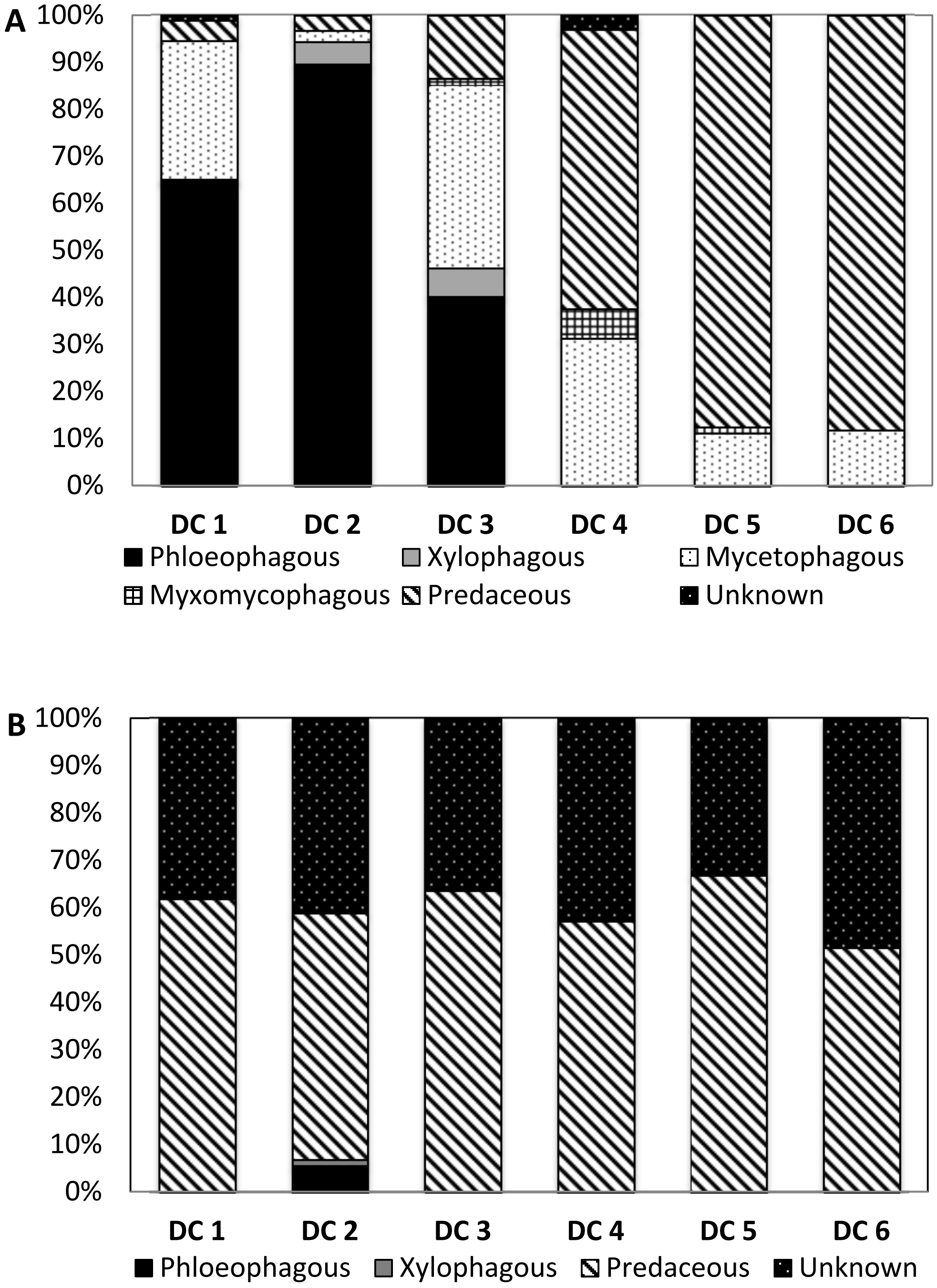


Fig. 2.5. Changes in percentage of feeding guilds on abundance of adult saproxylic beetles (A) and larvae (B) among different decay classes (DCs). Note that unknown feeding guild is most likely to be either mycetophagous or predaceous.

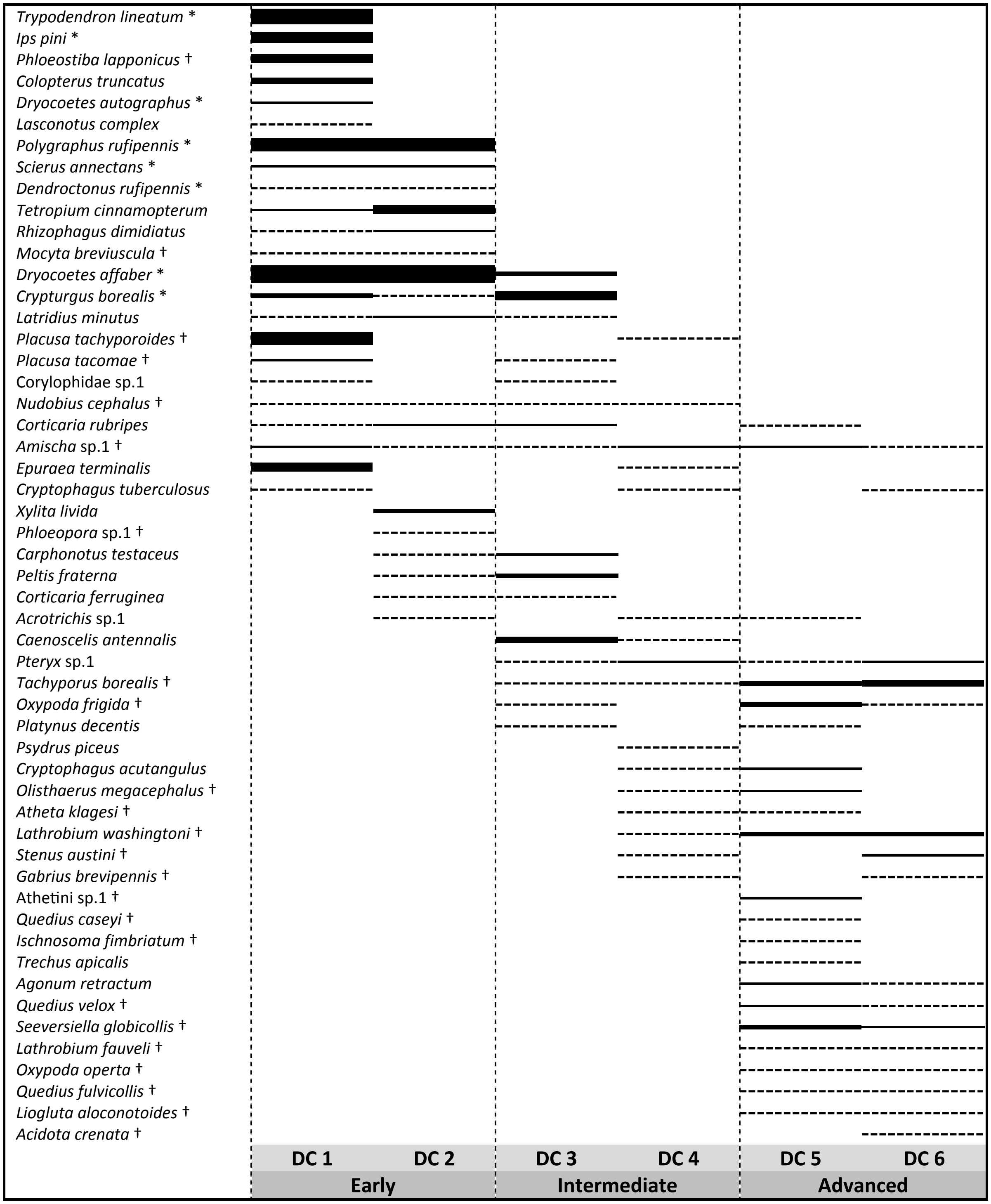


Fig. 2.6. Turnover in adult saproxylic beetle species along the decomposition gradient. The thickness of the lines represents the proportion of number of individuals. A dashed line indicates individuals appeared 1–2; the thinnest solid line indicates individuals

appeared 3–4; the thickest solid line indicates individuals appeared 257–512. Singletons were excluded in this figure. * indicates bark and ambrosia beetles (Curculionidae: Scolytinae). † indicates rove beetles (Staphylinidae). DC indicates decay class.

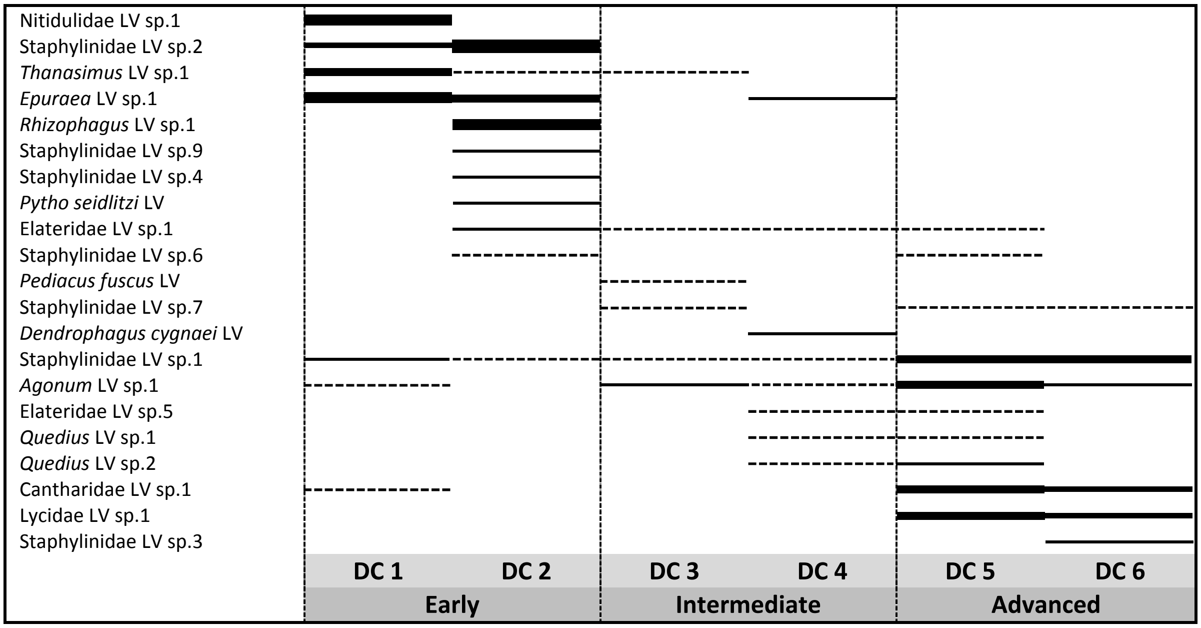


Fig. 2.7. Turnover in saproxylic beetle larvae along the decomposition gradient. The thickness of the lines represents the proportion of number of individuals. A dashed line indicates individuals appeared 1–2; the thinnest solid line indicates individuals appeared 3–4; the thickest solid line indicates individuals appeared 17–32. Singletons were excluded in this figure. DC indicates decay class. LV indicates larva.

CHAPTER 3

Retention patch size and conservation of saproxylic beetles in boreal white spruce stands

3.1. Introduction

Since its publication, the theory of island biogeography (MacArthur and Wilson, 1967) has strongly influenced conservation-oriented thinking about species distribution and permanence in fragmented landscapes (Laurance, 2008). For example, principles derived from island biogeography have been used for management of size, shape, dispersion, etc. of residual unharvested forest patches and legacies thought to function as biodiversity reserves for biota characteristic of pre-harvest conditions. Nonetheless, defining landscape targets for these traits remains a challenge for management of specific systems.

The general Natural Disturbance Model (NDM) was proposed as a new paradigm for guiding and improving forest landscape management over 20 years ago (Hunter, 1993). Proponents of the NDM approach hold that biodiversity and ecosystem functions can be maintained on forest landscapes by adopting logging practices that emulate dominant natural disturbances, e.g., wildfire, as much as possible to retain appropriate structural legacies (Hunter, 1993; Lindenmayer and Franklin, 2002). Under the broad NDM-based approach, retention of patches of uncut trees on harvested landscapes is promoted as an emulation of unburned ‘fire-skips’ that are thought to maintain populations of species that eventually colonize regenerating forest, thereby promoting recovery of biodiversity (Gandhi et al., 2001; Lindenmayer and Franklin, 2002; Work et al., 2003; Pinzon et al., 2012). Number and distribution of residual trees critically influence conservation and recovery of arthropod populations, especially ‘saproxylic’ insects that use deadwood as a resource (Langor et al., 2008; Hyvärinen et al., 2010; Légaré et al., 2011), because such elements provide the diverse characteristics of deadwood essential for persistence of such species (Siitonen, 2001). However, it remains unclear if conservation value is maximized by emulating post-fire patterns with harvest residuals (Gandhi et al., 2004).

Deadwood, especially as coarse woody debris (CWD), and associated organisms are critical to forest ecosystem function, because of connections to wood decomposition and nutrient cycling (Stokland et al., 2012). Saproxylic beetles (Insecta: Coleoptera) receive considerable attention in forest conservation science, because they are among the most diverse and abundant of deadwood-associated organisms, are sensitive to environmental change, their natural history is relatively well-known, and sufficient taxonomic resources for rigorous scientific work are available for many groups (Gibb et al., 2006; Langor et al., 2008; Cobb et al., 2011). In northern Europe, extensive forest harvest has led to reductions in amount and quality of coarse woody material, which has contributed to local extirpation of some saproxylic beetle species (Siitonen, 2001). Thus, there has been increasing focus on saproxylic insect assemblages worldwide in relation to forest management and conservation (Speight, 1989; Økland et al., 1996; Langor et al., 2008; Grove and Forster, 2011; Bouget et al., 2014), and deadwood management is widely accepted as an important part of sustainable forest management (Hagan and Grove, 1999; Langor et al., 2008).

Although better understanding of relationships between forest patch size and conservation potential is required to more effectively manage landscapes (Gustafsson et al., 2012), only a little research has addressed this issue for arthropod assemblages in boreal forests (e.g., Halme and Niemelä 1993; Gandhi et al., 2004; Pearce et al., 2005; Webb et al., 2008; Pyper, 2009). Work in North America and Europe has shown that relatively small patches (≤1-ha) are ineffective for conservation of epigaeic species (Matveinen-Huju et al., 2006; Halaj et al., 2008; Aubry et al., 2009). Pyper (2009) suggested that patch sizes of at least 2-ha in coniferous forests and 3-ha in deciduous forests should be retained to conserve assemblages of epigaeic carabid and staphylinid species. Several studies have concluded that even 3-ha patches were likely insufficient to conserve carabid beetles and spiders specialized in coniferous forest (Halme and Niemelä, 1993; Pearce et al., 2005). Larrieu et al. (2014) suggested that at least 20 ha of uncut patches are needed to conserve microhabitats required to maintain local biodiversity in montane beech-fir forests.

We examined relationships between retention patch size and saproxylic beetle assemblages in managed forest landscapes in the western boreal region of Canada. Ours is the first study to consider saproxylic insects in relation to patch size in these extensive forests. Furthermore, we considered the role of edge effects as drivers of response to patch size, and tried to link variation in deadwood qualities to differences in species composition. This study is part of a long-term study of biodiversity responses to logging on an operational forest landscape that is being broadly managed under the NDM paradigm. Thus, we can examine the ‘real-world’ utility of green-tree retention in an adaptive management framework that embraces practical application of biodiversity data. The overall goal of the study is to explore how retention patches of spruce function for saproxylic beetle conservation on harvested mixedwood landscapes in the boreal forest of western Canada.

3.2. Material and methods

3.2.1. Study area

This work was done in three large industrial harvest blocks (56.682°N−56.711°N, 118.605°W−118.781°W), located in the same area of originally homogenous boreal forest, ca. 100 km northwest of Peace River, Alberta, Canada. These blocks, designated A, B, and C (respectively, 379 ha, 44 ha, and 105 ha), were all harvested in 2000, leaving retention patches ranging from 0.03 to 6.64 ha in size in an early application of a NDM-inspired harvest design (Fig. 3.1). As part of this industrial harvest operation, patch sizes and distributions were arbitrarily chosen at harvest to place a variety of patch sizes on the harvested blocks under the constraint that total within-block retention would not exceed 30% of the original stem density. White spruce (*Picea glauca*) was the dominant tree species in all patches (>70% of all live trees), followed by lodgepole pine (*Pinus contorta*), with smaller numbers of trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), black spruce (*Picea mariana*), and balsam fir (*Abies balsamea*) sprinkled unevenly through the patches. White spruce and lodgepole pine seedlings were planted in the harvested 'matrix' surrounding patches one year after harvest.

3.2.2. Experimental design and sampling procedure

We focus on two variables in this study, patch size and tree location within a patch, either in the center or on the edge. We selected 15 retention patches for study, ranging in size from 0.63 to 5.93 ha. We were most interested in changes in species composition of retention patches with respect to possible edge effects, how these may be affected over the range of patch sizes presently left behind by the most progressive commercial forestry in this region. Therefore, we subjectively divided the available patches into the following three size categories, with five patches per category: Small, 0.63-1.06 ha; Medium, 1.43-2.93 ha; and Large, 3.34-5.93 ha (Fig. 3.1; Table 3.1). In order to better understand how size affects the ability of a patch to retain something close to the fauna of uncut forest, we also sampled five sites in the harvested matrix, and five sites in nearby intact forests.

We also studied the influence of location within a patch (i.e., possible edge effects) on the saproxylic fauna. To do this we girdled one white spruce tree at both the center and edge of every patch and characterized the saproxylic beetle assemblages that initially colonized dying trees in each within-patch location. In intact forests, five trees were girdled ca. 200 m from the harvest edge, four adjacent to harvest block A and one adjacent to block C. No trees of sufficient size remained in the harvested matrix but we sampled beetles there as described below. We also chose one white spruce natural snag near both the center and edge of each patch, and one snag in each intact forest to characterize the saproxylic beetle assemblages that colonize trees dying from natural causes. These snags had similar characteristics, consistent with early stages of decomposition (i.e., >90% of bark and >50% of branches), and were estimated to have died 5-10 years before sampling. We could not consider potential effects of distance of patches from intact forests (e.g., isolation), because all patches available for study were relatively close (<200 m) to continuous forest or other large patches (Fig. 3.1).

Saproxylic beetles were sampled with window traps attached perpendicularly to stems of girdled trees and snags at 1.3 m above the ground. Traps were a transparent plexiglass panel (20 × 30 cm) with a cloth funnel and plastic cup (100 mL) attached to the bottom of the panel (Hammond, 1997). Low-toxicity propylene glycol (30 mL) was added to the cups as a preservative. The 80 traps were distributed as follows: one was placed on each of two girdled trees and two snags in each of 15 patches; one was placed on each of five girdled trees and five natural snags in intact forests; and one was placed at breast height on each of ten living trees that had been planted in the harvested matrix. Traps were emptied and serviced every three weeks from early June to mid-September of 2010 and 2011.

Although we did not girdle trees in the harvested matrix, this is not likely to affect our results because diameters of 10-year-old coniferous trees were c. 5 cm, too small to colonize for the majority of saproxylic beetles in our study because they depend on relatively thick phloem as a feeding habitat. Also, there were no snags in the harvested matrix.

3.2.3. Identification and feeding guilds

Taxonomic literature, the arthropod reference collection at the Northern Forestry Centre (Canadian Forest Service) and available taxonomic expertise (see Acknowledgements) were used to identify saproxylic beetles to the lowest taxonomic level possible. Nomenclature follows that of Bousquet et al. (2013).

Each beetle species was assigned to one of eight feeding guilds based on available information (e.g., Klimaszewski et al., 2007; Dollin et al., 2008; Lee et al., 2014):

mycetophages (MYC, feeding on fungi), myxomycophages (MYX, feeding on slime molds), omnivores (OMN, feeding on a variety of materials), phloeophages (PHL, feeding in phloem tissues), predators (PRE, feeding on live invertebrates), rhizophages (RHI, feeding on plant roots), saprophages (feeding on decaying organic materials), xylophages (XYL, feeding in xylem tissues). Species that we could not confidently place in one of the above categories were assigned as unknown (UNK). In general, we selected the three most abundant species in each of the four major feeding guilds encountered (i.e., phloeophages, xylophages, mycetophages, and predators) to analyze individual species responses.

Voucher specimens for all taxa considered here have been placed in the Invertebrate Ecology Laboratory collection (Department of Renewable Resources at the University of Alberta, Edmonton, Alberta, Canada) and in the arthropod museum of the Northern Forestry Centre (Canadian Forest Service, Edmonton, Alberta).

3.2.4. Coarse woody debris characteristics and measurements

We measured both volume and decay class (DC) of downed CWD (diameter > 7 cm) in a 5 m × 5 m quadrat placed around each window trap. We did not segregate data by CWD species for analysis because it was not always possible to reliably identify highly decayed material to species. The combined volume of *Picea* spp. and *P. contorta* CWD represented 68.5% of total volume, and volumes of *A. balsamea*, *Populus* spp., and unknown CWD represented 10.9%, 5.1%, and 15.5% of the total, respectively. The six-grade DC system from Lee et al. (2014) was initially applied to describe decay of all white spruce CWD. For example, DC 2 CWD is fully covered by bark but has branches with no needles. In contrast, DC 4 CWD has little bark and few branches. DC 6 CWD is mostly covered by mosses and plants and partly sunken into the ground. In the following analyses, we combined DCs 1-2, DCs 3-4, and DCs 5-6 as early, intermediate, and advanced decay classes, respectively, to reduce the possible effect of high but idiosyncratic variation in volume between adjacent decay classes (see Lee et al., 2014).

3.2.5. Statistical analyses

Prior to analysis, we standardized species richness and catch data to number of species (and individuals)/trap days to reduce effects of unequal sampling effort due to trap disturbance by wildlife. Because of disturbance, 2.5% of traps were excluded from analyses.

Since the experimental design was unbalanced and sites were nested in each of the three harvest blocks, we used general linear mixed models (GLMM) with residuals following a Gaussian distribution to test for differences in standardized species richness, standardized beetle catches, and CWD volumes among treatments (i.e., harvested matrix, edge and center of three sizes of patches, and interior of intact forests). We considered treatment as a fixed effect, and incorporated harvest block as a random effect in the model. Data were transformed applying the square root or double square root to meet the assumptions of normality and homogeneity of variance. We also used generalized linear mixed models (GzLMM) with residuals following a Poisson distribution as appropriate for count data, to test for differences in amount of CWD among treatments. We performed the GLMM using the ‘nlme’ package (Pinheiro et al., 2015), and the GzLMM using the ‘lme 4’ package (Bates et al., 2015), both in R version 3.1.2 (R Development

Core Team, 2014). We also used the ‘lsmeans’ (Lenth and Hervé, 2015) and the ‘multcompView’ (Graves et al., 2015) packages to assess all pairwise comparisons ($\alpha = 0.05$) of least-squares means (lsmeans).

We tested the null hypothesis of no differences in species composition among treatments using permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001), using PERMANOVA+ add on package for PRIMER v7 (Anderson et al., 2008; Clarke and Gorley, 2015), with Bray-Curtis distance measures calculated from square root transformed data. We partitioned variation using the conservative Type III sums of squares, as appropriate for both balanced and unbalanced designs (Anderson et al., 2008). We used 9999 permutations in our PERMANOVAs for the main tests, and 999 permutations for *a posteriori* pairwise comparisons when significant results were detected in the main test ($p < 0.05$). We combined the data about girdled trees and snags for analyses because it is unlikely that window traps installed on a single girdled tree and snag in each patch center or edge adequately represent saproxylic beetle assemblages of the retention patch.

Redundancy analysis (RDA) was used to: (1) assess variation in saproxylic beetle assemblages among treatments according to the volumes of downed CWD for each DC category (i.e., DCs 1-2, DCs 3-4, and DCs 5-6); (2) visualize differences in species composition among treatments; and (3) further explore the results of PERMANOVAs using a different analytical approach. RDA is an asymmetric canonical analysis based on multiple linear regression that produces ordinations of response variables (i.e., species data) constrained by explanatory variables (i.e., DC categories) (Legendre et al., 2011). A Hellinger transformation was applied to species data prior to RDA to reduce possible ‘horseshoe effect’ in ordination (Legendre and Gallagher, 2001). RDAs were performed in R version 3.1.2 using the ‘vegan’ package (Oksanen et al., 2012).

3.3. Results

3.3.1. Coarse woody debris

Neither the overall number of pieces nor volume of downed CWD varied among treatments; however, volume of DCs 5-6 differed significantly among treatments (F = 3.86, p = 0.023; Table 3.2). In general, there were lower volumes of CWD in advanced decay stages in the matrix, edges of small and medium patches, and centers of medium patches, compared to intact forests (Table 3.2). There was a narrow range of deadwood quality in the matrix; i.e., there was no evidence of DCs 1-2 or DCs 5-6. In contrast, intermediate decay classes, and especially DC 4 (96.5%) comprised the great majority of CWD in these very dry environments ten years after harvest (Table 3.2).

3.3.2. Species richness and abundance

We tallied 8546 saproxylic beetles, representing 42 families and 260 species, over two sampling seasons (Appendix 3-A). Staphylinidae was the most species-rich family (58 species) followed by Curculionidae (27 spp.) and Cerambycidae (20 spp.). Curculionids were most abundant (6249 individuals), representing 73.1% of the total catch, followed by staphylinids (384) and monotomids (249). The nine most common species were bark beetles (Curculionidae: Scolytinae); among them, the most common species was *Scierus annectans* with 1536 individuals, representing 18% of total beetle catch.

Neither beetle abundance nor standardized richness varied in striking ways among patch sizes or between patch centres and edges. Standardized catches of beetles did not differ among treatments. Although GLMM gave a significant overall result ($F = 4.75$, $p = 0.011$) and trap mean catches were markedly higher in the centre of large patches, variances were high and *post hoc* multiple comparisons of adjusted means did not detect any significant differences (Fig. 3.2). Standardized species richness differed among treatments ($F = 3.14$, $p = 0.044$), reflecting mainly that richness in the harvested matrix was significantly lower than that from the edges of medium patches (Fig. 3.2). However, richness was similar in all other combinations of patch size and within-patch location.

3.3.3. Species composition

Species composition of the pooled catches differed among treatments (PERMANOVA: Pseudo-$F = 2.19$, $p < 0.001$), with *post hoc* pairwise comparisons indicating that species composition in the matrix differed significantly from that of all other treatments (Table 3.3). Saproxylic beetle assemblages associated with edges of small and medium patches differed from those in intact forests; however, the assemblages of large patch edges and centers of all patch sizes did not differ from those in intact forests (Table 3.3). Species composition of the pooled catches, analyzed without data from the harvested matrix, also showed significant variation in species composition (PERMANOVA: Pseudo-$F = 1.30$, $p < 0.012$). Catches from the edges of small and medium patches differed significantly in composition from intact forests underscoring edge effects in small and medium patches (Table 3.3). Our analyses did not identify other significant pairwise effects.

Redundancy analysis (RDA) revealed significant differences in species composition among patch size-location combinations ($F = 1.35$, $p = 0.046$), but explained only 10.1% of the total variance (Fig. 3.3a). Among environmental variables, volumes of CWD for DCs 1-2 ($F = 1.44$, $p = 0.040$) and DCs 3-4 CWD ($F = 1.49$, $p = 0.050$) significantly accounted for most of the constrained variance in species composition. Visual assessment of Fig. 3.3a largely corroborates the results of PERMANOVA: (1) saproxylic beetle assemblages collected from the harvested matrix were markedly distinct from those of patches and intact forests based on 95% confidence intervals (CIs) and the gradient explained by axis 1; (2) assemblages within patches roughly separated along axis 2 according to whether they were at the patch edge or center; and (3) edge effects increased with decreasing patch size and with increasing amounts of dried CWD (i.e., DCs 3-4). Faunal structure in the centers of all sizes of patches overlapped with that of intact forests, but edge faunas of small and medium patches differed from those of intact forests. Interestingly, the fauna in the center of small patches was completely incorporated into the ellipse for the fauna in the edge of large patches, suggesting that retention of large patches maintain faunas similar to those in the center of small patches.

Since beetle assemblages of the matrix were highly distinct from those of patches and intact forests, we performed separate PERMANOVAs excluding data from the harvested matrix for phloeophages, xylophages, mycetophages, and predators. Only predators showed significant differences in species composition among treatments (Pseudo-$F = 1.52$, $p = 0.004$). Pairwise comparisons of treatment effects on predators showed that assemblages in small patch edges differed from those of centers of all patches and intact forests (Table 3.3). Also, the assemblages of medium patch edges differed significantly from those of medium and large patch centers and intact forests. Edge assemblages of large patches, however, did not differ from other treatments or intact forests (Table 3.3), suggesting that effects are relatively weak.

Redundancy analysis related observed structure of saproxylic guilds to environmental characteristics. For example, volumes of CWD for DCs 1-2 ($F = 1.66$, $p = 0.030$) and DCs 3-4 ($F = 2.01$, $p = 0.010$) significantly explained xylophage species composition (Fig. 3.3b). Xylophage assemblages associated with the center of all patches overlapped with those of intact forests. Interestingly, the edge assemblages of large patches were completely included in those from the center of small patches based on 95% CIs, underscoring the likelihood that assemblages in the center of small patches are highly affected by edge effects for xylophages (Fig. 3.3b).

Volume of CWD for DCs 3-4 ($F = 1.85$, $p = 0.010$) significantly explained species composition of mycetophage assemblages (Fig. 3.3c). Mycetophages associated with patch edges differed markedly from those in patch centers and intact forests. Assemblages from the centers of small patches were least similar to those of intact forests, compared to assemblages of larger patch centers (Fig. 3.3c). Species composition of phloeophages (RDA: $F = 0.95$, $p = 0.540$) and predators (RDA: $F = 1.13$, $p = 0.170$) were not explained by environmental variables.

3.3.4. Response of common species

The most common phloeophages, the bark beetles (Curculionidae: Scolytinae) *S. annectans*, *Crypturgus borealis*, and *Xylechinus montanus,* tended to be caught more in the centers of medium and large patches than elsewhere (Fig. 3.4a). Catches of the most common xylophages, *Rhyncolus brunneus* (Curculionidae), *Serropalpus substriatus* (Melandryidae), and *Tetropium cinnamopterum* (Cerambycidae), did not differ among edges and centers of patches and in intact forests; however, these species were notably absent from the matrix (Fig. 3.4b). Among mycetophagous beetles, catches of *Cryptophagus tuberculosus* (Cryptophagidae) differed significantly among treatments ($F = 5.08$, $p = 0.009$), with highest catches in intact forests (Fig. 3.4c). *Corticaria rubripes* (Latridiidae) tended to be caught less in the harvested matrix and small patch edges. However, *Corticaria gibbosa* (Latridiidae) tended to be caught more in the matrix (Fig. 3.4c). Among the three most common predators that feed on many bark beetle species, the catch of *Rhizophagus dimidiatus* (Monotomidae) differed significantly among treatments ($F = 8.46$, $p = 0.001$) and was highest in the center of large patches (Fig. 3.4d). Catches of *Thanasimus undatulus* (Cleridae) also differed significantly among treatments ($F = 3.79$, $p = 0.024$), with the highest catches in the edge of medium patches (Fig. 3.4d).

Among saproxylic species considered in our analysis, only the mycetophagous latridiids, *C. rubripes* and *C. gibbosa*, occurred in more than two of the five replicates of matrix. Most species were absent in the matrix or were found in only one replicate, underscoring the important role of retention patches for conserving populations of even common saproxylic beetles in boreal spruce forest after logging.

3.4. Discussion

Determining a threshold patch size for conservation is challenging and, in fact, may be quite impractical as an approach, because thresholds doubtlessly vary with species, forest type, and change in relation to the characteristics of the surrounding matrix. Nonetheless, it is relevant and important for biodiversity conservation to understand responses of forest organisms to environmental features being created in a modern retention forestry framework.

3.4.1. Patch size and conservation of saproxylic beetles

Our study demonstrates that centers of the smallest patches considered here (0.63-1.06 ha) maintain saproxylic beetle assemblages broadly characteristic of intact forests for at least ten years. Although beetle assemblages in the center of small patches were not clearly separated from those of larger patch centers or intact forests, assemblages in the center of small patches were more similar to those at the edge of larger patches (3.34-5.93 ha). This suggests that retention of large patches may rather naturally maintain beetle assemblages associated with small patch centers, if we consider the assemblages in small patches have special conservation value.

Edge effects generally appear to have negative influence in small patches (Moen and Jonsson, 2003; Halaj et al., 2008). For saproxylic beetles, such effects are more serious in small patches because the proportion of edge habitat is larger than in large patches. Our work partially supports previous findings that interior forest species are not well maintained in forest patches less than one ha on harvested landscapes (Matveinen-Huju et al., 2006; Aubry et al., 2009; Pyper, 2009). In contrast, a study of saproxylic beetles in relation to patch size conducted in eastern Canada showed no clear differences in species composition between small forest remnants (<1 ha) and interior of large forest areas (>80 ha) (Webb et al., 2008). However, these authors did not explore the edge nature of small patches.

The influence of patch size on structure of saproxylic beetle assemblages varied according to trophic guild, at least among early post-harvest colonizers. Phloeophages and xylophages were least affected by edge effects or patch size. This is unsurprising because many phloem- and xylem-feeders are well adapted as early colonizers of ephemeral resources; they are strongly attracted to fresh phloem and sapwood in weakened or newly dead trees (Ås, 1993) in both open and interior habitats. Nonetheless, *S. annectans* and *X. montanus* showed strong affinity for centers of medium-to-large patches and intact forests, suggesting that they have a strong preference for effective colonization in interior forest habitat. In an earlier study of saproxylic beetles on white spruce in the same region (Jacobs et al., 2007b), *X. montanus* was strongly associated with intact undisturbed forests but *S. annectans* was not. In Finland, the congeneric species, *Xylechinus pilosus*, likewise has strong affinity with interior forests (Peltonen and Heliövaara, 1998). Thus, work on *X. montanus*, a species with limited distribution in western North America (Bright, 1976), seems warranted to understand specific habitat requirements and to ascertain whether this species is a useful indicator of interior forest habitats.

Mycetophages were most affected by edges and patch size. At least medium-size patches are required to retain an assemblage structure similar to that of intact forests. Similarly, Jacobs et al. (2007b) found that mycetophagous beetles were most affected by intensity of local harvest. They suggested that increased exposure to sunlight and wind in harvested areas results in drier CWD, lower fungal abundance and diversity, and ultimately greatly altered mycetophage assemblages compared to those of cooler and moister forest interior habitats. As a group, mycetophages may be the best indicators of forest interior habitats. We found that, among abundant mycetophages, *C. tuberculosus* is most indicative of interior habitats, supporting findings of Jacobs et al. (2007b).

We found that predaceous beetles, the most dominant of which were specialized predators of bark beetles, showed a similar response to that of all feeding guilds combined; i.e., increased edge effects as patch size decreased, with assemblages becoming less similar to those of intact forests. *Rhizophagus dimidiatus*, a predator of bark beetles, was previously reported to have strong association with closed canopies, showing large differences in abundance between old-growth forest and sites with severe selection cutting (Légaré et al., 2011). In our study, catches of *R. dimidiatus* tended to increase as patch size increased, supporting previous findings.

Structural persistence of retention patches through time is an important consideration for determining optimal patch size at time of harvest. In Sweden, for example, 46% of retained Norway spruce trees died within 18 years in a single 1-ha patch embedded in a single 41-ha clearcut block (Jönsson et al., 2007). In the Pacific Northwest of Canada and USA, increased windthrow rates were observed in retention patches less or equal than 1-ha 12-16 years after harvest (Steventon, 2011; Urgenson et al., 2013). Thus, leaving patches at harvest of < 1-ha is likely insufficient to meet long-term conservation objectives, partly because they will change in size and character due to blow-down and edge effects. We show that large patches (≥3.34 ha) are required to minimize negative edge effects on saproxylic beetle assemblages characteristic of intact forests for at least ten years post-harvest; however, the conservation benefits cannot be reasonably projected into the future. Thus, it will be important to revisit this conclusion in older harvested sites. Also, although not investigated in this study, patch shape will likely influence its conservation value for saproxylic beetles as minimization of edge to area ratio will likely minimize edge effects (Moen and Jonsson, 2003; Gandhi et al., 2004; Yamaura et al., 2008).

3.4.2. Character of the harvested matrix

An earlier study in the same forest blocks showed that epigaeic carabid and staphylinid beetle assemblages of the harvested matrix differed from those of the surrounding intact forests seven years after harvest (Pyper, 2009). Furthermore, Niemelä et al. (1993) showed that many forest specialists were absent or present at very low population size in regenerating pine stands, even 27 years after harvest. Webb et al. (2008) also demonstrated that species composition of saproxylic beetles differed between retention patches and harvested matrix 5-10 years post-harvest, although species richness did not differ between patches and the matrix. In our study, saproxylic beetles in the matrix ten years post-harvest showed significantly different assemblage structure compared to retention patches and intact forests, and tended to be lower in species richness. Many common species of phloeophages, xylophages and predators that prefer closed canopies were not recorded, or were scarce in the regenerating forest of the matrix. It is anticipated that many more years are required to allow canopy closure and recruitment of new CWD before saproxylic assemblages in harvested stands begin to recover. The presence of dispersed residual in the matrix may hasten the availability of CWD and contribute to faster recovery, but this requires further study.

Deadwood management is crucial for sustainable forest management, because deadwood is a critical element of forest ecosystem function, providing unique structural and ecological attributes critical to persistence of various saproxylic species (Hagan and Grove, 1999; Langor et al., 2008). In fact, beetle catches from ten-year-old harvested matrix in our study likely reflect both the complete absence of CWD in early and advanced decay classes and the prevalence of very dry DC 4 logs. The low variety and quality of downed CWD together with the lack of snags in the harvested matrix was clearly associated with reduced saproxylic beetle diversity. This is not surprising because particular species depend on habitat provided by different decay classes (Langor et al., 2008; Ferro et al., 2012b; Lee et al., 2014).

3.4.3. Caution in implementing natural disturbance model

Forest fire has historically been the major stand-replacing disturbance across the boreal region of Canada (Bergeron et al., 2002), thus some forestry companies in Canada and other countries have moved toward management that leaves a range of retention patches to emulate the patterns of fire skips and other characteristics of natural disturbance to enhance conservation of biodiversity (Work et al., 2003; Gustafsson et al., 2012). Although variability in patch size has been advocated as an important aspect of maintaining biodiversity in harvest blocks under the natural disturbance model, this approach does not consider that current area-specific rates of forest harvest may exceed local rates of stand replacement through natural disturbance (Kuuluvainen, 2009; Bergeron and Fenton, 2012). Thus, in this era of extensive resource extraction, we suggest that goals of variable retention harvesting, especially using aggregated retention, should focus on the ability of residual patches to conserve intact forest biota. Therefore, we highlight the option of leaving a sufficient number of large patches, rather than seeking to blindly emulate historical size distributions (mainly less than 1 ha) as observed for fire skips. Retaining small patches (<1 ha) will have more conservation impact than leaving nothing in a site after harvest; however, smaller patches do not effectively conserve saproxylic beetle assemblages characteristic of interior forests because of strong edge effects, and small patches likely will be rendered altogether ineffective as lifeboats for species characteristic of intact forests within few decades through blow-down (Jönsson et al., 2007; Steventon, 2011). Larger patches, on the other hand, have larger core areas capable of maintaining intact forest species as forest habitat recovers in the surrounding matrix. An early aspect of the natural disturbance model was providing insurance against ecological uncertainty by simply emulating patterns. As processes are better understood, we may find that some aspects of strict emulation do not best promote desired outcomes.

3.5. Conclusions

Our study clearly showed that, after 10 years of isolation, even centers of small forest patches successfully maintained saproxylic beetle assemblages that initially colonize white spruce deadwood. Such assemblages were notably absent from the harvested matrix. These early colonizers likely respond strongly to variable retention harvesting, because, as long as there are resources (i.e., deadwood), they visit and utilize them regardless of patch size (Webb et al., 2008). However, edge effects were found in patches less than 2.93 ha, suggesting that larger patches (3.34-5.93 ha in this study) are adequate to minimize negative edge effects. Although we now have better understanding of how early colonizing saproxylic beetles respond according to patch size, information about how saproxylic organisms associated with well-decayed deadwood in retention patches is still quite limited.

Crucial questions remain with respect to how quickly and well species characteristic of intact forests recolonize the regenerating matrix via emigration from retention patches and edges of intact forest. Unsurprisingly, ten years is insufficient for saproxylic species typical of old-growth forest to re-establish populations in the matrix. It is likely that at least 60-70 years will be required for regenerating spruce to reach a size sufficient to supply new suitable habitats for saproxylic species requiring intact forest habitats. Furthermore, it will take another few decades for stands to naturally develop advanced decay classes of large logs and snags that are critical habitats for many saproxylic species. Thus, we suggest that planning retention to maximally conserve the full range of habitats for saproxylic species is better than blind emulation of fire skip size distributions. Although it seems that the small patches (0.63-1.06 ha) effectively maintain early colonizing saproxylic beetles over ten years post-harvest, they may be inadequate in the future because of blow-down and encroachment of edge effects. Thus, the minimum patch size will need to be re-examined over time.

Table 3.1

Sizes of studied retention patches and surrounding harvest blocks.

Block	Patch	Retention patch size (ha)	Harvest block size (ha)
A	Small 1	0.63	379
A	Small 2	0.76	379
A	Small 3	0.77	379
A	Small 4	0.94	379
C	Small 5	1.06	105
C	Medium 1	1.43	105
A	Medium 2	1.59	379
A	Medium 3	1.71	379
B	Medium 4	2.29	44
C	Medium 5	2.93	105
B	Large 1	3.34	44
A	Large 2	4.47	379
C	Large 3	4.52	105
A	Large 4	4.58	379
A	Large 5	5.93	379

Table 3.2

Mean (± SE) number and volume of downed coarse woody debris (all species combined) in harvested matrix, edge and center of three sizes of retention patches, and intact forest of boreal white spruce stands.

Treatment[A]	Number of logs/50m^2	Volume of logs (m^3/50m^2)	DCs 1-2 (m^3/50m^2)	DCs 3-4 (m^3/50m^2)	DCs 5-6 (m^3/50m^2)[B]
HM	10.2 ± 1.2	0.36 ± 0.06	0	0.36 ± 0.06	0 a
ES	10.8 ± 1.8	0.94 ± 0.20	0.23 ± 0.09	0.68 ± 0.18	0.03 ± 0.02 a
EM	9.8 ± 2.7	0.78 ± 0.21	0.27 ± 0.14	0.47 ± 0.18	0.05 ± 0.02 ab
EL	6.4 ± 1.1	0.52 ± 0.06	0.10 ± 0.05	0.35 ± 0.08	0.07 ± 0.05 ab
CS	9.6 ± 1.2	0.58 ± 0.14	0.11 ± 0.05	0.37 ± 0.15	0.10 ± 0.04 ab
CM	7.6 ± 1.9	0.48 ± 0.24	0.18 ± 0.16	0.27 ± 0.08	0.03 ± 0.01 a
CL	6.0 ± 1.0	0.48 ± 0.11	0.08 ± 0.04	0.33 ± 0.11	0.07 ± 0.03 ab
IF	6.0 ± 1.4	0.40 ± 0.05	0.04 ± 0.02	0.16 ± 0.04	0.20 ± 0.05 b
	$p = 0.198$	$p = 0.074$	$p = 0.240$	$p = 0.106$	$p < 0.001$

Note: Decay classes (DCs) of coniferous and deciduous logs are adapted from Lee et al. (2014) and Wood (2012), respectively.

[A] Abbreviations: CL (center large), CM (center medium), CS (center small), EL (edge large), EM (edge medium), ES (edge small), HM (harvested matrix), and IF (intact forest).

[B] Different letters show significant differences according to GLMM results for each environmental factor (i.e., each column).

Table 3.3

Pairwise comparisons of assemblage composition among patch size-location combinations for all feeding guilds combined and for predators.

Treatments compared[A]	All feeding guilds (HM included)		All feeding guilds (HM excluded)		Predators (HM excluded)	
	t	*p*	*t*	*p*	*t*	*p*
HM vs. ES	1.78	**0.007**	-	-	-	-
HM vs. EM	2.27	**0.006**	-	-	-	-
HM vs. EL	2.12	**0.010**	-	-	-	-
HM vs. CS	2.18	**0.007**	-	-	-	-
HM vs. CM	2.62	**0.009**	-	-	-	-
HM vs. CL	2.11	**0.014**	-	-	-	-
HM vs. IF	2.25	**0.011**	-	-	-	-
ES vs. EM	1.08	0.227	1.08	0.234	1.21	0.114
ES vs. EL	0.98	0.517	0.98	0.525	0.72	0.935
ES vs. CS	1.12	0.177	1.19	0.183	1.36	**0.045**
ES vs. CM	1.57	**0.009**	1.57	**0.009**	1.37	**0.019**
ES vs. CL	1.22	**0.031**	1.22	**0.043**	1.58	**0.006**
ES vs. IF	1.30	**0.026**	1.30	**0.035**	1.45	**0.014**
EM vs. EL	0.88	0.911	0.88	0.916	1.10	0.216
EM vs. CS	1.11	0.170	1.11	0.168	1.39	0.055
EM vs. CM	1.51	**0.011**	1.51	**0.005**	1.66	**0.013**
EM vs. CL	1.17	0.085	1.17	0.082	1.53	**0.008**
EM vs. IF	1.28	**0.030**	1.28	**0.029**	1.61	**0.026**
EL vs. CS	1.01	0.467	1.01	0.461	1.20	0.143
EL vs. CM	1.33	**0.019**	1.33	**0.029**	1.20	0.089
EL vs. CL	0.94	0.660	0.94	0.699	1.06	0.304
EL vs. IF	1.02	0.471	1.02	0.455	1.02	0.465
CS vs. CM	1.14	0.139	1.14	0.141	0.81	0.881
CS vs. CL	1.02	0.408	1.02	0.414	1.08	0.277
CS vs. IF	1.04	0.389	1.04	0.408	1.11	0.281
CM vs. CL	1.05	0.257	1.05	0.265	1.08	0.273
CM vs. IF	1.12	0.168	1.12	0.153	0.97	0.554
CL vs. IF	0.84	0.892	0.84	0.897	0.90	0.730

Note: Pairwise comparisons were conducted in two ways: 1) all feeding guilds combined and 2) predators only, in which significant differences were detected on main tests of PERMANOVA. Significant differences ($p < 0.05$) are highlighted in bold.

[A] Abbreviations: CL (center large), CM (center medium), CS (center small), EL (edge large), EM (edge medium), ES (edge small), HM (harvested matrix), and IF (intact forest).

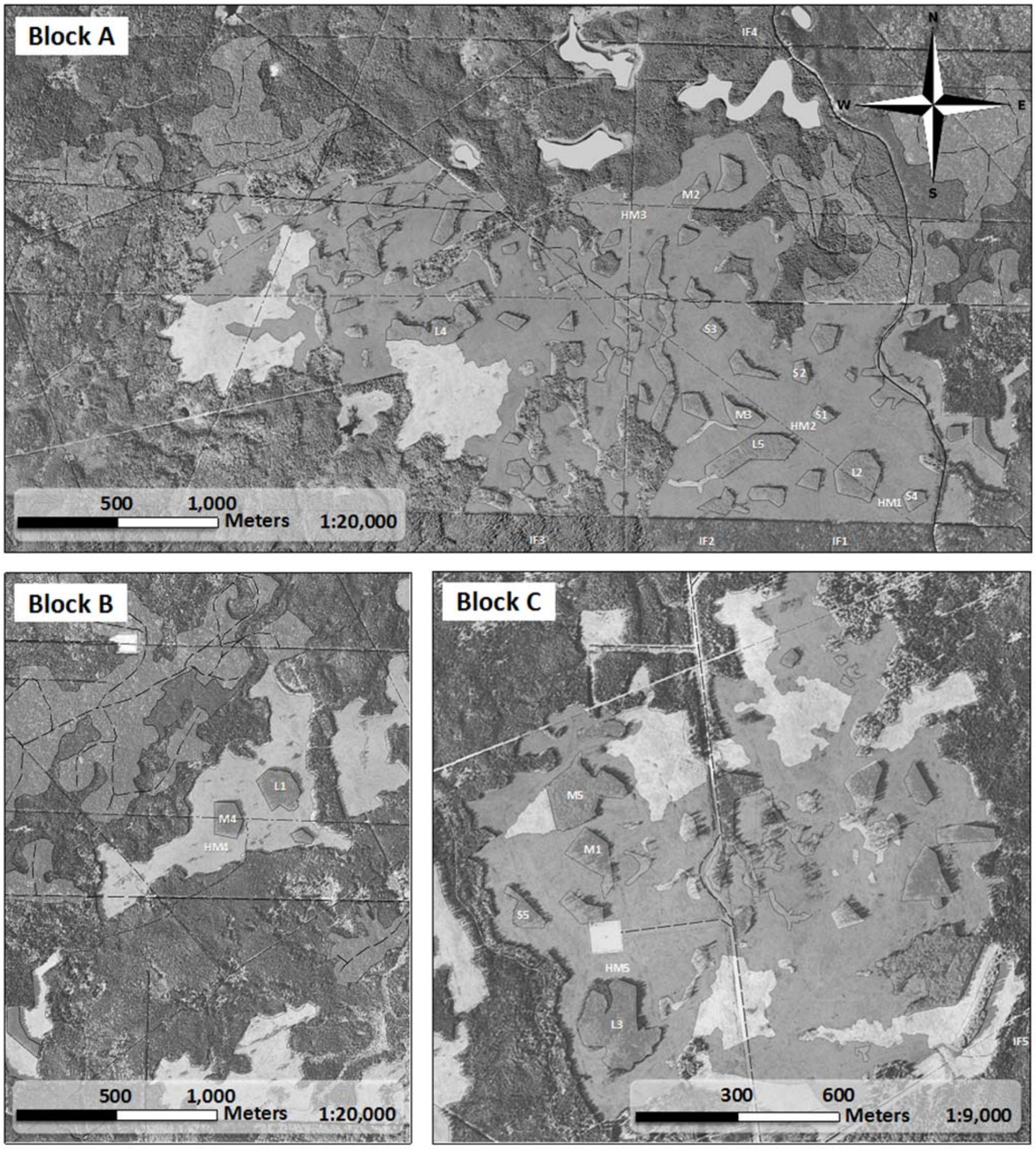


Fig. 3.1. Aerial views of the three studied harvest blocks harvested in 2000: A (379 ha), B (44 ha), and C (105 ha). Abbreviations: HM (harvested matrix), IF (intact forest), L (large), M (medium), and S (small). Each retention patch size is described in Table 3.1.

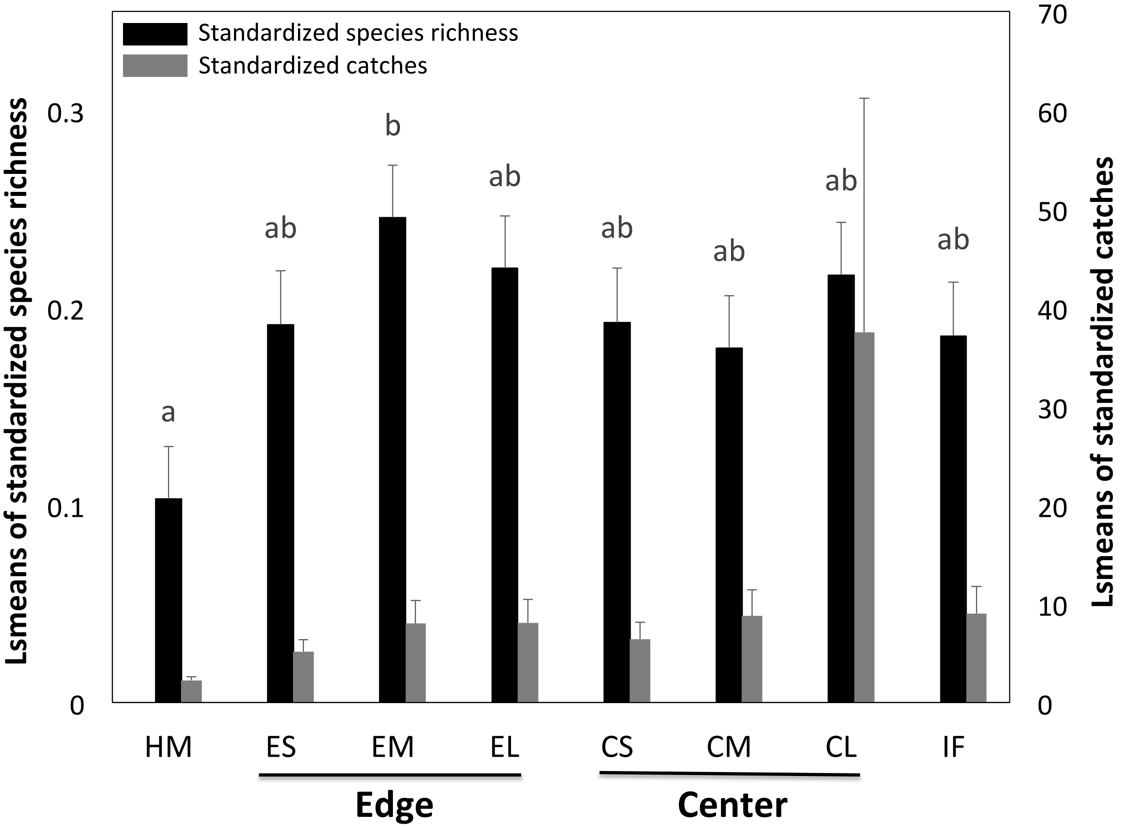
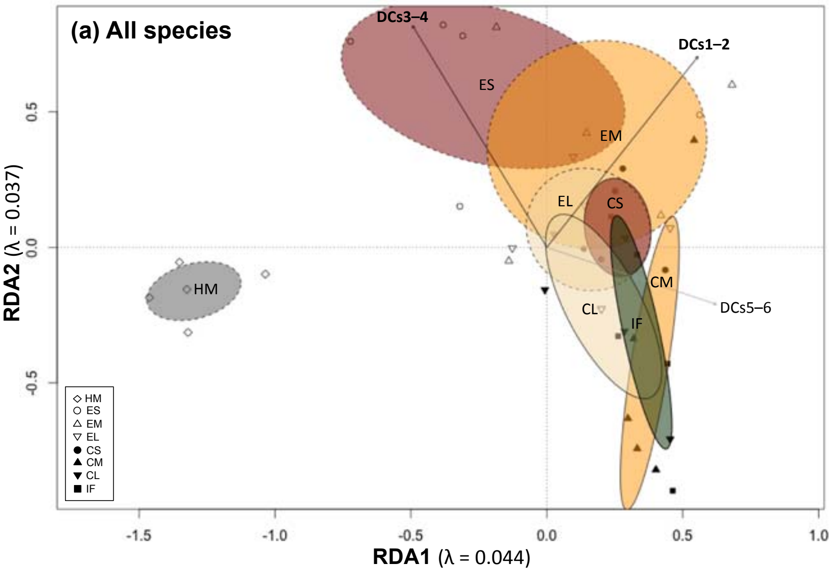
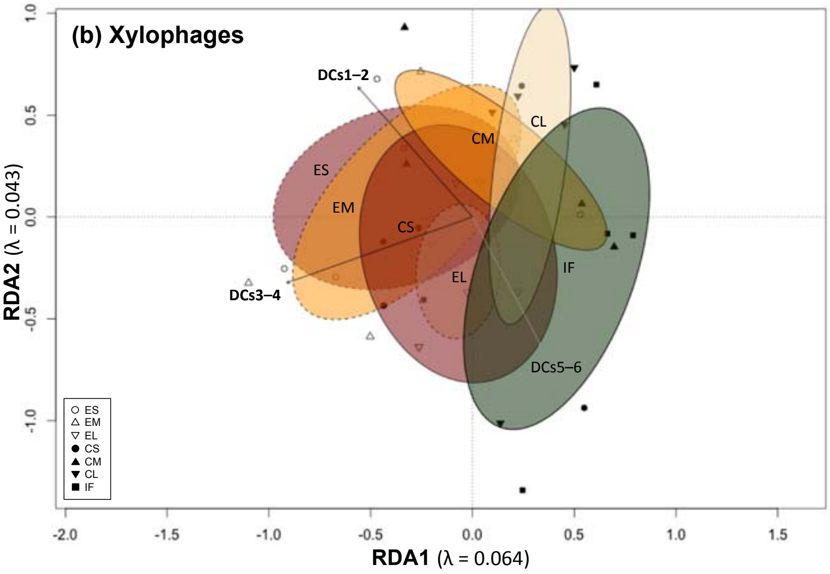


Fig. 3.2. Lsmeans of standardized species richness and standardized catches (number of beetles/trap days) of saproxylic beetles in 10-year-old harvested matrix, edge and center of three size classes of retention patches, and in intact forest of white spruce stands. Error bars represent the SE for five replicates of each treatment. Bars with different letters are significantly different according to GLMM. Abbreviations: CL (center large), CM (center medium), CS (center small), EL (edge large), EM (edge medium), ES (edge small), HM (harvested matrix), and IF (intact forest). There was no treatment effect on standardized catches.


(a) All species
DCs3–4
DCs1–2
DCs5–6
ES
EM
EL
CS
CM
CL
IF
HM
◇ HM
○ ES
△ EM
▽ EL
● CS
▲ CM
▼ CL
■ IF
RDA1 (λ = 0.044)
RDA2 (λ = 0.037)
-1.5
-1.0
-0.5
0.0
0.5
1.0
0.5
0.0
-0.5


(b) Xylophages
DCs1–2
DCs3–4
DCs5–6
ES
EM
EL
CS
CM
CL
IF
○ ES
△ EM
▽ EL
● CS
▲ CM
▼ CL
■ IF
RDA1 (λ = 0.064)
RDA2 (λ = 0.043)
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
1.0
0.5
0.0
-0.5
-1.0

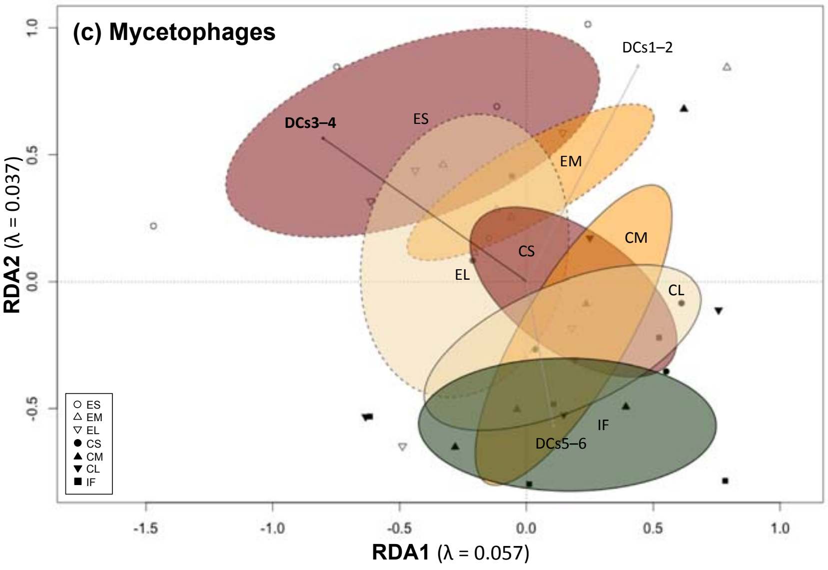

(c) Mycetophages
DCs1–2
DCs3–4
DCs5–6
ES
EM
EL
CS
CM
CL
IF
○ ES
△ EM
▽ EL
● CS
▲ CM
▼ CL
■ IF
RDA1 (λ = 0.057)
RDA2 (λ = 0.037)
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.0
0.5
0.0
-0.5

Fig. 3.3. Redundancy analysis (RDA) of saproxylic beetle assemblages of (a) all species combined, (b) xylophages, and (c) mycetophages among treatments. Note that we excluded harvested matrix for analyses of (b and c). Ellipses show 95% confidence intervals around group centroids. Significant and non-significant environmental variables are indicated with black and grey arrows, respectively. Colors of ellipses: grey (harvested matrix), red (small patch), orange (medium patch), beige (large patch), and green (intact forest). Abbreviations: CL (center large), CM (center medium), CS (center small), DCs (decay classes), EL (edge large), EM (edge medium), ES (edge small), HM (harvested matrix), and IF (intact forest).

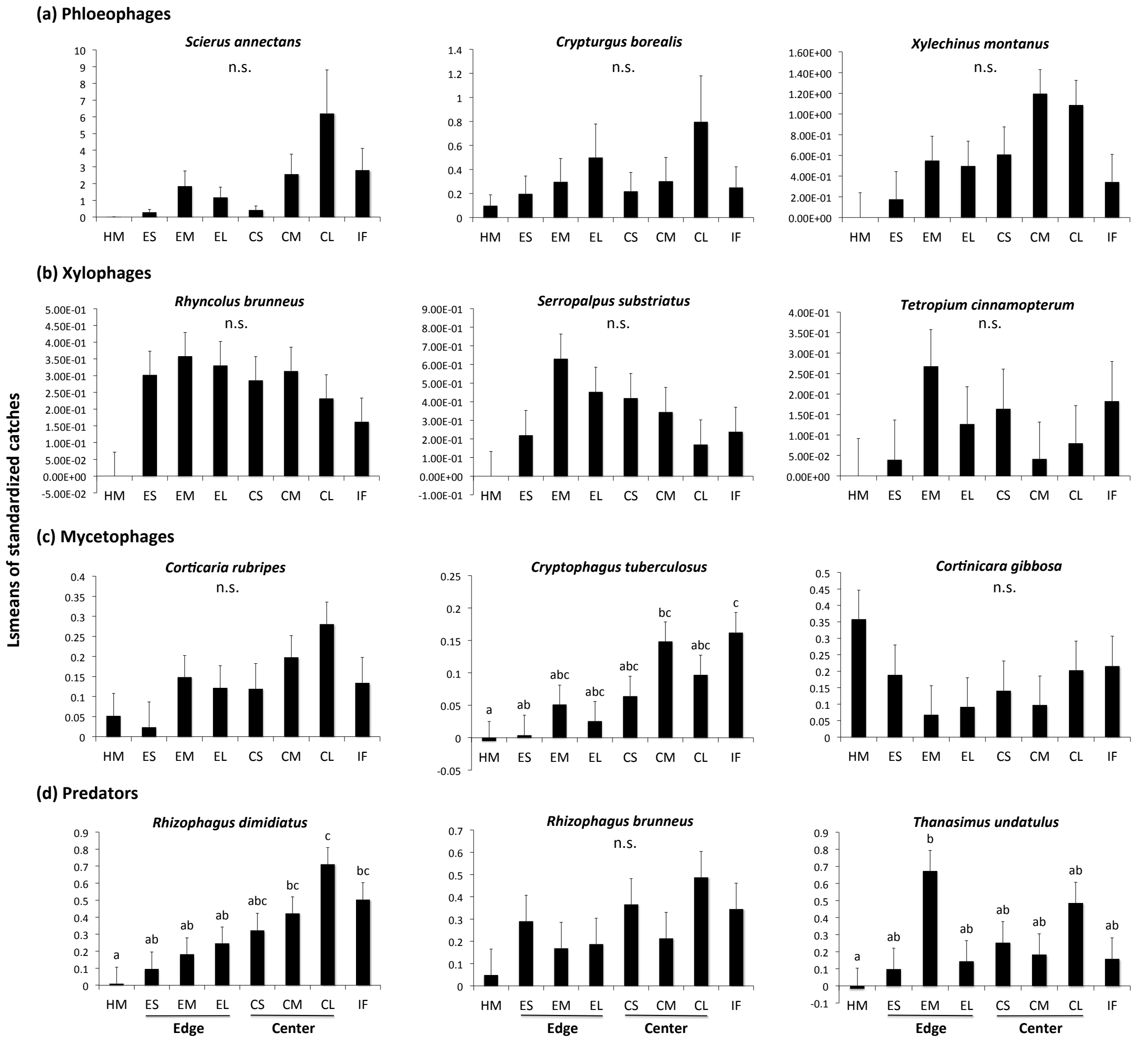


Fig. 3.4. Lsmeans of standardized catches (number of beetles/trap days) of 12 common saproxylic beetle species (three from each of the four major feeding guilds) in 10-year-old harvested matrix, edge and center of three size classes of retention patches, and in intact forest of white spruce stands. Error bars represent the SE for five replicates of each treatment. Bars with different letters are significantly different according to GLMM. Note that n.s. represents a non-significant result. Abbreviations: CL (center large), CM (center medium), CS (center small), EL (edge large), EM (edge medium), ES (edge small), HM (harvested matrix), and IF (intact forest).

CHAPTER 4

Combination of aggregated and dispersed retention conserve saproxylic beetles in boreal white spruce stands

4.1. Introduction

Retention forestry, variously also known as new forestry, green-tree retention and variable retention, has been increasingly adopted in North and South America, Australia and Scandinavian countries as a forest management approach to conserve biodiversity (Franklin et al., 1997; Lindenmayer and Franklin, 2002; Aubry et al., 2009; Work et al., 2010; Baker and Read, 2011; Lencinas et al., 2011; Gustafsson et al., 2012). In contrast to traditional forestry focused on timber production and rapid regeneration, retention forestry aims to promote heterogeneity of forest structure and composition that maintains biodiversity and ecological functions (Gustafsson et al., 2012). Inspired by natural disturbance such as wildfire, retention forestry is based on emulating patterns and processes inherent in natural disturbances, shaping spatiotemporally heterogeneous forests (Lindenmayer et al., 2012; Gustafsson et al., 2012).

Following harvest, retention may be left in aggregations, as patches of live and dead trees of various sizes, or dispersed more widely as individual trees (Franklin et al. 1997; Baker, 2010). Aggregated retention promotes persistence of live trees, undisturbed forest floor and interior forest specialist species (Franklin et al., 1997; Baker, 2011; Pinzon et al., 2012). Dispersed retention enhances distribution of deadwood, connectivity of belowground biota, edge-preferred species and forest aesthetics (Lindenmayer and

Franklin, 2002; Baker and Read, 2011; Pinzon et al. 2012). Combinations of aggregated and dispersed retention are generally advocated to accommodate the complementary advantages of both retention types (Baker, 2011), and this approach has been adopted by some forest products companies in Canada and the USA (Baker, 2011; Gustafsson et al., 2012). Although mixtures of aggregated and dispersed retention are thought to better conserve forest biodiversity compared to use of either approach alone, or to clearcuts, there has been little effort to test this hypothesis (e.g., Lencinas et al., 2011; Pinzon et al., 2012). Controlled, well-replicated experiments testing the efficacy of aggregated and dispersed retention for biodiversity conservation can contribute to guiding forest management practices and policy.

Deadwood management is recognized as a key component of sustainable forest management (Hagan and Grove, 1999; Siitonen, 2001; Lindenmayer and Franklin, 2002; Langor et al., 2008; Hjältén et al., 2012; Stokland et al., 2012). Deadwood is intimately involved with nutrient cycling and carbon dynamics (Harmon et al., 1986), provides seedbeds for plant germination to promote forest regeneration (Gray and Spies, 1997), and serves as important habitats for many saproxylic species (Hammond, 1997; Ferro et al., 2012; Lee et al., 2014). In fact, it is well established that the variation in deadwood (e.g., species, sizes, decay classes, and types such as snags or logs) provides essential habitats for a variety of species (Grove, 2002; Ferro et al., 2012; Wood, 2012; Lee et al., 2014). Populations of saproxylic organisms have been drastically impacted by extensive harvesting in the boreal forests of northern Europe, leading to extirpation of many species and perhaps even some examples of extinction (Siitonen, 2001; Djupström et al., 2008; Stokland et al., 2012). In Finland, for example, reductions in volume of dead or dying trees are thought to have been the most common cause of decline and the second-most important cause of extinction for threatened forest species (Rassi et al., 2010). As a result, the importance of deadwood for conserving saproxylic biodiversity is well established (Siitonen, 2001; Jonsson et al., 2005; Franc, 2007; Jonsell et al., 2007; Stokland et al., 2012).

Saproxylic beetles provide excellent model organisms for study of forestry impacts on biodiversity because they are taxonomically and functionally diverse and are well known to be sensitive to forestry practices (Siitonen, 2001; Langor et al., 2008; Bouget et al., 2014). Beetles are also one of the best-known groups of saproxylic organisms in Canada, and their taxonomy and ecology has recently been well documented in our study area (Jacobs et al., 2007a, 2007b; Wood, 2012; Lee et al., 2014). The main objective of the present study is to test the efficacy of combining aggregated retention and various degrees of dispersed retention on saproxylic beetle assemblages 10-11 years post-harvest in boreal white spruce stands. I hypothesize that as the amount of dispersed retention increases, the capacity of aggregated retention patches to conserve saproxylic beetle assemblages will also increase.

4.2. Material and methods

4.2.1. Study area and experimental design

The study was conducted in three white spruce [*Picea glauca* (Moench) Voss] dominated stands (56°74′95″N–56°80′75″N, 118°32′23″W–118°41′90″W) at the Ecosystem Management Emulating Natural Disturbance (EMEND) research site, located in northwestern Alberta, Canada. EMEND is a fully replicated 4 × 8 factorial experiment designed to test the natural disturbance paradigm by asking specifically how variable retention harvesting affects biodiversity, forest regeneration, nutrient cycling, water, public perception, etc. Five harvest treatments, and three replicates of each, were applied to 10 ha compartments of each of four forest cover-types (deciduous-dominated, deciduous with white spruce understory, mixed, and coniferous-dominated stands) during the winter of 1998-99. Each harvested compartment included two aggregated retention patches (one 0.20 ha and one 0.46 ha) within the matrix of dispersed retention [2% (standard clearcut), 10%, 20%, 50%, and 75%] (see Work et al. (2010) for a detailed description of the design of the EMEND experiment).

We studied saproxylic beetle assemblages in retention patches in three of the dispersed retention harvest treatments, 2%, 20%, and 50%, in white spruce-dominated stands (Fig. 4.1; Fig. 4.2), and compared them to assemblages in unharvested control compartments.

4.2.2. Saproxylic beetle sampling

Saproxylic beetles were sampled from June to September of 2009 and 2010 using window traps and emergence traps. Window traps have been widely used for collecting invertebrates because they yield large numbers of species and individuals, allowing statistically reliable samples. However, the species assemblages and relative abundances collected in a window trap attached to a snag do not perfectly reflect the assemblages actually using the snag, i.e., there are also incidental captures of non-saproxylic insects captured in flight (Siitonen, 1994; Hammond, 1997; Langor et al., 2008). Thus, emergence traps were also deployed to provide information about beetles that actually emerged from snags and this information helped us to interpret the window trap captures (Wood, 2012).

Window traps were placed on girdled trees and snags (all 30-40 cm DBH) in retention patches of both sizes in white spruce dominated compartments. Four window traps were deployed in each patch and in unharvested controls, two on newly girdled trees and two on natural snags of decay class 2. Beetles were sampled from one girdled tree and one natural snag at both the edge and in the center of each patch, whereas all traps were deployed in the interior of control compartments. The experiment was replicated three times to study a total of 18 retention patches (nine of each size) and three unharvested controls. Natural snags selected for sampling were at an early stage of decomposition; all had more than 90% bark cover and 50% of fine branches remaining, but no needles.

Window traps were transparent plexiglass panels (20 × 30 cm) with cloth funnels attached to the bottom of each panel (Hammond, 1997). Plastic cups (100 mL), containing approximately 30 mL of propylene glycol as a killing-agent and preservative, were attached to the bottom of the funnels. The traps were attached with the panel perpendicularly to the trunk at breast height (ca. 130 cm) using wire. In total, 84 window traps were deployed for the study. Saproxylic beetles were collected every three weeks, preserved, and later identified to species in the laboratory.

Emergence traps were installed in the same patches and control compartments as were window traps, but only in the centers of the patch. In each patch and control compartment, two emergence traps were set on each of two decay classes (DCs) of downed wood, one in an early stage of decay (DC 2) and one in an intermediate stage

(DC 4). Logs selected for these emergence traps were cut c. 3 m in length and elevated to lean against live trees before installing emergence traps, mainly because traps deployed on logs on the forest floor are subject to high levels of animal disturbance near the EMEND site (Wood, 2012). Emergence traps were constructed by wrapping a ca. 1 m length of a log with no-see-um mesh (0.6 mm × 0.6 mm), and stapling the sides together to form a tube. The mesh tube was fastened to the trunk with wire, and glue was used to fill any spaces between the wire and the trunk to prevent beetle escape. Plastic bottles (300 mL, diameter of spout = 25 mm), containing approximately 50 mL of propylene glycol, were attached to the bottom of the mesh to collect emerging beetles. A total of 84 emergence traps were deployed, and the beetles were collected periodically and on the same day as those in window traps.

4.2.3. Identification of saproxylic beetles and trophic guilds

Beetles were identified using taxonomic literature (e.g., Arnett and Thomas, 2001; Arnett et al., 2002) and the reference collections at the Northern Forestry Centre (Canadian Forest Service) and E. H. Strickland Entomological Museum (University of Alberta). Specimens of taxonomically difficult taxa, such as aleocharine rove beetles (Staphylinidae: Aleocharinae), were dissected to reveal genital characters and identified by taxonomic experts (see Acknowledgements). For names, I followed Bousquet et al. (2013).

Non-saproxylic beetle taxa collected from window traps were not included in analyses. Two species of Nitidulidae [*Epuraea avara* (Randall) and *E. terminalis* (Mannerheim)] and three species of Staphylinidae [*Placusa incompleta* Sjöberg, *P.*

pseudosuecica Klimaszewski, and *P. tachyporoides* (Waltl)] were classified and tallied as *Epuraea* spp. and *Placusa* spp., respectively, because certain identification of females of these species was not possible. Saproxylic species were each categorized into eight functional trophic guilds (detritivores, mycetophages, myxomycophages, omnivores, phloeophages, predators, rhizophages, and xylophages) based on information in the literature (e.g., Klimaszewski et al., 2007; Dollin et al., 2008; Wood, 2012; Lee et al., 2014).

Voucher specimens for all taxa have deposited in the Invertebrate Ecology Laboratory (Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada) and in the Arthropod Museum (Northern Forestry Centre, Canadian Forest Service, Edmonton, Alberta, Canada).

4.2.4. Coarse woody debris and live tree measurements

The volumes and decay class of every piece of CWD were measured in each small retention patch, and for half of each large patch. Data for all species of deadwood were combined for analyses because there were uncertainties in identification of highly decayed CWD. *Picea* CWD (mostly *P. glauca*) represented 67.3% of total volume, while *Populus* spp. and unidentified CWD represented 25.2% and 7.5 % of the total, respectively. We used a six-grade decay classification system (Wood, 2012; Lee et al., 2014) to assign class of decay to each piece of CWD. However, we combined DCs 1–2, DCs 3–4, and DCs 5–6, respectively, as early, intermediate, and advanced decay classes for our analyses (see Lee et al., 2014). The total number of live trees was counted in each small and large retention patch.

4.2.5. Statistical analyses

All trap catch data were standardized to number of individuals per trap-day prior to analysis to adjust for uneven sampling efforts due to disturbance by animals and small differences in sampling periods. We analyzed data from window and emergence traps separately because each trap samples even saproxylic beetle assemblages somewhat differently and the emergence data was confined to particular decay classes. Window trap data from girdled trees and snags were combined to reflect overall patterns of beetle responses to treatments. Emergence trap data from DC 2 and DC 4 were combined for rigorous analysis because too few beetles (i.e., 196 individuals) emerged from DC 4 logs.

We tested for significant differences in species richness, abundance of saproxylic beetles, and CWD volumes among treatments (i.e., aggregated retention patches surrounded by different levels of dispersed retention, and unharvested controls), using generalized linear models (GLMs). Errors were modeled as negative binomial distributions when the data were counts and overdispersed, and as Gaussian distributions when the data were continuous. We applied Tukey's Honestly Significant Difference to test *post-hoc* pairwise comparisons when the results of GLMs were significant ($p < 0.05$). We use R version 3.1.2 (R Development Core Team, 2014) to compute GLMs and subsequent pairwise comparisons using the 'MASS' (Venables and Ripley, 2002) and the 'multcomp' packages (Hothorn et al., 2008), respectively.

To measure species diversity, we adopted Hill numbers (i.e., the effective numbers of species or numbers equivalents) (Jost, 2007; Chao et al., 2014). Hill numbers are a parametric family of diversity indices, providing a more unified framework than classical indices. Hill numbers indicate the sensitivity of the relative frequencies of species along several ordered levels of q. For example, $q = 0$ simply means total species richness. When $q = 1$, the estimation becomes the exponential of Shannon entropy, or the Shannon index. When $q = 2$, the measure becomes Gini-Simpson concentration, and can be interpreted as the effective number of dominant species. As an order of q increases, the sensitivity of the index to common species increases, which means that dominant species are more important [See Jost (2007) and Chao et al. (2014) for the algorithm and formula]. For these calculations we used the 'd' function in the 'vegetarian' package (Charney and Record, 2009) in R (R Development Core Team, 2014).

We performed a permutational multivariate analysis of variance (PERMANOVA) to test null hypothesis of no differences in species composition among treatments. PERMANOVA is a non-parametric multivariate method that partitions variation and it may be based on any measure of distance (Anderson, 2001). Since there was no difference in species composition between small and large aggregated retention patches within the same level of dispersed retention based on the initial result of PERMANOVA, we pooled data from the two sizes of aggregated retention for further community analyses. This resulted in unbalanced data, i.e., there are still only three replicates of the unharvested control, but now there are six replicates for each harvest treatment. For this work, we used the PERMANOVA+ add on package for PRIMER v7 (Anderson et al., 2008; Clarke and Gorley, 2015) with Bray-Curtis distances on square-root-transformed data. We corrected for the unbalanced designs by using the conservative Type III sums-of-squares. PERMANOVAs for main tests used 9999 permutations, followed by *a* *posteriori* pairwise comparisons with 999 permutations when significant results were detected ($p \leq 0.05$).

We used non-metric multidimensional scaling (NMS) to visualize the structure of saproxylic beetle assemblages among the treatments and to provide visual tests of the results of PERMANOVA. NMS is an unconstrained ordination technique well-suited for ecological data because it avoids the assumption of linear relationships among variables and reduces the zero-truncation problem by using ranked distances (McCune and Grace, 2002). We performed the analysis using the 'metaMDS' function with Bray-Curtis distances from square-root-transformed data using 500 random starts in the 'vegan' package (Oksanen et al., 2012) in R (R Development Core Team, 2014). Confidence ellipses (95%) were calculated to help evaluate differences in assemblage composition in the ordination space

Both PERMANOVA and NMS were performed on the saproxylic beetles of all feeding guilds combined and also performed individually on the most common four feeding guilds, i.e., phloeophages, xylophages, mycetophages, and predators.

We used Indicator Species Analysis (Dufrêne and Legendre, 1997) to identify significant associations between species and treatments, using the 'labdsv' package (Roberts, 2013) in R (R Development Core Team, 2014). Indicator Values (IV) and probabilities ($\alpha = 0.05$) were calculated based on 4999 permutations.

4.3. Results

4.3.1. General results

A total of 45 042 saproxylic beetles were collected from the patches and control compartments, using both window traps and emergence traps (see Appendix A for breakdown by trap type). Overall, these represented 40 families and 289 species. Sixty-nine species were recorded by singletons (64 spp. and 50 spp. in window and emergence traps, respectively). Staphylinidae (55 spp.) was the most species-rich family in the window traps, followed by Curculionidae (28 spp.) and Cerambycidae (22 spp.). Curculionidae dominated the catch of window traps, with 36 818 individuals representing 90.3% of the total catch, followed by Cerambycidae (511 individuals) and Monotomidae (455 individuals). The ten most common species were all bark beetles (Curculionidae: Scolytinae); *Crypturgus borealis* was most common with 20 659 individuals accounting for 50.6% of the total catch, followed by *Dryocoetes affaber* (4868 individuals, 11.9%) and *Trypodendron lineatum* (2777 individuals, 6.8 %). A total of 210 species (34 919 individuals) and 212 species (5872 individuals) were sampled from girdled trees and snags, respectively.

In emergence traps, the most species-rich family was also Staphylinidae (34 spp.), followed by Curculionidae (16 spp.), Cryptophagidae (8 spp.) and Latridiidae (8 spp.). Curculionidae was the most abundant family with 3743 individuals, accounting for 88.0% of the total catch, followed by Staphylinidae (73 individuals) and Colydiidae (48 individuals). *Dryocoetes affaber* was the most common species in emergence traps with 2214 individuals, accounting for 52.1% of the total catch, followed by *Polygraphus rufipennis* (584 individuals) and *C. borealis* (464 individuals). A total of 108 species (4055 individuals) and 79 species (196 individuals) were sampled from DC 2 and DC 4, respectively.

4.3.2. Species diversity

Neither species richness nor catch of saproxylic beetles collected from window traps differed significantly among treatments (deviance = 26.84, $p = 0.431$ for species richness; deviance = 460624.00, $p = 0.629$ for catch) (Table 4.1).

Species richness of saproxylic beetles collected from emergence traps differed significantly among treatments (deviance = 46.94, $p < 0.001$); subsequent pairwise comparisons revealed that mean species richness in small patches surrounded by 2% retention was significantly lower than in large patches surrounded by 20% and 50% dispersed retentions ($p = 0.038$ and $p < 0.010$, respectively) (Table 4.1). No treatment differed in species richness from that of unharvested control. Mean standardized catch of beetles showed exactly the same trends as observed for species richness, i.e., there was lower catch in small patches surrounded by 2% retention than in large patches surrounded by either 20% or 50% dispersed retentions ($p = 0.038$ and $p < 0.001$, respectively) (Table 4.1).

Hill numbers suggested an interesting species diversity pattern for saproxylic beetles (Fig. 4.3). In window traps, Hill numbers dropped rapidly between $q = 0$ and $q = 1$, suggesting highly uneven assemblages irrespective of treatments (Fig. 4.3a). When $q = 1$, Hill number in small patches surrounded by 20% dispersed retention was slightly higher than those in other treatments, and Hill numbers in small patches surrounded by 2% and 50% retention were slightly lower than those in other treatments (Fig. 4.3a). As an order of q increased, however, Hill numbers became similar among treatments (Fig. 4.3a).

Hill numbers indicated by emergence trap data were somewhat different than those based on data from window traps (Fig. 4.3b). In emergence traps, although Hill numbers in most treatments dropped sharply between $q = 0$ and $q = 1$, Hill numbers in small patches surrounded by 2% and 50% retention showed gradual declines along an order of q, suggesting fairly even assemblages in those two treatments (Fig. 4.3b). When $q = 1$ and $q = 2$, Hill numbers were notably highest in small patches surrounded by 50% dispersed retention and were lowest in small patches surrounded by 20% dispersed retention (Fig. 4.3b). Interestingly, when $q \geq 1$, Hill numbers in large patches and unharvested controls had values between both extremes.

4.3.3. Structure of assemblages captured by window traps

Significant differences in species composition among treatments were evident in the window trap data pooled over trophic guilds (PERMANOVA; Pseudo-$F = 1.72$, $p = 0.018$) (Table 4.2). Subsequent pairwise comparisons showed that species composition in aggregated retention patches surrounded by 2% retention significantly differed from both that of aggregated patches surrounded by 50% dispersed retention ($t = 1.43$, $p = 0.029$) and the unharvested controls ($t = 1.84$, $p = 0.012$) (Table 4.2). Results of PERMANOVA were supported by NMS; however, NMS also showed that assemblages from patches embedded in 20% and 50% dispersed retention treatments were intermediate between those from the 2% treatment and controls, and were more similar to each other than to those of the controls (Fig. 4.4a).

PERMANOVAs were also performed separately for the most common four trophic guilds (i.e., phloeophages, xylophages, mycetophages, and predators). There were no significant differences in species composition among treatments for phloeophages, xylophages or mycetophages; however, predator assemblage composition differed significantly among treatments (Pseudo-$F = 2.21$, $p < 0.001$) (Table 4.2). Subsequent pairwise comparisons revealed that composition of predator assemblages in patches surrounded by 2% retention differed significantly from that of patches surrounded by either 20% dispersed retention ($t = 1.80$, $p = 0.004$), 50% dispersed retention ($t = 1.89$, $p = 0.002$), or unharvested controls ($t = 1.93$, $p = 0.012$) (Table 4.2).

Results of NMS using data from different trophic guilds largely supported the results of PERMANOVA; however NMS depicted some interesting patterns that PERMANOVA did not reveal (Fig. 4.5). Phloeophage and mycetophage assemblages in patches surrounded by 2% retention did not overlap with those of controls on the basis of 95% CIs, but assemblages in the patches surrounded by 20% and 50% dispersed retentions were intermediate between the two extremes (Figs. 4.5a, 4.5c). In contrast, NMS strongly supported the results of PERMANOVA for xylophage and predator assemblages (Figs. 4.5b, 4.5d). Variation in assemblage structure of xylophages and mycetophages was much higher in data from control compartments than in treatments, but this pattern was not evident for the other two trophic groups.

4.3.4. Structure of assemblages captured by emergence traps

For data from emergence traps, PERMANOVA revealed a significant difference in species composition of the entire saproxylic beetle assemblage among the treatments (Pseudo-$F = 1.50$, $p = 0.041$) (Table 4.2). *A posteriori* pairwise comparisons showed that species composition of aggregated retention surrounded by 2% residual differed significantly from that of retention patches surrounded by both 20% ($t = 1.52$, $p = 0.034$) and 50% dispersed retention ($t = 1.38$, $p = 0.028$), and that of controls ($t = 1.43$, $p = 0.012$). NMS supported the PERMANOVA results but also suggested that faunal structure of patches in 20% and 50% dispersed retention treatments were somewhat intermediate between those in 2% retention and controls, and were more similar to each other than either was to control compartments (Fig. 4.4b), as seen for the window trap data (Fig. 4.4a).

PERMANOVAs were also performed separately for data partitioned by trophic group (Table 4.2). As on the data from window traps, only predator assemblages were significantly affected by treatment (Pseudo-$F = 1.40$, $p = 0.050$). Pairwise comparisons revealed that predator assemblage composition in patches in 2% retention differed significantly from those both in patches surrounded by 50% dispersed retention ($t = 1.32$, $p = 0.047$) and in control compartments ($t = 1.33$, $p = 0.013$). Results of NMS strongly supported the results of PERMANOVAs for each trophic guild (Fig. 4.6). Assemblages of phloeophages, xylophages and mycetophages in every treatment overlapped each other due to very high variability among replicates (Figs. 4.6a, 4.6b, 4.6c). There was considerably less variability among replicates for predator assemblages (Fig. 4.6d).

4.3.5. Indicator species

Overall, twenty species from window traps and one species from emergence traps were significant indicators of some combination of treatments (Table 4.3). For assemblages sampled by window traps twelve species indicated aggregated retention surrounded by the clearcuts and half of these were predators. The predaceous flat bark beetle, *Pediacus fuscus*, was the strongest indicator species (IV = 90.7), followed by the minute tree-fungus beetle, *Cis striolatus* (IV = 89.3), and the predatory rove beetle, *Acidota crenata* (IV = 81.5). Eight species were identified as indicators of controls. The bark beetle, *Xylechinus montanus*, was the strongest indicator species (IV = 73.6), followed by the predatory rove beetle, *Phloeonomus* sp.1 (IV = 73.2), and the sap beetle, *Epuraea linearis* (IV = 72.8) (Table 4.3). For emergence trap data, only the predaceous soldier beetle, *Dichelotarsus piniphilus,* was identified as an indicator of controls (Table 4.3). Given that there were no indicators of aggregated retention patches surrounded by 20% and 50% dispersed retention, these habitats appear to harbour more generalist species.

4.3.6. Live trees and coarse woody debris in aggregated retention

The total number of live trees in retention patches differed among treatments (deviance = 57134.00, $p = 0.002$), but there was extremely high within-group variation (Table 4.4). Pairwise comparisons revealed that significantly fewer live trees were standing in large patches surrounded by 2% retention than those surrounded by 20% dispersed retention ($p = 0.002$; Table 4.4). The number of live trees in small patches was not significantly affected by the amount of surrounding dispersed residual, although small patches surrounded by 2% retention tended to have fewer live trees than those surrounded by higher levels of retention (Table 4.4).

Total volumes of downed CWD differed among treatments (deviance = 8296.10, $p < 0.001$). Subsequent pairwise comparisons showed that the volumes of CWD in small and large patches surrounded by 2% residual were significantly greater than in other treatments (Table 4.4). Total volumes of DCs 1–2 showed this same pattern; however, volume of older logs (DCs 3–4 and DCs 5–6) did not differ among treatments (Table 4.4).

4.4. Discussion

4.4.1. Combined effects of aggregated and dispersed retention on biodiversity

A critical set of questions surrounding variable retention harvesting revolves around how retention is best distributed across harvested blocks to maximize its biodiversity conservation value. Given that retention may be aggregated (i.e., patches), dispersed, or both, some specific questions that arise are: What proportion of retention is best aggregated in large harvest blocks? What are the optimal sizes of retained patches within harvested areas? Does the amount of surrounding dispersed retention affect the conservation value of patches? To date in Canadian forests, there has been little progress in answering the first question; however, recent advances in understanding optimal patch size suggest that 3 ha of aggregated retention may not be effective (Pearce et al., 2005; Pyper, 2009; Lee et al., 2015), and size of patch with the highest conservation value depends on distance from unharvested forest edge, at least for beetles (Pyper, 2009). The present research marks one of the first attempts to understand the influence of residual left as dispersed retention in the surrounding harvested matrix on the capacity of patches to serve as conservation 'lifeboats' for saproxylic beetles. Data presented above strongly indicate that dispersed retention can influence the conservation value of aggregated retention patches, and that this should be considered in designing large areas harvested to variable retention prescriptions.

Data from both window and emergence traps were consistent in showing that in stands harvested 10-11 years previously, saproxylic beetle assemblages were better conserved in aggregated retention patches (0.20 ha and 0.46 ha) embedded in a harvest matrix containing both 20% and 50% dispersed retention, than in patches surrounded by traditional clearcuts (c. 2% retention). This result corroborates the findings of Pinzon et al. (2012), also based on research at the EMEND site; they showed that spider assemblages in patches surrounded by 10% dispersed residual did not retain structure and composition similar to those of unharvested controls, whereas assemblages were largely conserved in patches surrounded by 75% residual. In an old-growth *Nothofagus pumilio* forest in Argentina, however, understory plant assemblages in small aggregated retention patches (0.28 ha) within low levels of dispersed retention (about 10%-20%) did not differ from those in similar patches surrounded by clearcut four years after treatments (Lencinas et al., 2011). The limited data available suggest that low levels of dispersed retention are of little conservation benefit, but that higher levels associated with small retention patches can provide advantages. In my study, such advantages were evident even for 20% dispersed retention.

Different feeding guilds of saproxylic beetles responded differently to our treatments. Although assemblages of phloeophages, xylophages, and mycetophages did not differ among treatments as determined statistically by PERMANOVA, NMS suggested a consistent tendency for all three groups to be more similar to those of unharvested controls when embedded in 20% or 50% retention than in harvest blocks with 2% residual. For predators, the same pattern was more strongly evident in NMS but it was also statistically significant in the PERMANOVA analyses. Interestingly, predators sampled directly from CWD in emergence traps, were mainly specialized predators of bark beetles that were not apparently affected by treatment. Furthermore, these predators were less sensitive to levels of surrounding dispersed retention than were those found in window traps, which included many generalist species as well as bark beetle specialists. This suggests that deadwood may provide relatively stable habitats for specialist predators (and their hosts) but perhaps not so for generalist predators. Our results contrast with those from earlier work at the same location that showed that fungivores were the most sensitive among trophic guilds to harvest of white spruce (Jacobs et al., 2007b). Thus, it is possible that early post-harvest effects differ from those that evolve over time as landscape forces come into play.

Although placing aggregated retention patches within a clearcut matrix appears to make them less useful as lifeboats for saproxylic beetles, we could identify no specific additive benefit of leaving 50%, rather than 20%, retention for any trophic group or for the saproxylic assemblage as a whole. Thus, in situations where the total within-block retention is >20% but ≤50% for a harvested white spruce stand, residual beyond 20% will likely be better placed in aggregated patches than allocated to additional dispersed retention.

4.4.2. Patterns of species diversity

Rapid declines of diversity profiles (i.e., Hill numbers along the order ranks of q) suggests that saproxylic beetle assemblages sampled from both window traps and emergence traps are composed of few highly dominant species and many rare species. In spite of the consistent results proved by PERMANOVA and NMS that assemblages in patches surrounded by 2% retention differed from those in unharvested controls, our analysis of Hill numbers underscores contrasting patterns of species diversity between window and emergence trap catches. In window traps, for example, homogenization of beetle assemblages was noticeable in small patches surrounded by 2% and 50% retention, suggesting that larger patches will in general maintain higher species diversity. On the other hand, species diversity as assessed from emergence trap data was highest in small patches surrounded by 2% and 50% retention, possibly resulting from low species richness represented in low catches from single lengths of CWD, especially in small patches. These completely opposite results of the diversity pattern between two sampling methods require further studies for better understanding species diversity. Nonetheless, species diversity in large patches and unharvested controls always placed between both extremes regardless of trapping methods.

4.4.3. Structural stability of aggregated retention

Projecting and managing blow down among live trees left as residual is critical to the success of retention forestry (Beese et al., 2003; Scott and Mitchell, 2005). Immediately following harvest, both aggregated and dispersed retention starts to fall down due to increased wind exposure; however, aggregated retention is less susceptible to windthrow than dispersed retention (Scott and Mitchell, 2005; Aubry et al., 2009). Although aggregated retention left in circular shapes reduces edge effects, elliptical patches oriented with the direction of prevailing winds may better minimize adverse edge effects in relation to solar radiation and increases in temperature (Heithecker and Halpern, 2007). One goal of variable retention harvesting is to leave live trees in place that will be gradually recruited as deadwood (standing and fallen) over time, in an attempt to provide a continuous supply of habitat for saproxylic organisms until a new forest regenerates sufficiently to provide a natural flow of CWD into the system. However, if retention patches experience high levels of windfall soon after harvest of the surrounding area, their utility as lifeboats likely will deteriorate quickly, and before the surrounding regenerating stand can accept immigration of forest specialists from forest patches of adequate size to retain them.

Some patches among our clearcuts were highly susceptible to blowdown, e.g., one small (0.20 ha) patch retained only nine and another only 20 live trees 10-11 years after harvesting, and the remaining live trees appeared weakened and likely to blow down in the near future. Even 0.46-ha-patches surrounded by 50% residual had high amounts of blowdown, although variability in percent blowdown was higher, e.g., two patches retained only 50 and 54 live trees, respectively, after windthrow, but the other patch had nearly three times more (160) live trees. Nonetheless, and despite significant windthrow in the aggregated retention patches in all treatments, patches surrounded by 20% and 50% dispersed retention appeared to experience a much slower rate of blowdown than those surrounded by clearcuts. Thus, the changes in saproxylic beetle assemblage structure in aggregated retention associated with different levels of dispersed retention may simply reflect deterioration of the patch associated with blowdown. A study of tree mortality in Sweden showed that retention patches (≤ 1 ha) of Norway spruce (*Picea abies* (L.) Karst.) maintained neither structure or microclimate similar to adjacent unharvested control areas 18 years after treatments, but suffered 76% and 53% tree mortality in 0.25 ha and 0.50 ha patches, respectively (Jönsson et al., 2007). Although not investigated directly in our experiment, high rates of blowdown also appears to reduce both quality and quantity of deadwood habitats due to drying caused by sun exposure. This, in turn, should also influence assemblage composition.

4.4.4. The balance of aggregated and dispersed retention in cut-block management

The goals of retention forestry vary (See Aubry et al., 2009; Baker and Read, 2011; Gustafsson et al., 2012). In this paper, I focused on managing retention in large cutovers, i.e., at the within cut-block level. I recognize that this scale of focus does not accommodate all species and that additional complexities arise for effective management of whole landscapes. Nonetheless, for much invertebrate biodiversity, the within-block focus is useful (Spence et al. 2008), and thus, this is a useful component of sustainable forest management. A central point, however, is to balance timber production and biodiversity conservation, ensuring long-term persistence of forest dependent species in the context of sustainable forest management. This conservation-oriented approach is not only important for promoting biodiversity, but also crucial for sustaining ecosystem function (Lindenmayer et al., 2012; Gustafsson et al., 2012). Many important within stand processes are mediated by saproxylic beetles (e.g., Cobb et al., 2010).

So, how should forest managers respond? Most ecologists agree that aggregated retention has the following advantages over dispersed retention: 1) it retains overstorey trees and multiple canopy levels, 2) it maintains undisturbed soil and leaf litter, 3) it ameliorates local microclimate conditions, reducing tree mortality, and conserving structurally complex old-growth characteristics along with elements of the original fauna and flora (Franklin et al., 1997; Aubry et al., 2009; Baker and Read, 2011; Lencinas et al., 2011; Pinzon et al., 2012; Urgenson et al., 2013). Nonetheless, dispersed retention can 1) enhance connectivity of belowground biota across harvest blocks, 2) promote growth of seedlings, 3) benefit and sustain species with edge preference, 4) increase the evenness of CWD distribution, and 5) elevate aesthetic perceptions of harvested landscapes (Franklin et al., 1997; Aubry et al., 2009; Baker and Read, 2011; Gustafsson et al., 2012; Pinzon et al., 2012; Urgenson et al., 2013). Moreover, my study suggests that dispersed retention can play an important role as a windbreak, protecting and extending the physical structure of aggregated retention as stands recover after harvest. I also think that dispersed retention can supply large CWD across space and time throughout regenerating stands as live trees fall down in regenerating blocks. Such natural additions of deadwood are expected to promote biodiversity into regenerating matrix.

Nevertheless, there are problems associated with both aggregated and dispersed retention. For example, the positive effects of aggregated retention are locally limited, leaving large post-harvest areas (i.e., harvested matrix) as hostile habitat for many original forest organisms (Dynesius and Hylander, 2007; Pinzon et al., 2012). On the other hand, dispersed retention cannot be expected to fully protect the forest biota unless high levels of retention are left (Pinzon et al., 2012), an approach incompatible with economic demands for maximizing timber production.

Overall retention forestry aims to achieve continuity of forest structure, composition, and complexity that maintains biodiversity and ecological functions at different spatial scales (Gustafsson et al., 2012; Lindenmayer et al., 2012). In this sense, use of a single spatial pattern of variable retention will not achieve the fundamental goal of retention forestry. I argue that aggregated retention and dispersed retention are tools that have complementarily been used in an overall strategy for harvest block management. By implementing both aggregated and dispersed retention, managers can strengthen function of retention patches as ‘life boats’ for multiple forest organisms that inhabited the area pre-harvest. In our study, it is obvious that relatively small aggregated patches ($\leq$ 0.46 ha) can function well even 10-11 years after harvest when surrounded by dispersed retention, which contributes to the structural stability and survival of saproxylic organisms in the patch.

4.5. Conclusions

This work demonstrates that aggregated retention patches of 0.20 ha and 0.46 ha conserve saproxylic beetle assemblages similar to those of unharvested forest 10-11 years post-harvest, if the patches are embedded in areas with dispersed retention. However, important questions remain about whether such patches will maintain their structural stability or simply collapse as habitats before regenerating stand can sustain saproxylic beetle assemblages similar to unharvested forest. Because blowdown was severe even in some patches surrounded by 20% or 50% dispersed retention, the answer is unclear. Therefore, we recommend leaving aggregated patches larger than 0.50 ha in harvest blocks harvested to dispersed retention prescriptions in efforts to maintain biodiversity.

Of necessity, our study is focused largely on responses of early post-disturbance colonists, which are well adapted to find and occupy to trees that are dying or very recently dead. As such, these species may be rather tolerant of forestry practices if potential deadwood sources are left behind a site. This work did not consider saproxylic beetles that may depend on advanced decay classes common in old-growth forests and it is unreasonable to speculate that these species will respond similarly to early colonizers under the combined retention approach we suggest. Thus, long-term study is critical, because the success of retention forestry in conserving biodiversity depends on both structural persistence of aggregated retention patches and their ability to maintain organisms associated with intact forests.

Table 4.1

Catch and species richness of saproxylic beetle assemblages in boreal white spruce in small (S; 0.20 ha) and large (L; 0.46 ha) aggregated retention patches surrounded by three dispersed retention levels (2%, 20%, 50%) and in unharvested controls (CT). Assemblages sampled by window traps and emergence traps are presented separately. Replicates were ca. 10 ha in size and harvesting was applied 10-11 years before sampling.

Trapping method	Treatments	Mean species richness[a]	Mean standardized catch[a]
Window trap	2%-S	79.33 ± 19.10	229.40 ± 210.04
	2%-L	74.00 ± 3.06	37.50 ± 17.35
	20%-S	55.67 ± 7.17	21.42 ± 8.48
	20%-L	68.00 ± 13.53	111.04 ± 63.70
	50%-S	75.33 ± 6.36	130.07 ± 107.81
	50%-L	69.33 ± 4.26	71.18 ± 32.46
	CT	67.33 ± 3.84	90.23 ± 34.13
Emergence trap	2%-S	10.67 ± 1.76 a	0.69 ± 0.14 a
	2%-L	16.33 ± 0.88 abc	1.75 ± 0.34 abc
	20%-S	21.67 ± 6.89 abc	15.51 ± 9.31 abc
	20%-L	24.67 ± 4.84 bc	18.19 ± 9.23 bc
	50%-S	14.67 ± 6.17 ab	1.31 ± 0.27 ab
	50%-L	32.67 ± 2.33 c	28.56 ± 11.99 c
	CT	16.00 ± 1.15 abc	5.02 ± 2.42 abc

[a] Different letters show significant differences according to Tukey's pot-hoc test (α = 0.05).

Table 4.2

Results of one-way PERMANOVA testing the impacts of retention treatment (2%, 20%, 50%, 100% [control=CT]) on saproxylic beetle assemblage composition [null hypothesis: no treatment effects]. Tests were applied to the entire saproxylic beetle fauna and separately for four common trophic groups. Results from window traps (WT) and emergence traps (ET) are presented separately.

Trapping methods	FG[a]	Source	df	MS	Pseudo-*F*	*p* (perm)[b]	Pairwise comparisons
WT	All	Retention type	3	2720.6	1.72	**0.018**	2% ≠ (50%, CT)
		Residual	17	1583.9			
		Total	20				
	PHL	Retention type	3	2102.0	1.43	0.167	
		Residual	17	1473.6			
		Total	20				
	XYL	Retention type	3	2232.5	1.39	0.054	
		Residual	17	1608.0			
		Total	20				
	MYC	Retention type	3	2537.2	1.36	0.122	
		Residual	17	1867.4			
		Total	20				
	PRE	Retention type	3	3469.7	2.21	**< 0.001**	2% ≠ (20%, 50%, CT)
		Residual	17	1571.2			
		Total	20				
ET	All	Retention type	3	4652.3	1.50	**0.041**	2% ≠ (20%, 50%, CT)
		Residual	17	3109.7			
		Total	20				
	PHL	Retention type	3	3935.3	1.26	0.211	
		Residual	17	3122.0			
		Total	20				
	XYL	Retention type	3	3848.7	1.50	0.124	
		Residual	17	2569.5			
		Total	20				
	MYC	Retention type	3	3656.6	1.28	0.168	
		Residual	17	2854.8			
		Total	20				
	PRE	Retention type	3	5334.8	1.40	**0.050**	2% ≠ (50%, CT)
		Residual	17	3811.3			
		Total	20				

[a] FG (feeding guild): MYC (mycetophagous), PHL (phloeophagous), PRE (predaceous).

[b] Significant differences ($p \leq 0.05$) are highlighted in bold.

Table 4.3

Significant ($\alpha = 0.05$) indicator species of saproxylic beetle assemblages in aggregated retention patches surrounded by 2%, 20% and 50% dispersed retention, and in unharvested control (CT) of white spruce stands using window traps (WT) and emergence traps (ET). Indicator values (IV) are given for each species.

Trapping methods	Treat -ments[a]	Families	Species	Trophic guilds	IV	*p*
WT	2%	Cucujidae	*Pediacus fuscus*	Predators	90.7	< 0.001
	2%	Ciidae	*Cis striolatus*	Mycetophages	89.3	< 0.001
	2%	Staphylinidae	*Acidota crenata*	Predators	81.5	0.005
	2%	Corylophidae	*Clypastraea* sp.1	Mycetophages	74.5	< 0.001
	2%	Elateridae	*Ampedus luctuosus*	Predators	72.1	0.006
	2%	Tenebrionidae	*Corticeus praetermissus*	Predators	67.5	0.038
	2%	Scraptiidae	*Canifa pallipes*	Unknown	66.7	0.011
	2%	Elateridae	*Setasomus nitidulus*	Predators	66.7	0.011
	2%	Elateridae	*Ampedus nigrinus*	Predators	62.9	< 0.001
	2%	Cerambycidae	*Acmaeops proteus*	Xylophages	58.2	0.021
	2%	Melandryidae	*Dolotarsus lividus*	Xylophages	52.9	0.018
	2%	Cerambycidae	*Pygoleptura nigrella*	Xylophages	46.8	0.046
	CT	Curculionidae	*Xylechinus montanus*	Phloeophages	73.6	0.003
	CT	Staphylinidae	*Phloeonomus* sp.1	Predators	73.2	0.030
	CT	Nitidulidae	*Epuraea linearis*	Omnivores	72.8	0.002
	CT	Curculionidae	*Cryphalus ruficollis*	Phloeophages	66.7	0.012
	CT	Leiodidae	*Anisotoma globososa*	Myxomycophages	57.7	0.014
	CT	Clambidae	*Calyptomerus oblongulus*	Mycetophages	57.3	0.032
	CT	Carabidae	*Calathus advena*	Predators	53.1	0.045
	CT	Cerambycidae	*Pogonocherus penicillatus*	Xylophages	44.0	0.039
ET	CT	Cantharidae	*Dichelotarsus piniphilus*	Predators	66.7	0.013

Table 4.4

Mean ± SE number of live trees and volumes (m^3/ patch) of downed coarse woody material (CWD) in small (S; 0.20 ha) and large (L; 0.46ha) aggregated white spruce retention patches in 10 ha harvested compartments 10-11 years post-harvest. Volume of CWD is calculated for all DCs combined and for early (DCs 1-2), intermediate (DCs 3-4) and advanced (DCs 5-6) decay classes. Within each column, values followed by the same letter are n.s. according to Tukey's pot-hoc test (α = 0.05).

Treatm -ents	Mean number of live trees	Total volume (m^3) of downed CWD	Volume (m^3) of DCs 1–2	Volume (m^3) of DCs 3–4	Volume (m^3) of DCs 5–6
2%-S	25.00 ± 10.97 a	57.46 ± 7.24 a	31.27 ± 5.10 a	25.70 ± 9.25	0.50 ± 0.25
2%-L	34.33 ± 3.84 a	64.12 ± 7.41 a	35.12 ± 2.82 a	27.09 ± 10.78	1.91 ± 0.72
20%-S	79.67 ± 38.71 ab	24.80 ± 8.14 b	13.47 ± 5.38 b	9.15 ± 2.61	2.18 ± 0.93
20%-L	162.67 ± 11.68 b	16.69 ± 5.19 b	7.34 ± 0.54 b	8.77 ± 4.84	0.58 ± 0.18
50%-S	58.00 ± 17.21 a	18.12 ± 2.74 b	6.72 ± 2.20 b	9.58 ± 0.61	1.82 ± 0.64
50%-L	88.00 ± 36.02 ab	21.18 ± 6.76 b	10.17 ± 1.89 b	9.81 ± 5.59	1.20 ± 1.11

NOTE: Total volume of downed CWD and volume of each DC were measured in every small retention patches, and for half of each large patch

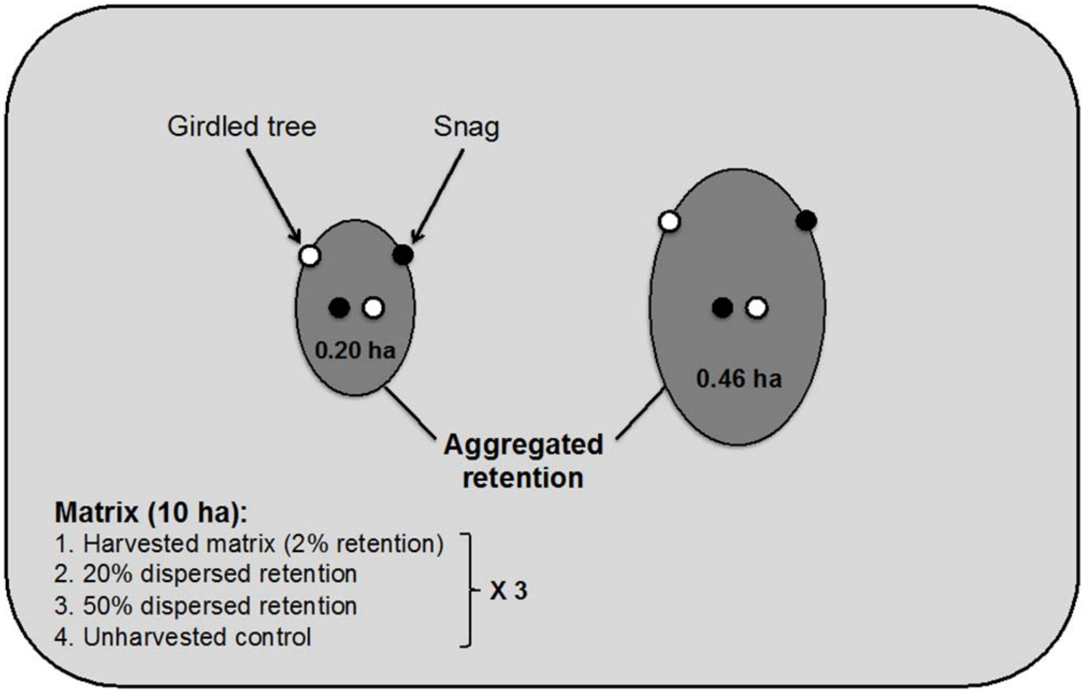


Fig. 4.1. Schematic diagram of the experimental design, illustrating two sizes of aggregated retention patches (0.20 ha and 0.46 ha) surrounded by three different retention levels (2%, 20%, 50%), as deployed in 10 ha compartments of boreal white spruce-dominated stands included in the EMEND experiment. Three unharvested control stands were chosen as comparisons. Open and closed circles indicate girdled trees and natural snags, respectively, on which four window traps were placed on each retention patch. Four emergence traps were also installed on two different pieces of spruce logs in decay class 2 or 4 that were exposed in the center of each patch.

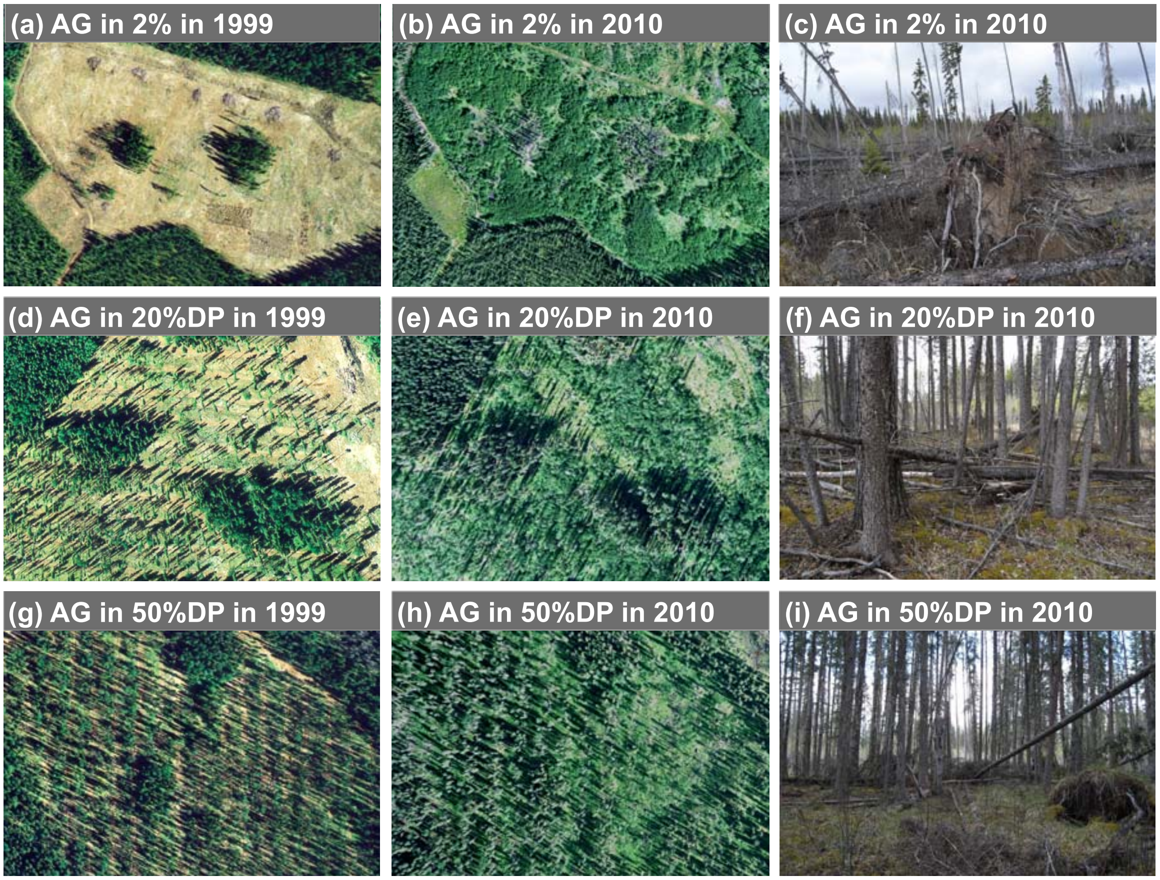
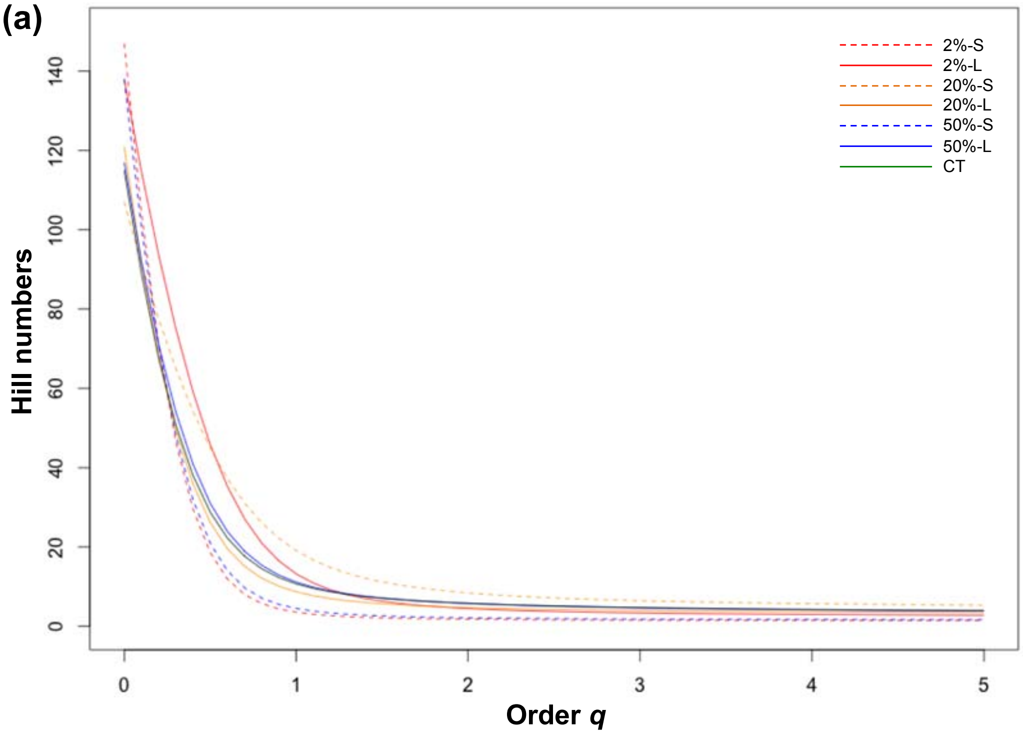


Fig. 4.2. Aerial and ground photographs of aggregated retention patches showing two sizes of aggregated retention patches (0.20 ha and 0.46 ha) surrounded by three different retention levels (2%, 20%, 50%) in 10 ha compartments of boreal white spruce-dominated stands included in the EMEND experiment. The aerial photos were taken in 1999 (a, d, g) and 2010 (b, e, h), and the ground photos were taken in large aggregated retention (0.46 ha) in 2010 (c, f, i). AG, aggregated retention; DP, dispersed retention. Aerial photos (a, b, d, e, g, h) from the EMEND Project (http://www.emendproject.org); ground photos (c, f, i) were taken by Seung-Il Lee.

(a)


Hill numbers
0
20
40
60
80
100
120
140
Order q
0
1
2
3
4
5
2%-S
2%-L
20%-S
20%-L
50%-S
50%-L
CT

(b)

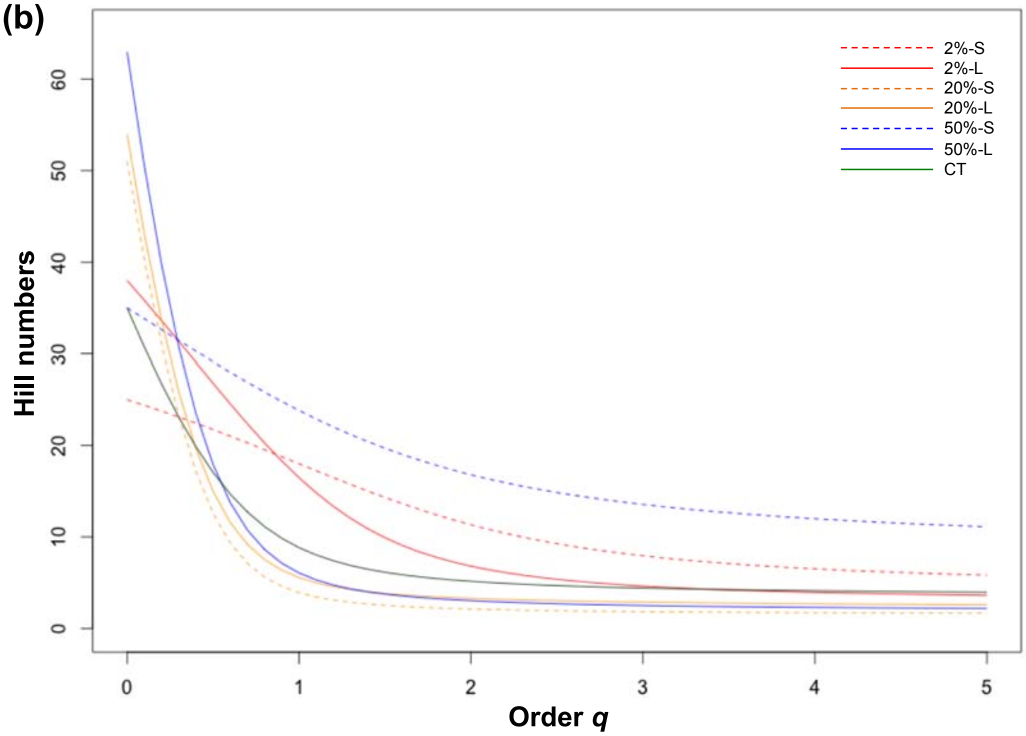

Hill numbers
0
10
20
30
40
50
60
Order q
0
1
2
3
4
5
2%-S
2%-L
20%-S
20%-L
50%-S
50%-L
CT

Fig. 4.3. Hill numbers characterizing saproxylic beetle samples collected with (a) window traps and (b) emergence traps in two sizes of aggregated retention patches surrounded by three different retention levels (2%, 20%, 50%) in10 ha compartments of boreal white spruce. Unharvested controls were chosen as comparisons. Abbreviations: CT (unharvested control), L (large aggregated retention = 0.46 ha), and S (small aggregated retention = 0.20 ha). q_0 indicates total species richness of each treatment. As the ranked order of q increases, the contribution of rare species to the function decreases.

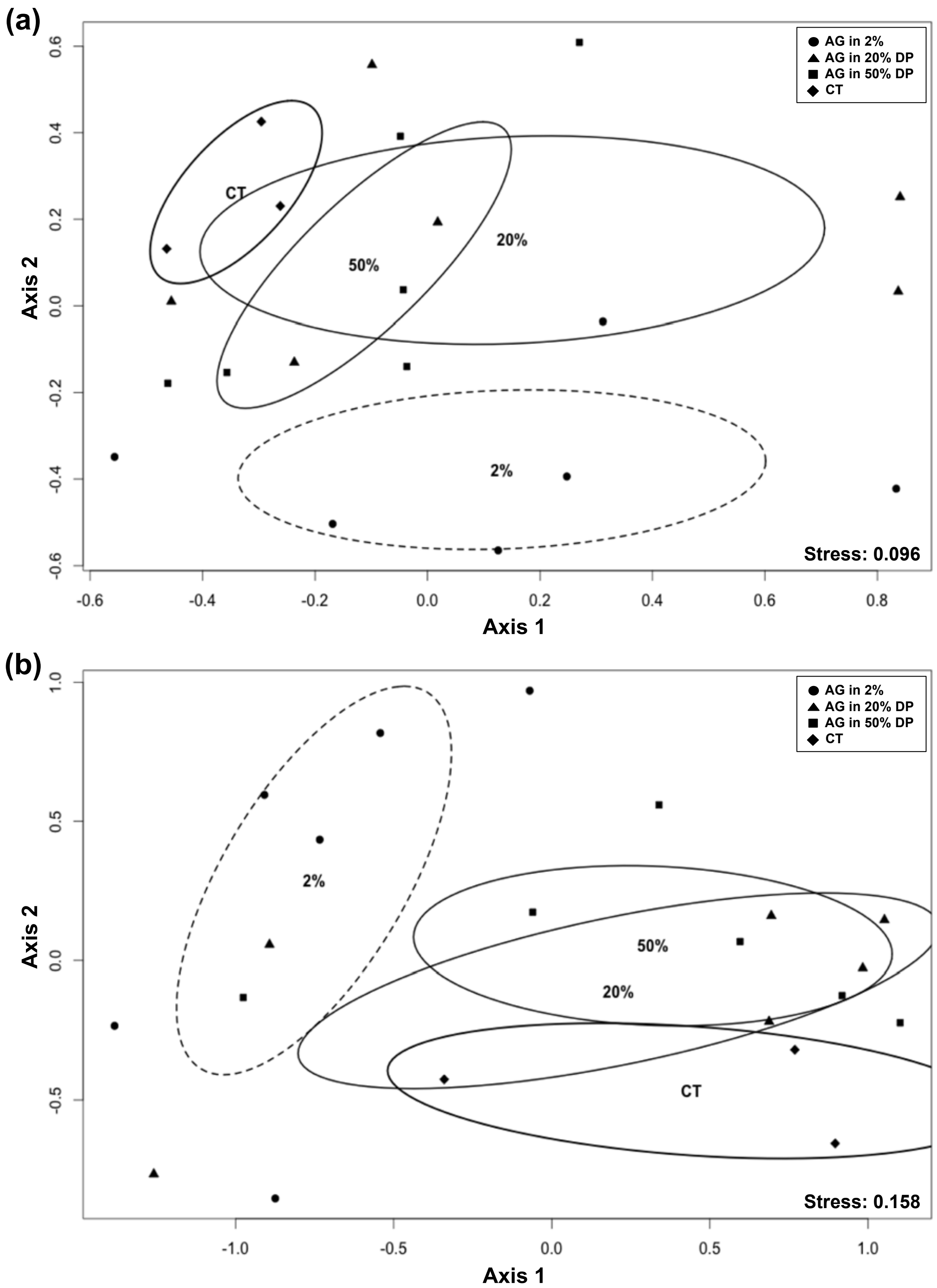


Fig. 4.4. Non-metric multidimensional scaling (NMS) of saproxylic beetle samples from (a) window traps and (b) emergence traps placed in two sizes of aggregated retention

patches (0.20 ha and 0.46 ha) surrounded by three different retention levels (2%, 20%, 50%) in 10 ha compartments of boreal white spruce. Unharvested control stands were chosen as comparisons. Ellipses show 95% confidence intervals around treatment centroids; the dotted line represents aggregated retention in 2% retention, and solid lines represent aggregated retentions surrounded by 20% and 50% dispersed retention, and the unharvested controls. Abbreviations: AG (aggregated retention), CT (unharvested control), DP (dispersed retention).

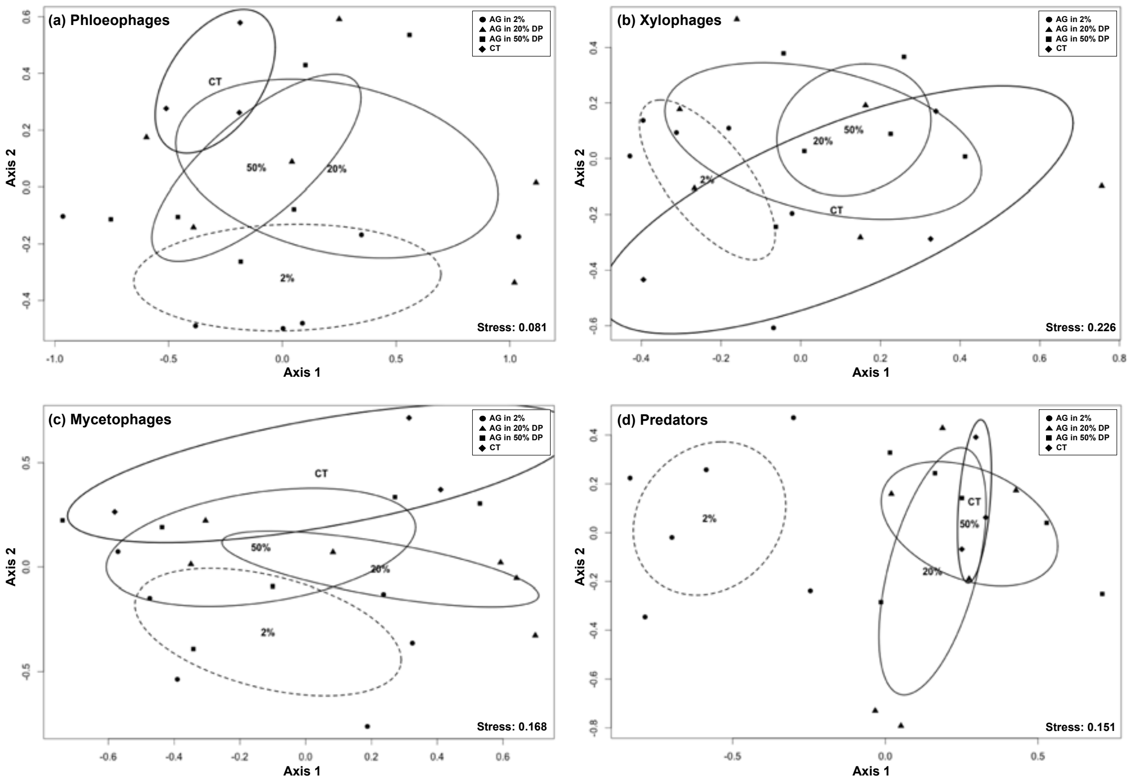


Fig. 4.5. Non-metric multidimensional scaling (NMS) of frequency-abundance data for four different trophic guilds of saproxylic beetles sampled with window traps in two sizes of aggregated retention patches (0.20 ha and 0.46 ha) surrounded by three different retention levels (2%, 20%, 50%) in10 ha compartments of boreal white spruce and in unharvested control compartments. Ellipses are 95% confidence intervals around treatment centroids; the dotted line represents aggregated retention in 2% retention, and solid lines represent aggregated retentions surrounded by 20% and 50% dispersed retention, and unharvested controls. Abbreviations: AG (aggregated retention), CT (unharvested control), DP (dispersed retention).

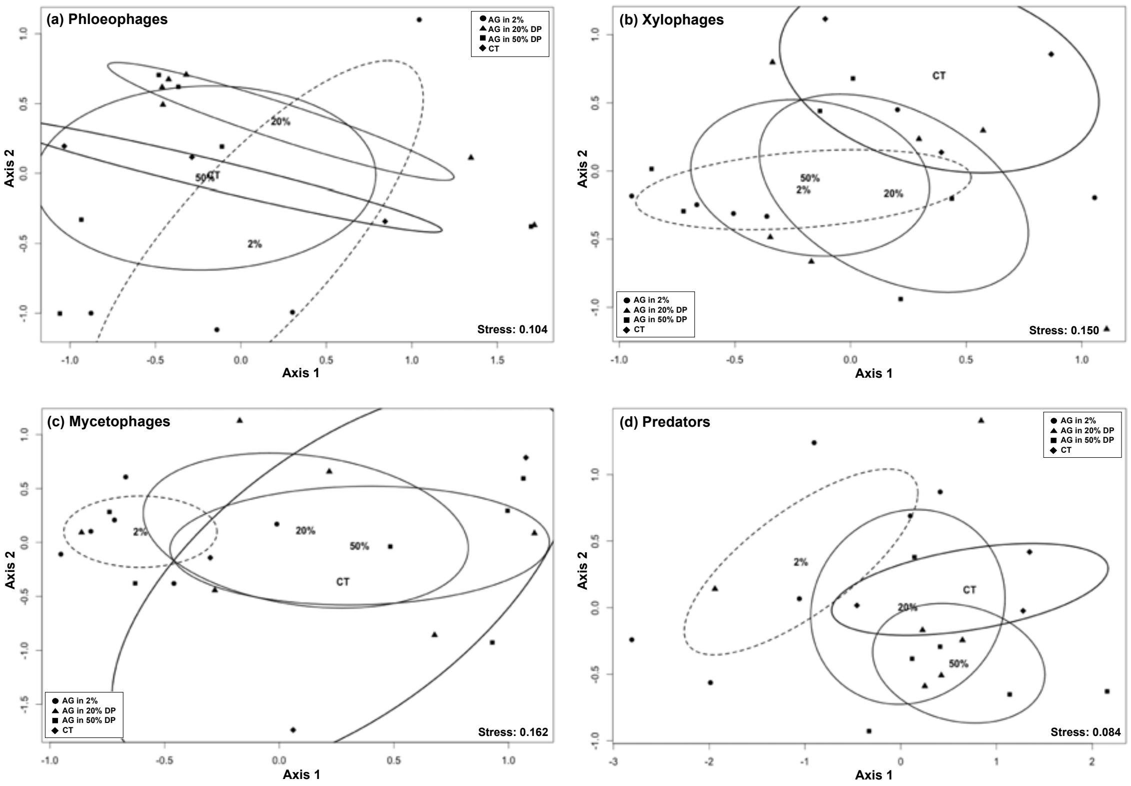


Fig. 4.6. Non-metric multidimensional scaling (NMS) of data from four different trophic guilds of saproxylic beetles sampled by emergence traps in two sizes of aggregated retention patches (0.20 ha and 0.46 ha) surrounded by three different retention levels (2%, 20%, 50%) in10 ha compartments of boreal white spruce, and unharvested control compartments. Ellipses are 95% confidence intervals around treatment centroids; the dotted line represents aggregated retention in 2% retention, and solid lines represent aggregated retentions surrounded by 20% and 50% dispersed retention, and unharvested controls. Abbreviations: AG (aggregated retention), CT (unharvested control), DP (dispersed retention).

CHAPTER 5

Early colonization of white spruce deadwood by saproxylic beetles and combined effects of aggregated and dispersed retention in boreal mixedwood stands

5.1. Introduction

Balancing timber harvest with biodiversity conservation is a key aspect of modern industrial forestry (Gustafsson et al., 2012; Fedrowitz et al., 2014). Retention harvests were incorporated into forestry practice, mainly as a conservation tool, nearly 25 years ago. The approach has been employed mainly in North and South America, Australia, and Scandinavian countries as an alternative to conventional clearcut harvesting to better maintain biodiversity and ecosystem function (Franklin, 1989; Lindenmayer and Franklin, 2002; Halaj et al., 2008; Work et al., 2010; Baker and Read, 2011; Lencinas et al., 2011; Gustafsson et al., 2012; Koivula et al., 2014).

Retention may be aggregated or dispersed in harvested blocks (Lindenmayer and Franklin, 2002; Baker, 2010). Groups of trees left behind in cut-overs are referred to as aggregated retention. A system of aggregated retention patches promotes multiple tree cohorts in the overstory, stand-level diversity in understory plant assemblages, areas of undisturbed soils, and local conservation of some fauna and flora requiring interior forest habitat (Franklin et al., 1997; Baker, 2011). In contrast, application of dispersed retention leaves single trees throughout a harvested area, and benefits are seen mainly as conservation of deadwood and belowground biota, and to some extent species of edge habitats (Franklin et al., 1997; Baker and Read, 2011).

Despite much work to explore consequences of aggregated and dispersed retention worldwide (Aubry et al., 2009; Work et al., 2010; Baker and Read, 2011; Lencinas et al., 2011; Fedrowitz et al., 2014), few authors have considered the possible interactive effects of these two kinds of retention left on single cut-blocks (e.g., Lencinas et al., 2011; Pinzon et al., 2012). Nonetheless, some forestry companies in North America have applied the combination of aggregated and dispersed retention in harvest design, actively implementing new findings from the science that exists (Baker, 2011; Gustafsson et al., 2012).

The EMEND (Ecosystem Management Emulating Natural Disturbance) experiment in western Canada is one of the early attempts to test effects of stand cover type (deciduous, coniferous and mixed), disturbance type (clear-cut harvest, retention harvest and burning), and amount of retained trees (retention level) on biodiversity, ecosystem function, economic viability and public perceptions (see Spence et al. (1999), Work et al. (2004) and www.emendproject.org). The experimental design of EMEND includes two sizes of aggregated retention patches (0.20 ha and 0.46 ha) embedded inside replicated 10 ha compartments, otherwise harvested to several dispersed retention prescriptions. Although this design can support study of interaction of retention types, all but two EMEND studies (Pinzon et al., 2012; Lee, Chapter 4) over the last 15 years have focused on biotic responses measured at the whole compartment level in a way that blurs distinction between retention types. Because saproxylic organisms are well known to be threatened by industrial forestry (Siitonen, 2001; Langor et al., 2008; Stokland et al., 2012), aggregated retention was included in the EMEND design to provide a continuous supply of deadwood into the regenerating matrix. Thus, the design supports study of conservation potential of aggregated retention for saproxylic organisms (i.e., deadwood-associated biota) in interaction with different levels of dispersed retention in the matrix.

A recent study conducted at EMEND revealed that even small aggregated retention patches of white spruce (*Picea glauca* (Moench) Voss) conserve saproxylic beetle biodiversity when combined with dispersed retention on spruce cut-blocks (Lee, Chapter 4). As study organisms, saproxylic beetles have advantages over other saproxylic groups because they are abundant and diverse both taxonomically and ecologically, and their taxonomy and natural history are relatively well-known, facilitating species level analyses (Jacobs et al., 2007b; Wood, 2012; Lee et al., 2014).

The specific objectives of the study were to: 1) identify saproxylic beetle species that initially colonize logs and snags of white spruce; and 2) evaluate the combined influence of aggregated and dispersed retention on early colonization of saproxylic beetle assemblages in mixedwood forests. We expected that saproxylic beetle assemblages would respond differently to logs and snags (Franc, 2007; Bouget et al., 2012; Wood, 2012), and that beetle assemblage structure in aggregated retention patches would differ depending on quality of the surrounding matrix.

5.2. Material and methods

5.2.1. Study area

This work was conducted on the EMEND experimental site, located in northwestern Alberta, Canada (56°46′N, 118°22′W) at elevations ranging from 677 m to 880 m above sea level. The forest at EMEND originated from a mosaic of wildfires (Bergeron, 2012) and had not been subject to commercial harvest before 1999. Merchantable stands there are dominated by two deciduous species, trembling aspen (*Populus tremuloides* Michaux) and balsam poplar (*Populus balsamifera* L.), and one coniferous species, white spruce, but also include less-abundant lodgepole pine (*Pinus contorta* Dougl. ex Loud.), black spruce (*Picea mariana* (Mill.) B.S.P.), balsam fir (*Abies balsamea* (L.) Mill.), and paper birch (*Betula papyrifera* Marsh.).

During the winter of 1998-1999, variable retention harvest treatments were applied to c. 10-ha compartments in each of four different stand-types (i.e., deciduous-dominated, deciduous with spruce understory, mixed, and conifer-dominated stands) on the EMEND landscape. Treatments included clear-cuts (2% retention), partial retention prescriptions (10%, 20%, 50%, 75% dispersed retention), and unharvested controls. Retention prescriptions also included two sizes of aggregated retention patches (0.20 ha and 0.46 ha) in each compartment to provide a continuous supply of CWD in regenerating stands (see Work et al., 2010 for further information). In this study, we focused on aggregated retention patches surrounded by clear-cuts, and 20% and 50% dispersed retention in mixedwood stands (canopy cover of both deciduous and coniferous 35%-65%), which mainly comprise trembling aspen, balsam poplar, and white spruce (Fig. 5.1).

5.2.2. Experimental design and beetle sampling

In mid-July 2010, one mature white spruce tree (> 80 years old) was felled in each of small (0.20 ha) retention patches surrounded by 20% and 50% dispersed retention, large (0.46 ha) patches surrounded by 2%, 20%, 50% dispersed retention and in unharvested control (CT) compartments to achieve the treatment combinations described in Table 5.1. Each treatment combination was repeated in three different stands. We were unable to sample saproxylic beetles in small patches surrounded by clear-cuts (2% retention) because there were too few live spruce trees left standing in two of the three replicate small patches, and felling a tree for this work was judged to have probable negative impacts on other ongoing studies. Two bolts, 120 cm long, were cut starting ca. 2 m from the base of each felled tree; one was left on the forest floor as a 'log', and the other was propped up against a nearby tree to simulate a 'snag'. The diameter of most of these bolts was ca. 30 cm, and did not exceed 40 cm. A pair of bolts was left in the center of each patch or unharvested control compartment and beetles were allowed to colonize until mid-June 2011, i.e., one year after cutting.

In mid-June 2011, half of each bolt (i.e., a 60 cm length) was cut and placed in a plastic 121-L bin (diameter 60 cm, height 91 cm) used as a rearing cage (see Lee et al., 2014). A screw-top canning jar (250 mL) containing approximately 50 mL of propylene glycol as killing agent and preservative was attached to the bottom of each bin to collect beetles. Saproxylic beetle species that emerged from the CWD sections were sampled every three weeks from June to September 2011 and again in mid-June 2012 before bolts were discarded. The remaining bolts that had been exposed to colonization for about two years were then placed in rearing drums in mid-June 2012 and sampled as as described above, with the last beetle samples collected in mid-June 2013.

5.2.3. Saproxylic beetle identification and trophic guilds

Both adult and larval saproxylic beetles emerged from the bolts. Although larval emergences are documented below, only coarse identification was possible for larvae and so these data cannot be included in detailed analyses. Adult beetles were identified mostly to the species level using relevant taxonomic literature (e.g., Arnett and Thomas, 2001; Arnett et al., 2002), the arthropod reference collections at the Northern Forestry Centre and the University of Alberta (E. H. Strickland Entomological Museum), and the help of taxonomic experts (see Acknowledgements). Data about specimens of two non-saproxylic families, Chrysomelidae and Coccinellidae, considered to have been on bolts by chance when they were put into the drums were removed before analysis. Individuals belonging to three species of Staphylinidae, *Placusa incompleta* Sjöberg, *P. pseudosuecica* Klimaszewski, and *P. tachyporoides* (Waltl), were pooled as *Placusa* spp. because they could not be reliably separated. In application of names we followed the 'Checklist of Beetles (Coleoptera) of Canada and Alaska' (Bousquet et al., 2013).

Each beetle species was assigned to one of six functional trophic guilds, i.e., mycetophages, omnivores, phloeophages, predators, rhizophages, and xylophages, based on published information (Klimaszewski et al., 2007; Dollin et al., 2008; Wood, 2012; Lee et al., 2014). Voucher specimens of all taxa identified were deposited in the Invertebrate Ecology Laboratory (Department of Renewable Resources, University of Alberta, Edmonton, Alberta, Canada) and in the arthropod collection of the Northern Forestry Centre, Canadian Forest Service, Edmonton, Alberta, Canada.

5.2.4. Live tree and coarse woody debris measurements

In order to better understand implications of retention treatments for resource availability a decade after harvest, live trees were enumerated in both small and large aggregated patches surrounded by 2%, 20% and 50% dispersed retention. Volumes of downed CWD and decay classes (DCs) were measured using a 40 m and 60 m line transect in each small and large patch, respectively, crossing from the east end to the west end of each patch. For unharvested control compartments, CWD volumes were measured using a 60 m east-west line transect through the center of the stump of the tree felled for bolts. We measured diameter and length of every piece of downed CWD (> 7 cm in diameter) that intersected the line transect. If sections of various decomposition stages existed in one piece of CWD, we calculated separate volumes for each decay class. For analysis, we pooled all deadwood across species because we could not identify well-decayed CWD to species.

A decay classification system (Lee et al., 2014) was applied to describe physical characters in decomposition of CWD. Although the basic system uses six classes, we combined DCs 1–2, DCs 3–4, and DCs 5–6 and denoted the combinations as early, intermediate, and advanced decay classes for analyses (Lee et al., 2014).

5.2.5. Data analyses

I used Venn diagrams to partition species richness between our experimental logs and snags. Unless stated specifically below, all analyses were run in R version 3.1.2 (R Development Core Team, 2014).

I used generalized linear models (GLM), to compare species richness and catches for all saproxylic beetles combined and for each of the three most abundant feeding guilds, phloeophages, mycetophages, and predators, among treatments. Error distributions in the factorial design, substrate position × habitat configuration (see Table 5.3), were generally modeled as Poisson, or as negative binomial when data were overdispersed. I used GLM with negative binomial distribution of error to test for treatment effects on data about the 12 most common species from abundant feeding guilds, six spp. for phloeophages, three spp. for mycetophages, and three spp. for predators. Tukey's honestly significant difference tests for *post-hoc* pairwise comparisons were applied when results from a GLM were significant ($p < 0.05$).

A paired *t*-test was used to test mean differences in numbers of live trees between small and large patches surrounded by each dispersed retention treatment. We generated the 't.test' function using the 'stats' package (R Development Core Team, 2014).

We used a GLM with Gaussian distribution of error, as implemented in R (Oksanen et al., 2015) to test differences in CWD volumes across habitat treatments, with pairwise comparisons applied subsequent to significant GLMs, using the 'MASS' (Venables and Ripley, 2002) and the 'multcomp' packages (Hothorn et al., 2008).

A two-way permutational multivariate analysis of variance (PERMANOVA+ add on package for PRIMER v7 (Anderson et al., 2008; Clarke and Gorley, 2015) was performed using a crossed design to test the null hypothesis of no difference in species composition among treatments (Anderson et al., 2008). For this analysis the first factor was 'substrate position' (i.e., logs and snags) and second factor was 'treatment combination', as described in the experimental design above. This non-parametric multivariate analysis uses permutations that require no explicit assumptions and partitions variation based on any distance measure (Anderson, 2001; Anderson et al., 2008). Bray-

Curtis distance calculations were performed on square-root-transformed data with 9999 permutations for main tests of PERMANOVA, and 999 permutations for *a posteriori* pairwise comparisons when significant results were detected in the main test ($p < 0.05$). We partitioned variation using the default conservative Type III sums-of-squares because it is satisfactory for both balanced ANOVAs and those unbalanced due to missing data (Anderson et al., 2008).

I used non-metric multidimensional scaling (NMS) to visualize community structure of saproxylic beetle assemblages and to further interpret the PERMANOVA results. This ordination technique is widely used in community ecology because it avoids the assumption of linear relationships among variables, decreases the zero-truncation issue by using ranked distances, and supports use of a variety of distance measures to describe the data (McCune and Grace, 2002). We generated the 'metaMDS' function using Bray-Curtis distance, as described above, on square-root-transformed data using 500 random starts in the 'vegan' package (Oksanen et al., 2015). The three decay class groups were overlaid on the ordination space to visualize relationships between species composition and CWD quality. We also calculated 95% confidence ellipses (CIs) to help assess differences in species composition among harvesting treatments.

Indicator species analysis (ISA) (Dufrêne and Legendre, 1997) was used to identify significant associations between species and harvest treatments separately for logs and snags. ISA considers both relative abundance and relative frequency in providing an indicator value (IV). We generated the 'indval' function using 4999 randomizations to calculate IV and probabilities ($p < 0.05$) in the 'labdsv' package (Roberts, 2013).

5.3. Results

5.3.1. Live trees and coarse woody debris in aggregated retention

There was high variance among patches in number of live trees and total volume of CWD 12 years after harvest (Table 5.2). The high variation was especially remarkable for live trees in patches surrounded by clear-cuts; the three replicates of small patches retained 3, 23 and 150 live trees, and large patches in the same compartments respectively retained 32, 35 and 183 trees. Nonetheless, there were significantly fewer live trees in 2%-S patches than in 2%-L patches in the same compartment (paired $t = -3.83$, $p = 0.031$). In contrast, number of standing trees in small and large patches did not differ in 20% dispersed retention ($t = -2.84$, $p = 0.053$) or 50% dispersed retention ($t = -0.77$, $p = 0.260$). No harvest treatments had fewer than 48 live trees except for patches surrounded by clear-cuts (Table 5.2). The only apparent trend with regard to CWD volume was for plots in the control stands that showed lower overall volume of CWD and higher volume of advanced decay classes (DCs 5-6) relative to earlier decay classes.

5.3.2. The beetle fauna

A total of 20 367 adult saproxylic beetles were collected from white spruce bolts representing 24 families and 78 species (Appendix 5-A). Among these, 6808 (66 spp.) and 13 559 individuals (52 spp.) emerged from simulated logs and snags, respectively (Appendix 5-A; Fig. 5.2a). The proportion of species shared between logs and snags was 51% (Fig. 5.2a). Thus, despite overlapping use of substrates about half of the species appeared to occur disproportionately in bolts presented either as logs or snags.

The Staphylinidae was the most species-rich family, accounting for 24 species, followed by Curculionidae (13 spp.) and Nitidulidae (5 spp.). However, most individuals were attributed to Curculionidae, which accounted for 18 668 individuals and 91.7% of the total catch, followed by Staphylinidae (1031) and Monotomidae (236). A single bark beetle species, *Dryocoetes affaber* (Mannerheim), was most common with 9631 individuals accounting for 47.3% of the total catch, followed by the ambrosia beetle, *Trypodendron lineatum* (Olivier) (3691), and the bark beetle, *Polygraphus rufipennis* (Kirby) (2136) (Appendix 5-A).

Overall, 925 (27 spp.) and 1251 individuals (22 spp.) of beetle larvae emerged from logs and snags, respectively (Appendix 5-B). The proportion of apparent species shared between logs and snags was 44% for larvae (Fig. 5.2b). Thus, both adults and larvae suggest that logs and snags have substantially different species composition. As with adults, the most abundant family among larvae was the Staphylinidae, accounting for 10 spp. with 966 individuals (Appendix 5-B). The emergence of larvae from deadwood in nature is an interesting phenomenon as it suggests that during development larvae of some saproxylic species may move within pieces of CWD by dispersing on the wood surface and may even move among pieces of CWD. Most emerged larvae seem to be predatory; larvae of most members of other trophic guilds, such as bark beetles, are more restricted to single pieces of wood during development.

5.3.3. Species richness and catches

There were a few significant effects of CWD position or treatment combinations on catches of beetles from particular guilds (Table 5.3). Emergence of mycetophages was significantly higher from simulated snags than from logs, and also significantly higher in bolts from CT, 50%-L and 50%-S patches than in those from 20%-S patches (Table 5.3). Emergence of predators was significantly higher in bolts from CT than in other treatments (Table 5.3). There were no significant interactions. Species richness was not affected by main effects or their interactions (Table 5.3).

5.3.4. Assemblage composition

Two-way PERMANOVA suggested significant differences in species composition between logs and snags (Pseudo-$F = 3.25$, $p < 0.001$). Species composition also differed among retention treatments (Pseudo-$F = 1.63$, $p = 0.007$) with *post hoc* pairwise comparisons suggesting that species composition in CT differed significantly from that in 2%-L, 20%-S, 20%-L and 50%-S (Table 5.4). Thus, although diversity and catches of saproxylic groups were not much affected by the treatments, it appears that retention combinations did affect the relative abundance of species and thus the structure of saproxylic beetle assemblages.

The PERMANOVA results were supported by NMS as 95% CIs indicated that species composition in CT differed from that in all other treatments except 50%-L (Fig. 5.3). Although assemblages in 50%-L overlapped with those in the other retention treatments, demonstrating high within-group variation, they also overlapped with the CT assemblages, showing that they were intermediate between uncut forest and the other retention treatments (Fig. 5.3). Assemblages associated with logs were roughly separated from those associated with snags, scattering in the upper right of the ordination space (Fig. 5.3). Assemblages collected from CT were strongly associated with DCs 5-6, whereas assemblages from 2%-L were associated with either DCs1-2 or DCs 3-4 (Fig. 5.3).

PERMANOVAs applied to each of the three most common trophic guilds showed that different feeding guilds were affected differently by treatments. Species composition of phloeophage assemblages differed significantly between logs and snags (Pseudo-F = 4.95, $p < 0.001$), and among harvest treatments (Pseudo-F = 1.77, $p = 0.014$) (Table 5.4). Although species composition of mycetophage assemblages also differed between logs and snags (Pseudo-F = 2.18, $p = 0.042$), they did not differ among harvest treatments (Table 5.4). In contrast to effects of stand characteristics on predator emergence, composition of predator assemblages did not apparently differ across treatments (Table 5.4).

Results of an NMS ordination for common trophic guilds supported the PERMANOVA results. For example, 95% CIs for phloeophage assemblages from CT samples completely overlapped with those from 50%-L; however, they were distinct from those from both 2%-L and 20%-S (Fig. 5.4a). Phloeophage assemblages in 2%-L were strongly associated with DCs 1-4 (Fig. 5.4a). Mycetophage assemblages were roughly separated by substrate position, but confidence ellipses for harvest prescriptions overlapped considerably (Fig. 5.4b). Predator assemblages from all treatment combinations overlapped considerably (Fig. 5.4c). Interestingly, assemblages from CT samples were the most homogeneous in all ordinations (Fig. 5.3; Fig. 5.4) suggesting that harvest increases variation in assemblage composition.

5.3.5. Response of common species

The six most common phloeophagous species were bark beetles (Curculionidae), and they responded differently to local forest conditions (Figs. 5.5a-5.5f). The most common species, *D. affaber*, was more common in snags than in logs and tended to be most abundant in bolts from CT (Fig. 5.5a). However, the second most captured bark beetle, *P. rufipennis*, was most common in the 2%-L treatment (Fig. 5.5b), a pattern also exhibited by *Orthotomicus caelatus* (Eichhoff) (Fig. 5.5f). *Crypturgus borealis* Swaine (Fig. 5.5c) and *Scierus annectans* LeConte (Fig. 5.5e) tended to be more abundant in 20%-L than in other harvest treatments; however, the pattern for *S. annectans* was less clear as there was a significant interaction between substrate position and harvest treatment (Deviance = 34.31, $p = 0.011$). *Dryocoetes autographus* (Ratzeburg) emerged more commonly from logs than snags, and was more abundant in 2%-L than in 20%-S (Fig. 5.5d). Thus, phloeophages respond in species-specific ways to the treatments, and their responses must depend on interactions between their biological characteristics and environmental variation generated by the harvest prescriptions.

The most common mycetophage, *T. lineatum* (Curculionidae), tended to be most abundant in bolts from CT compartments (Fig. 5.5g). More of the second-most common mycetophage, *Placusa* spp. (Staphylinidae), emerged from snags than logs, and catches were higher from CT than from 2%-L (Fig. 5.5h). For many species, unfortunately, the data were too few to permit inferences. For example, the minute hooded beetle, *Clypastraea* sp.1 (Corylophidae), emerged from only one snag in 2%-L (Fig. 5.5i).

Among predators, more *Rhizophagus dimidiatus* Mannerheim (Monotomidae) and *Phloeopora* spp. (Staphylinidae) emerged from bolts in CT plots (Figs. 5.5j-5.5k). In contrast, emergence of *Lasconotus complex* LeConte (Colydiidae) tended to be lowest from bolts in CT compartments (Fig. 5.5l).

5.3.6. Indicator species

Only two species were identified as significant indicators in this work. The monotomid beetle, *R. dimidiatus*, a specialist predator of bark beetles, was indicative of both logs (IV = 56.1, $p = 0.034$) and snags (IV = 68.0, $p = 0.021$) in CT compartments. The bark beetle, *P. rufipennis,* was a significant indicator of snags in 2%-L (IV = 54.0, $p = 0.007$). Interestingly, no species had indicator value for logs or snags in retention patches surrounded by 20% and 50% dispersed retention.

5.4. Discussion

5.4.1. Combined effects of aggregated and dispersed retention

Structure of saproxylic beetle assemblages in aggregated retention patches generally differed from assemblages in controls, regardless of the surrounding matrix quality. Only large patches (0.46 ha) surrounded by 50% dispersed retention harbored assemblages somewhat similar to those from CT stands. These results differ from those of a previous study conducted in the same area but in stands with a higher proportion of white spruce and dealing with significantly different assemblages (Chapter 4). In the previous study, assemblages in retention patches surrounded by 20% or 50% dispersed retention did not differ from those of unharvested control sites, while those in patches surrounded by clear-cuts differed from both unharvested controls and patches surrounded by dispersed retention (Chapter 4). Although the results are not directly comparable because of differences in taxa, stand type, and sampling methods, Pinzon et al. (2012) concluded that epigaeic spider assemblages in spruce patches did not differ from those of CT stands when surrounded by 75% dispersed retention. Results from this chapter suggest that unharvested mixedwood forest patches with dispersed retention left at economically feasible levels does little to buffer changes in assemblages of saproxylic beetles using white spruce in mixed stands. Nonetheless, the adjacent matrix can influence these assemblages, but this effect clearly depends on patch size. Structure of saproxylic assemblages was largely conserved in the larger patches if surrounded by 50% retention. In short, processes affecting outcome of forest retention conservation strategies for saproxylic organisms will likely depend on forest cover type.

Although the overall effects of retention combinations on saproxylic beetles are hard to interpret, there were interesting patterns when the analysis was partitioned among the three most common feeding guilds. For example, phloeophage assemblages (mostly bark beetles) in large patches surrounded by dispersed retention did not differ from those in CT plots unless patches were surrounded by clear-cuts. Assemblages from small patches, however, differed from those of CT plots regardless of the amount of retention surrounding the patches. Therefore, both patch size and matrix quality are important factors for shaping phloeophage assemblages. Jacobs et al. (2007b) focused on the effect of dispersed retention on saproxylic beetles in the same experimental area, and also demonstrated that assemblage structures of phloeophages and xylophages differed between all levels of dispersed retention (10%-75%) and unharvested compartments 1.5 years post-harvest, although this difference did not persist into the next year.

Neither assemblage structure nor common species of mycetophages differed among harvest treatments. Mycetophages are known to be sensitive to variable retention harvest (Jacobs et al., 2007b); however, results presented above suggest that patches 0.46 ha in area, can conserve early-colonizing mycetophage assemblages even when surrounded by only 2% retention.

Assemblages of predatory saproxylic beetles are also known to be sensitive to harvest, with species composition in patches depending on levels of dispersed retention around the residual patches in white spruce stands (Chapter 4). However, in the present study in mixedwood forests, predator assemblages in residual patches were not affected by level of dispersed retention in the matrix. Several explanations are possible for the difference in results between the two stand types. For example, dispersed mixedwood retention may sustain insufficient spruce deadwood to satisfy search needs of some predatory species and thus concentrate them into residual patches. We note that in using the rearing approach in this study we focused on resident saproxylic species, and this group of species may be less sensitive collectively to the surrounding matrix than is the more diverse fauna collected in window traps from pure spruce stands. Another explanation for lack of impact on the guild of predatory beetles in mixedwood stands may reflect general suitability of the deadwood environment in early decay classes for meeting needs of many generalist predatory beetles. Such early colonizing generalists could be maintained even in relatively small patches as long as there are broadly acceptable deadwood resources. Nonetheless, the two most common predators, *R. dimidiatus* and *Phloeopora* spp., were negatively affected by harvest treatments, indicating that relatively small-sized aggregated retention (≤ 0.46 ha) with high matrix quality did not maintain populations of these sensitive species similar to CT plots. Strong association of *R. dimidiatus* with CT plots in the present study supports association of this species with intact forest, as suggested from studies in both eastern Canada (Légaré et al., 2011) and white spruce retention patches of industrial harvest blocks in the western Canada (Lee et al., 2015).

5.4.2. Saproxylic beetles in logs and snags

Comparisons of species richness and abundance of saproxylic beetles between logs and snags in other studies have given conflicting results. For example, species richness are sometimes reported to be higher in logs than snags (Franc, 2007; Ulyshen and Hanula, 2009; Wood, 2012); however, both species richness and catches are higher in snags than logs of European oaks (Bouget et al., 2012). In the present study, there was no difference in mean species richness or mean emergence between bolts exposed as logs and snags, supporting the results from spruce-dominated forest in Sweden (Hjältén et al., 2010). Nonetheless, more mycetophages emerged from snags than logs in our study, contrary to a study of oak deadwood (Franc 2007). It thus seems that there is likely no general pattern of species richness or abundance of saproxylic beetles in logs and snags, but rather that patterns depend on tree species, geographical regions and life-histories of species in particular saproxylic assemblages (Bouget et al., 2012).

Nonetheless, both logs and snags clearly contribute to the structure of saproxylic arthropod assemblages, and that effective conservation measures will require consideration of both substrates. Unlike the variable results about species richness and relative abundance, the structure of beetle assemblages always differs between logs and snags (Franc, 2007; Ulyshen and Hanula, 2009; Hjältén et al., 2010; Bouget et al., 2012; Wood, 2012). Although my study shows overlap between assemblages characteristic of these two substrate positions, it also documents variation in saproxylic species composition that depends on CWD position. Nonetheless, it is interesting that assemblages of predators did not differ between logs and snags. This could reflect the more generalized feeding habits of predators, or mainly reflect the narrow range of decay class (i.e., DC 1) in this study (Bouget et al., 2012).

5.4.3. Windthrow

Long-term structural stability of aggregated retention is essential to the proposed benefits of retention forestry (Beese et al., 2003; Scott and Mitchell, 2005). Although aggregated retention is generally more resistant to wind than is dispersed retention (Scott and Mitchell, 2005; Aubry et al., 2009), relatively small (≤ 1 ha) aggregated retention patches are highly susceptible to windthrow (Jönsson et al., 2007; Aubry et al., 2009; Urgenson et al., 2013). We found remarkable variation in numbers of live trees in the relatively small patches (≤ 0.46 ha) of our study throughout all retention levels 12 years after harvest. More interestingly, small patches retained fewer live trees than in large patches, but only when surrounded by clear-cuts, suggesting that surrounding matrix affects the break-up of retention patches. Nonetheless, in the first 12 years after harvest, most trees had blown down in more than half of the patches surrounded by 2% residual. Such retention patches will not serve as long-term and continuous sources of CWD recruitment as a forest regenerates on a cut-block.

Persistence of aggregated retention appears to be a general concern for northern forest systems. A recent study conducted in white spruce stands at EMEND also reports that such relatively small patches surrounded by clear-cuts collapse as sources of CWD recruitment 10 years after harvest (Chapter 4). There is also a strong evidence of high mortality in similar-sized Norway spruce (*Picea abies* (L.) Karst.) patches 18 years after harvest in Sweden (76% and 53% mortality in 0.25 ha and 0.50 ha patches) (Jönsson et al., 2007). Nonetheless, we note a tendency for even such small patches to maintain more live trees 12 years after harvest if they were surrounded by dispersed retention.

5.5. Implications

Saproxylic beetle assemblages in two sizes of retention patches were dissimilar to those in unharvested control plots, regardless of matrix quality 12-13 years post-harvest, except in 0.46 ha patches surrounded by the highest level of dispersed retention (50%) studied. Patches of 0.20 ha were ineffective in conserving saproxylic assemblages characteristic of unharvested forest. Thus, even combination of aggregated and dispersed retention does not fully maintain obligatory saproxylic beetle assemblages of species that initially colonize in deadwood if patches are not large enough. Collectively, the results from EMEND (this study and Chapter 4) reflect the influence of variation among stand types, use of different trapping methods, and time since harvest across studies, perhaps muting the direct effects of retention harvest. It is nonetheless safe to suggest that leaving patches with higher quality matrix (i.e., 20% and 50% dispersed retention) will preserve patch structures better than leaving a harvested matrix typical of clear-cuts. We note that four out of six patches surrounded by clear-cuts were almost eliminated due to windthrow 12 years post-harvest.

Canopy closure is one of the most important factors that shapes species composition of saproxylic beetles (Stokland et al., 2012; Bouget et al., 2014), so aggregated retention is the only method that is likely to conserve species requiring intact forest. However, positive effects on biodiversity can be maximized by combinations of aggregated and dispersed retention, which not only protects patches as windbreaks, but also naturally injects CWD into the surrounding matrix as habitat for saproxylic beetles during the regeneration phase. In order to promote useful progress, future studies of retention forestry should focus on: 1) investigating long-term structural persistence of retention patches combined in dispersed retention matrices differing in quality, 2) assessing responses of forest organisms associated with later decompositional stages of CWD in retention patches because these organisms are thought to be more susceptible to environmental changes associated with forestry operations, and 3) testing the interaction of patch size and level of dispersed retention required to promote biodiversity conservation. The EMEND experiment was not designed to fully investigate this latter interaction but the data available suggest that patches of the size incorporated into the EMEND design will not maintain obligatory saproxylic beetle assemblages associated with unharvested forests, given feasible levels of dispersed retention.

Table 5.1

Abbreviations for the combination of treatments used for the study.

Abbreviations	Descriptions
2%-S	Small patch (0.20 ha) surrounded by 2% retention (standard clear-cut)
2%-L	Large patch (0.46 ha) surrounded by 2% retention (standard clear-cut)
20%-S	Small patch (0.20 ha) surrounded by 20% dispersed retention
20%-L	Large patch (0.46 ha) surrounded by 20% dispersed retention
50%-S	Small patch (0.20 ha) surrounded by 50% dispersed retention
50%-L	Large patch (0.46 ha) surrounded by 50% dispersed retention
CT	Unharvested control (10 ha)

NOTE: Saproxylic beetles were not sampled in 2%-S. Environmental factors were measured in all treatment combinations.

Table 5.2

Mean (± SE) numbers of total live trees and mean volumes of downed CWD quantity and quality in aggregated retention patches surrounded by 2%, 20% and 50% dispersed retention, and unharvested control of mixed stands.

Patch Sizes	Treatm -ents[a]	Total numbers of live trees[b]	Proportion of coniferous and deciduous trees	Volumes of downed CWD (m^3)	Volumes of DCs[c] 1–2 (m^3)	Volumes of DCs 3–4 (m^3)	Volumes of DCs 5–6 (m^3)
0.20 ha	2%-S	58.67 ± 46.03 (3-150)	55:45	8.29 ± 3.42	1.21 ± 0.71	6.95 ± 3.19	0.13 ± 0.07
	20%-S	103.33 ± 41.68 (48-185)	70:30	6.41 ± 2.94	2.73 ± 1.37	3.67 ± 2.25	0.02 ± 0.02
	50%-S	70.67 ± 8.41 (57-86)	60:40	4.40 ± 1.75	2.44 ± 1.94	1.40 ± 0.29	0.57 ± 0.44
0.46 ha	2%-L	83.33 ± 49.84 (32-183)	58:42	14.06 ± 6.94	6.71 ± 6.39	6.16 ± 1.45	1.19 ± 0.61
	20%-L	158.33 ± 56.89 (97-272)	58:42	11.28 ± 5.66	6.49 ± 2.70	4.09 ± 2.94	0.69 ± 0.41
	50%-L	104.33 ± 40.48 (52-184)	73:27	8.24 ± 4.02	4.41 ± 3.21	2.60 ± 1.26	1.23 ± 0.47
CT	CT	-	-	2.91 ± 0.98	0.29 ± 0.24	1.05 ± 0.85	1.58 ± 0.58
		$p = 0.608$	-	$p = 0.361$	$p = 0.502$	$p = 0.173$	$p = 0.058$

NOTE: Total numbers of live trees were not measured in unharvested control.

[a] CT (unharvested control), L (large aggregated retention = 0.46 ha), and S (small aggregated retention = 0.20 ha).

[b] Numbers in parenthesis indicate ranges.

[c] DCs (decay classes).

Table 5.3

GLM results testing effects of position and harvesting treatments on species richness and catches of saproxylic beetles.

Trophic guilds	Source[a]	df	Deviance	AIC	p[b]	Pairwise comparisons[c]
GLM species richness						
All trophic guilds	Pos	1	44.49	222.78	0.128	
	Trmt	5	51.48	221.77	0.097	
	Pos × Trmt	5	39.09	229.38	0.688	
Phloeophages	Pos	1	29.96	158.40	0.392	
	Trmt	5	34.98	155.41	0.332	
	Pos × Trmt	5	27.33	167.76	0.863	
Mycetophages	Pos	1	19.92	133.35	0.326	
	Trmt	5	23.80	129.22	0.436	
	Pos × Trmt	5	15.43	140.86	0.620	
Predators	Pos	1	26.17	154.92	0.231	
	Trmt	5	29.00	149.74	0.512	
	Pos × Trmt	5	22.57	163.31	0.825	
GLM catches						
All trophic guilds	Pos	1	44.21	531.87	0.064	
	Trmt	5	49.29	528.95	0.130	
	Pos × Trmt	5	38.55	538.21	0.815	
Phloeophages	Pos	1	44.76	510.77	0.122	
	Trmt	5	49.26	507.27	0.230	
	Pos × Trmt	5	40.77	518.77	0.900	
Mycetophages	Pos	1	53.75	390.27	**0.001**	Snags > Logs
	Trmt	5	59.95	388.47	**0.006**	(CT, 50%-L, 50%-S) > 20%-S
	Pos × Trmt	5	36.65	385.17	0.233	
Predators	Pos	1	41.48	269.19	0.253	
	Trmt	5	76.66	296.37	**< 0.001**	CT > all treatments
	Pos × Trmt	5	37.89	277.60	0.809	

[a] Pos (Position) and Trmt (Treatment).

[b] Significant differences ($p < 0.05$) are highlighted in bold, followed by *a posteriori* pairwise comparisons.

[c] CT (unharvested control), L (large aggregated retention = 0.46 ha), and S (small aggregated retention = 0.20 ha).

Table 5.4

Two-way crossed design of PERMANOVA results testing effects of position and harvesting treatments on saproxylic beetle assemblages.

Trophic guilds	Source[a]	df	SS	MS	Pseudo-*F*	*p* (perm)[b]	Pairwise comparisons[c]
All trophic guilds	Pos	1	6306.8	6306.8	3.25	**< 0.001**	Log ≠ Snag
	Trmt	5	15814.0	3162.8	1.63	**0.007**	CT ≠ (2%-L, 20%-S, 20%-L, 50%-S), 2%-L ≠ 50%-L
	Pos × Trmt	5	6387.5	1277.5	0.66	0.978	
	Residual	24	46610.0	1942.1			
	Total	35	75119.0				
Phloeophages	Pos	1	7430.9	7430.9	4.95	**< 0.001**	Log ≠ Snag
	Trmt	5	13273.0	2654.7	1.77	**0.014**	CT ≠ (2%-L, 20%-S, 50%-S), 2%-L ≠ (20%-L, 50%-L, CT)
	Pos × Trmt	5	4734.6	946.9	0.63	0.938	
	Residual	23	34552.0	1502.3			
	Total	34	60113.0				
Mycetophages	Pos	1	5788.8	5788.8	2.18	**0.042**	Log ≠ Snag
	Trmt	5	13621.0	2724.2	1.03	0.418	
	Pos × Trmt	5	11818.0	2363.7	0.89	0.632	
	Residual	23	61050.0	2654.3			
	Total	34	93099.0				
Predators	Pos	1	1860.1	1860.1	0.74	0.624	
	Trmt	5	17497.0	3499.4	1.40	0.090	
	Pos × Trmt	5	4399.0	879.8	0.35	0.999	
	Residual	24	59976.0	2499.0			
	Total	35	83732.0				

[a] Pos (Position) and Trmt (Treatment).

[b] Significant differences ($p < 0.05$) are highlighted in bold, followed by *a posteriori* pairwise comparisons.

[c] CT (unharvested control), L (large aggregated retention = 0.46 ha), and S (small aggregated retention = 0.20 ha).

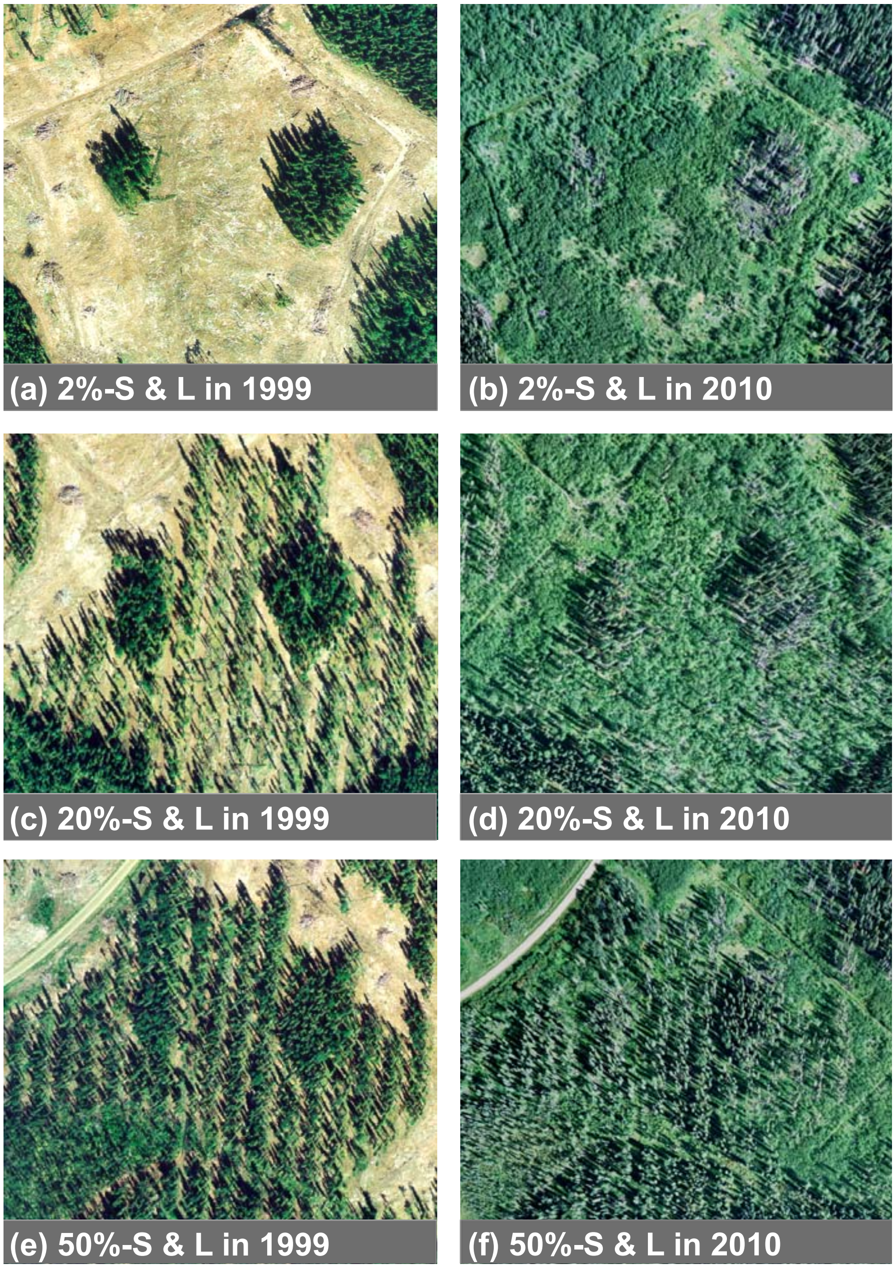


Fig. 5.1. Aerial photos of aggregated retention patches illustrating small (S) and large (L) patches (0.20 and 0.46 ha) surrounded by three different retention levels of 10 ha matrix (i.e., 2% retention (a, b), 20% dispersed retention (c, d), and 50% dispersed retention (e, f)) in mixedwood stands of EMEND landscape. Note that left and right aerial photos were taken in 1999 (a, c, e) and 2010 (b, d, f), respectively. Courtesy of photos: EMEND.

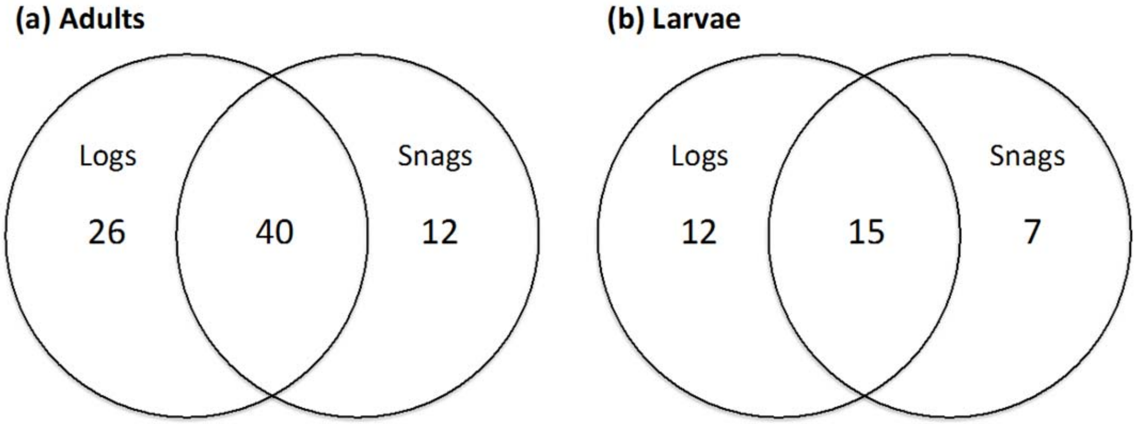


Fig. 5.2. Venn diagrams showing number of saproxylic beetle species between experimental logs and snags and their shared species richness for (a) adults and (b) larvae.

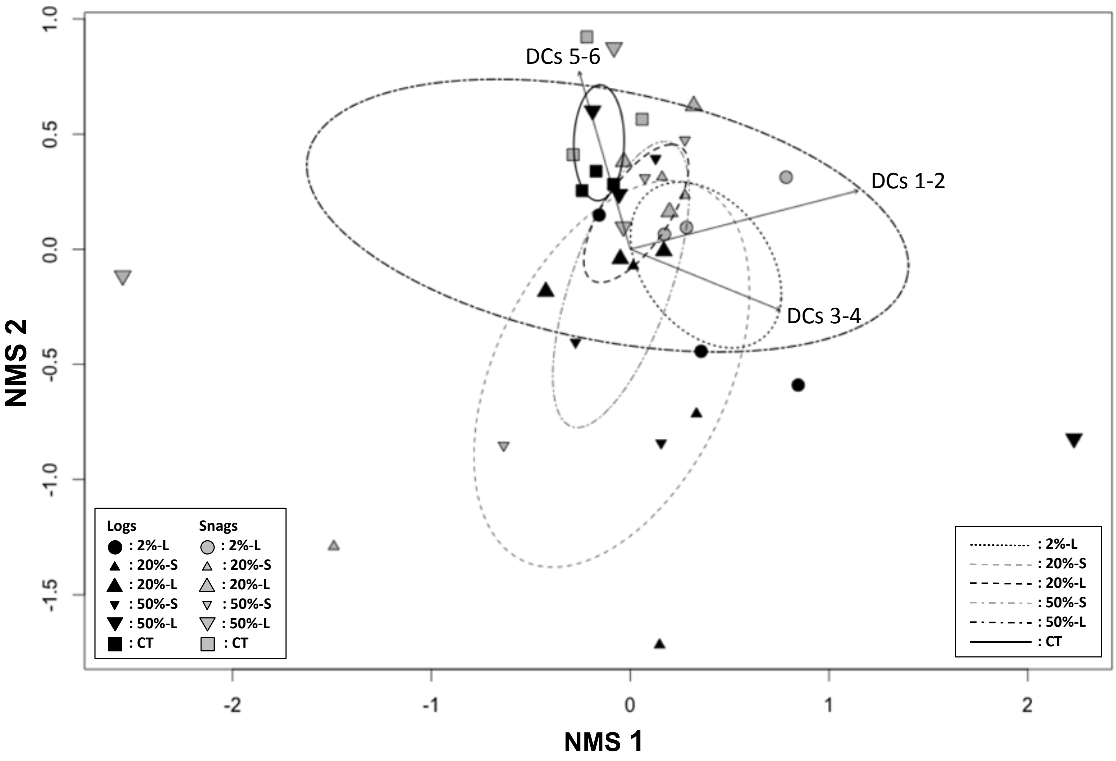


Fig. 5.3. Non-metric multidimensional scaling (NMS) of saproxylic beetle assemblages. Final stress is 14.4. Black and gray symbols represent beetles sampled from logs and snags, respectively. Small and large symbols represent small (0.20 ha) and large (0.46 ha) patches, respectively. Ellipses show 95% confidence intervals around treatment centroids. Note that the ellipses are applied to combined data of logs and snags of each treatment. Abbreviations: CT (unharvested control), DCs (decay classes), L (large aggregated retention), and S (small aggregated retention).

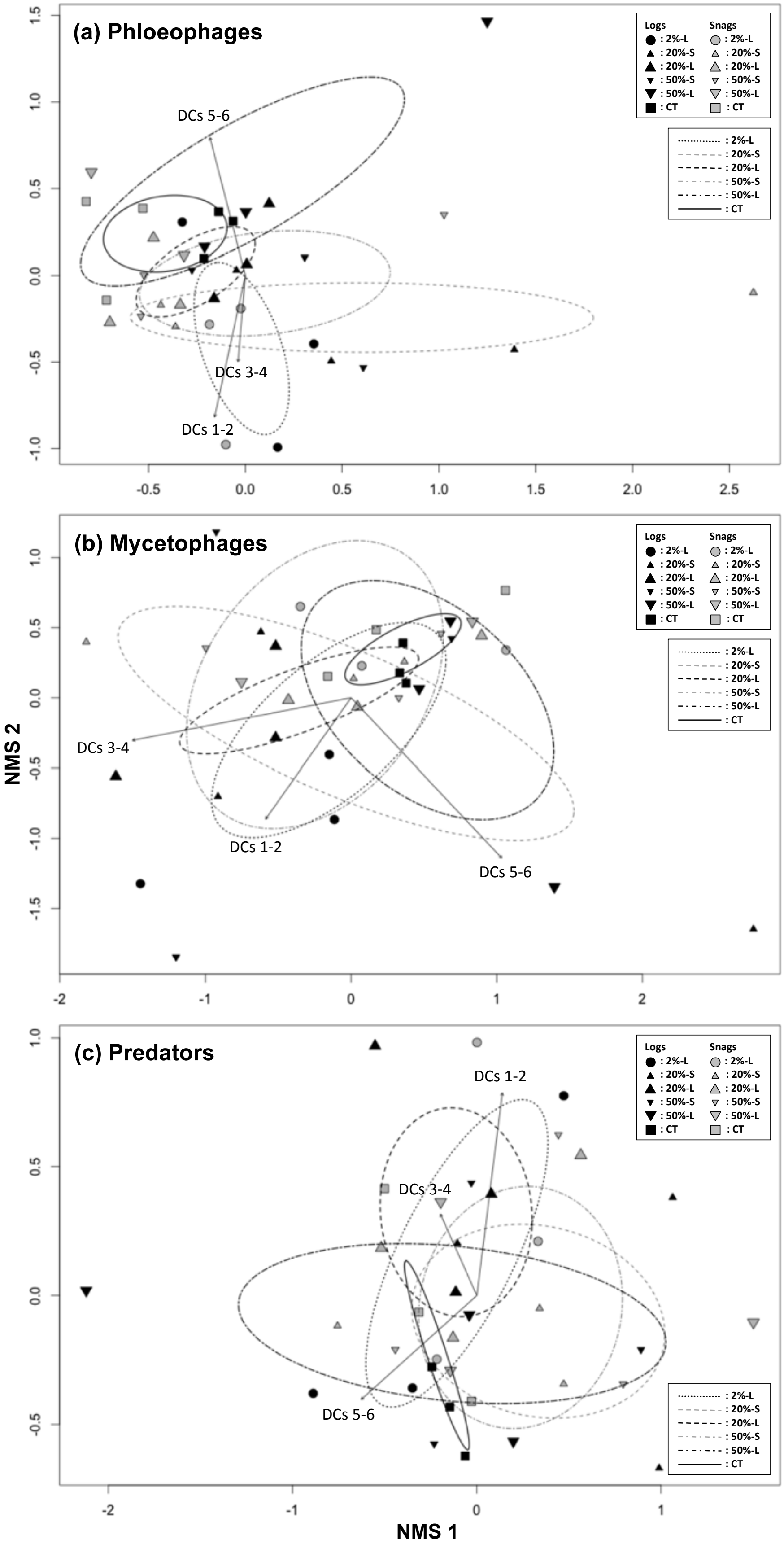

(a) Phloeophages
(b) Mycetophages
(c) Predators
Logs
Snags
: 2%-L
: 20%-S
: 20%-L
: 50%-S
: 50%-L
: CT
DCs 1-2
DCs 3-4
DCs 5-6
NMS 1
NMS 2
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
-1.0
-1.5
-2
-1
0
1
2

Fig. 5.4. Non-metric multidimensional scaling (NMS) of three trophic guilds (i.e., (a) phloeophages, (b) mycetophages, and (c) predators) saproxylic beetle assemblages. Final stresses of (a), (b), and (c) are 12.7, 10.7, and 17.1, respectively. Black and gray symbols represent beetles sampled from logs and snags, respectively. Small and large symbols represent small (0.20 ha) and large (0.46 ha) patches, respectively. Ellipses show 95% confidence intervals around treatment centroids. Note that the ellipses are applied to combined data of logs and snags of each treatment. Abbreviations: CT (unharvested control), DCs (decay classes), L (large aggregated retention), and S (small aggregated retention).

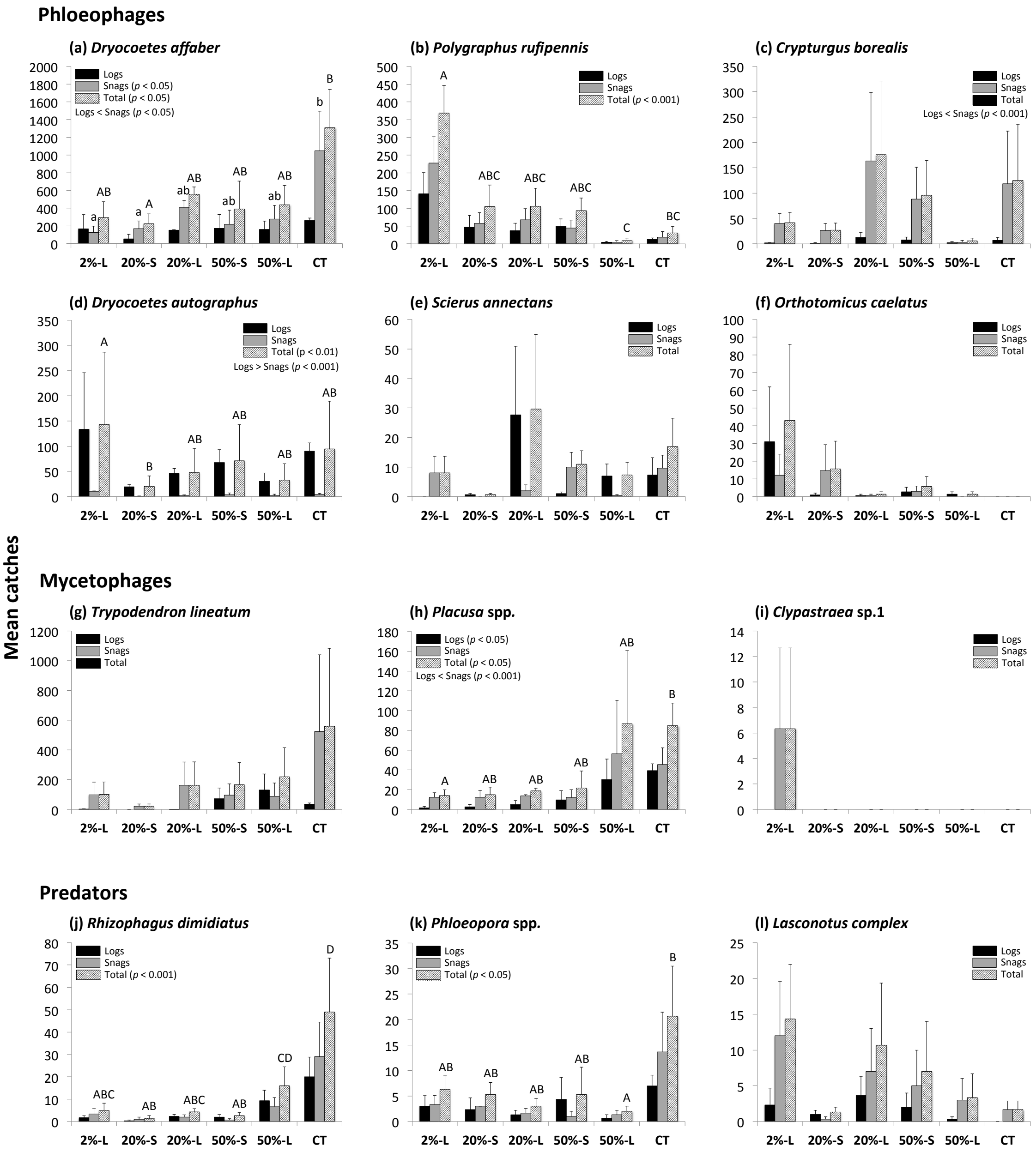


Fig. 5.5. Mean catches (+SE) of common species of phloeophages (a-f), mycetophages (g-i), and predators (j-l) in large patches surrounded by 2% retention, small (S) and large (L) patches surrounded by 20% and 50% dispersed retention, and unharvested control (CT). Different letters indicate significant *post-hoc* results (Tukey's honestly significant difference test, $p \leq 0.05$).

CHAPTER 6

General discussion

6.1. Main findings

In Chapter 2, I showed that structure of saproxylic beetle assemblages in the boreal mixedwood forest change progressively with increasing decomposition of white spruce downed CWD. In relation to a six-grade decay classification system, it was also clear that beetle assemblages of adjacent decay classes were highly similar, and that similarity decreased with increasing difference in decay classes. This carries an important message for conservation, as retention of the entire range of decay classes is necessary to conserve this saproxylic beetle fauna on post-harvest landscapes.

Using formal Indicator Species Analysis, I also found that phloeophagous and predaceous species were strong indicators for early decay stages, and that predatory species were the main indicators for advanced decay stages. Larvae that emerged from rearing drums were disproportionately predaceous, suggesting that movement of juveniles within and among CWD substrates is likely an important aspect of the life history for these species. Retention of CWD in advanced decay stages, which harbor species not found in earlier decay classes, presents a particular challenge in forest management because of the long time required to develop CWD in the later stages of decomposition. As suggested throughout the thesis, a conservation enlightened forest management regime will provide for some continuous entry of dead trees into decomposition cycles during in-block regeneration through green tree retention at harvest.

In Chapter 3, I examined how retention patches of white spruce function for saproxylic beetle conservation on industrially harvested landscapes, and sought to evaluate the ‘real-world’ utility of green-tree retention in an adaptive management framework. I compared saproxylic beetle assemblages among patches of three size categories (Small: 0.63-1.06 ha, Medium: 1.43-2.93 ha, and Large: 3.34-5.93 ha) left standing in harvested areas with those in intact forests and in the harvested matrix. A major finding of this chapter is that centers of patches ≥ 0.63 ha maintained saproxylic beetle assemblages similar to intact forests ten years postharvest. Although small retention patches maintained or attracted populations of species deemed to be ‘initial colonizers’, beetle assemblages in patches ≤ 2.93 ha were strongly influenced by edge effects and were less similar to those in intact forests. I suggest that patches ≥ 3.34 ha are sufficient to minimize negative edge effects.

Trophic guilds showed distinct and different responses to patch size. In particular, predator assemblages in smaller patches differed greatly from those of intact forests, while phloeophage assemblages were affected little by patch size.

Although smaller patches may better emulate historical size distributions of fire skips, they have limited conservation value for the deadwood-dependent fauna. Thus, I conclude that large patches are required to maintain local saproxylic beetle assemblages similar to those of intact forests. These findings provide practical guidance to the forest industry with respect to how best to leave aggregated retention on harvested landscapes. Since many forestry companies now leave very small forest patches, blindly emulating natural disturbance pattern, I recommend against this trend now prevailing in boreal forestry by underscoring the importance of larger patches for maintaining native saproxylic beetle assemblages.

In Chapter 4, I sought to understand how variable retention harvesting influences the composition and diversity of saproxylic beetle assemblages in boreal white spruce forests. Specifically, I compared saproxylic beetle assemblages in unharvested forest retention patches of two sizes (0.20 ha and 0.46 ha) that were embedded in 10 ha compartments harvested to different levels of dispersed retention (2%, 20% and 50%) in the context of the EMEND experiment. I compared assemblages with those from similar sized plots in 10 ha unharvested control compartments. By using two different trap types (i.e., window and emergence traps), I sampled both facultative and obligatory saproxylic beetles.

The most important finding of this chapter was that retention patches surrounded by 2% retention (i.e., clear-cuts by Canadian standards) were nearly eliminated through windthrow by 11 years after harvest. However, patches surrounded by 20% and 50% dispersed retention retained much of their basic structure, providing intact and continuous habitat for saproxylic beetles. My results demonstrate that saproxylic beetle assemblages characteristic of pre-harvest condition will not likely be maintained in retention patches left in clear-cuts, but should be better conserved in patches surrounded by 20% and 50% dispersed retention. Among different trophic guilds, predators were especially vulnerable to increasing harvest intensity in the surrounded matrix. Thus, my work underscores the value of using combinations of aggregated and dispersed retention on harvested landscapes to better maintain saproxylic beetle assemblages similar to those in unharvested control stands.

In Chapter 5, I examined the combined effects of aggregated retention patches (0.20 ha and 0.46 ha) and surrounding dispersed retention (2%, 20%, and 50%) on saproxylic beetle assemblages as in Chapter 4, but instead of working in spruce-dominated stands, I studied mixed stands 12-13 years post-harvest at the EMEND experiment. In this study, I sampled obligatory saproxylic beetles that emerged from freshly cut-bolts of white spruce and exposed as logs and snags in unharvested forest retention patches, and compared to assemblages from similar-sized plots in 10 ha unharvested control stands.

Neither species richness nor abundance differed significantly among combinations of aggregated and dispersed retention or between the two patch sizes studied. Clearly, however, composition of assemblages in retention patches 12-13 years post-harvest differed from those in unharvested controls, except in the largest patches surrounded by 50% dispersed retention. Species composition also differed between logs and snags for all feeding guilds except predators. Thus, patch size, matrix quality and the mix of logs and snags are important considerations for conservation of saproxylic beetle faunas in boreal mixedwood stands.

The results from Chapter 5 conflict somewhat with those from Chapter 4, in which I showed that saproxylic beetle assemblages in patches surrounded by 20% and 50% dispersed retention maintained similar to those of unharvested control. I point out that optimizing conditions for conservation of this fauna may vary according to forest composition, although commonly focused on beetles in white spruce. Thus, such considerations of context should be built into future research about combined effects of aggregated and dispersed retention to better understand how retention forestry practices affect the dynamics of saproxylic beetles.

With application of my taxonomic skills to identify 75 719 saproxylic beetles to species level, I was able to tally 377 species in 44 families in this dissertation. I found many beetle species new to the province of Alberta, and these results represent a significant contribution to the knowledge of Canadian biodiversity and the association of species with specific habitats. As a result, I recently contributed to a paper about new jurisdictional records of rove beetles in Canada (Klimaszewski et al., 2015) by reporting 14 new aleocharine rove beetle species in Alberta and describing their natural history and relationships to white spruce CWD. These species are: *Atheta fanatica* Casey, *Atheta pseudosubtilis* Klimaszewski & Langor, *Boreophilia davidgei* Klimaszewski & Godin, *Boreophilia islandica* (Kraatz), *Dinaraea worki* Klimaszewski & Jacobs< , *Homalota plana* (Gyllenhal), *Liogluta aloconoides* Lohse, *Oxypoda hiemalis* Casey, *Placusa incompleta* Sjöberg, *Placusa pseudosuecica* Klimaszewski, *Placusa tachyporoides* (Waltl), *Schistoglossa campbelli* Klimaszewski, *Schistoglossa hampshirensis* Klimaszewski, and *Trichiusa pilosa* Casey.

6.2. Future of retention forestry and saproxylic beetle conservation

6.2.1. Aggregated retention VS dispersed retention VS combination

Although clear-cutting is still a prevalent harvesting method in the world's forests, various silvicultural approaches such as variable retention have been suggested as better alternatives to improve conservation of forest biodiversity (Franklin et al., 1997; Lindenmayer and Franklin, 2002; Gustafsson et al., 2012). Among these alternatives, aggregated retention has been largely advocated as an effective way of maintaining biodiversity because it maintains intact forest structures and associated microhabitats and thereby conserves interior forest species (Franklin et al., 1997; Baker, 2011). Most researchers have agreed that patches ≤ 1 ha do not conserve arthropods characteristic of forest interior habitats (Halme and Niemelä, 1993; Pearce et al., 2005; Matveinen-Huju et al., 2006; Aubry et al., 2009). My research (e.g., Chapter 2) supports previous findings, and further emphasizes the need for larger patches (≥ 3.34 ha) to maintain the original saproxylic beetle assemblages associated with spruce deadwood in managed boreal landscapes in western Canada.

Several experiments have been conducted in western Canada and the USA during the last 20 years to test variable retention harvesting (Baker, 2011; Gustafsson et al., 2012). For example, the Ecosystem Management Emulating Natural Disturbance (EMEND) experiment in northwestern Alberta (Spence et al., 1999; Work et al., 2004), the Variable-Retention Adaptive Management (VRAM) project in British Columbia (Beese et al., 2005), and the Demonstration of Ecosystem Management Options (DEMO) study in the Pacific Northwest of the USA (Aubry et al., 2009) are designed to demonstrate the efficacy of retention forestry, focusing on both aggregated and dispersed retention. A general conclusion drawn from these large-scale experiments is that low levels of dispersed retention are not effective to alleviate negative effects of forest harvest on native biodiversity (Aubry et al., 2009; Work et al., 2010). In fact, even 50% dispersed retention, a level that is unlikely to be economically viable, does not maintain arthropod species characteristic of interior forest habitats (Work et al., 2010; Pinzon et al., 2012). Dispersed retention of 75% may preserve some interior forest species in situ (Work et al., 2010; Pinzon et al., 2012); however such a high amount of retention is not practical to apply in industrial harvesting systems.

Although the prevailing opinion is that dispersed retention alone cannot serve as lifeboat for conserving characteristics of interior forest and the species that depend upon them, dispersed retention is a highly important component of modern ‘green forestry’, and should be applied together with aggregated retention to maximize effectiveness. Based on my examination of the benefits of dispersed retention (Chapters 4 and 5), there are unique aspects of dispersed retention that aggregated retention cannot provide. Most importantly, dispersed retention strengthens connectivity on harvest block between adjacent aggregated retention patches and surrounding intact forests (Lindenmayer and Franklin, 2002), and belowground processes and organisms benefit through such connectivity (Franklin et al., 1997). Evenly dispersed live trees eventually die and supply standing and fallen deadwood continuously throughout harvest blocks, at least during the early phases of forest regeneration, and such CWD will provide an array of decay classes and habitats in the regenerating stands to help biodiversity recover following harvest. These are important characters of dispersed retention, missing from conventional clear-cut harvests. Moreover, my work suggests that dispersed retention plays a pivotal role in providing windbreaks that minimize blowdown of aggregated retention at least 10 years post-harvest.

Thus, the combined use of aggregated and dispersed retention on the same harvest blocks should be beneficial for conservation of forest biodiversity. In fact, many forestry companies have recently implemented this combined approach to enhance biodiversity conservation (Baker, 2011). Despite the emerging practice in North America of combining aggregated and dispersed retention on harvested blocks, only few studies of limited taxa have tested the hypothesis that combinations of dispersed and aggregated retention will lead to superior results, e.g., spiders (Pinzon et al., 2012) and saproxylic beetles (Chapters 4 and 5). Therefore, the combined value of both types of retention should be examined for other taxa in order to formulate recommendations that are optimal for a broad suite of organisms. To my knowledge, the EMEND project is the only study in the world that experimentally tests the conservation value of both dispersed and aggregated retention; however, the limited size of retained patches at EMEND (i.e., 0.20 and 0.46 ha) is likely too small to fully test these effects. Thus, future field experiments are needed to test the combined effects of aggregated and dispersed retention using larger patch sizes. Work presented in this dissertation and elsewhere to date suggests that patches of 3-4 ha will be required to demonstrate positive effects over reasonable time frames.

6.2.2. Adaptive management and current forest management guidelines

Adaptive management is applying lessons learned through operational work in a continuous feedback cycle of learning and application. In forest management this approach supports exploring new approaches while, at the same time, accommodating uncertainty to better attain management goals (Walters and Holling, 1990; Lindenmayer and Franklin, 2002; Bunnell, 2005; Baker, 2011; Van Damme et al., 2014). Biodiversity protection is a relatively new management priority for the Canadian forest sectors (Work et al., 2003) that was not accommodated in design of the previous clear-cut approaches. Although many forestry companies have implemented adaptive management for biodiversity conservation, currently there is little effective guidance about retention levels or approaches (Work et al., 2003; Van Damme et al., 2014).

In Alberta, for example, there is no legislative framework, and forest industries engage in voluntary land management planning (Van Damme et al., 2014). Therefore, some companies leave only 3–6% retention, including unmerchantable volume, which is only a slight improvement on traditional clear-cuts. Nonetheless, other companies leave more. For example, Daishowa-Marubeni International Ltd. (DMI), voluntarily leaves an average of 15% retention on their harvested landscapes, ranging from 0–30% at the cut block level, not including wetlands, buffers and inoperable slopes (DMI, 2013; Van Damme et al., 2014). Although all harvest plans must be approved, both extremes are acceptable under the current provincial guidelines (Van Damme et al., 2014). On the other hand, current standards and guidelines in the Pacific Northwest region of USA are more prescriptive, demanding that at least 15% retention is required, of which 70% must be aggregated retention in areas larger or equal than 0.2 ha (Aubry et al., 2009; Urgenson et al., 2013). Research such as that outlined in this dissertation is critical to provide science-based input into development of future policies and regulations in Canada concerning desired retention levels.

Research to date, including that presented in this dissertation, however, suggests that the small aggregated retention patches (≤ 1 ha) widely implemented in industrial forestry are insufficient for maintaining arthropod assemblages characteristic of interior forest (Matveinen-Huju et al., 2006; Aubry et al., 2009; Lee et al., 2015). Thus, I have advocated that more large patches should be left at harvest, and that combinations of aggregated and dispersed retention should be investigated for extending patch persistence, improving retention of characteristics of interior forest and thereby enhancing biodiversity conservation.

6.2.3. Beyond strict emulation of natural disturbance regimes

The natural disturbance emulation (NDE) approach is now widely accepted by the science community, regulators and forestry industry, and thus leaving various sizes of uncut forest patches to mimic the distribution of fire skip patterns within large fires is widely endorsed (e.g., Work et al., 2003; Lee et al., 2015). There is no doubt that this shift to NDE has positively influenced conservation of forest biodiversity over conventional clear-cut harvesting that removes nearly all merchantable timber from large blocks (Jacobs et al., 2007b; Pinzon et al., 2012; Lee et al., 2015). Although this approach to forest management is thought to benefit many forest organisms and ecosystem functions, there are intrinsic differences between natural disturbance and natural disturbance-emulating forest management. Most obvious among these is the amount and pattern of deadwood left after disturbance; wildfires leave huge amounts of dead and fire-damaged wood on landscape (Hunter, 1993) but most of this volume is trucked to mills as a result of harvest. Patterns of burnt, damaged and non-damaged trees may also vary according to fire intensity and severity as well as be affected by the natural history of specific ecosystems. Additionally, under the current NDE approach to forest management, only relatively small amounts of sufficiently large deadwood are left in the harvested matrix in the process of resource extraction (Schneider, 2002). Therefore, we cannot exactly emulate all ecosystem characteristics of natural disturbance.

At the landscape level, variability in retention patch size has been an important feature for biodiversity conservation under the natural disturbance model. However, as I address in Chapter 3, the present approach may be inadequate when considering that current area-specific rates of industrial harvest will likely exceed local rates of stand replacement through natural disturbance (Kuuluvainen, 2009; Bergeron and Fenton, 2012). If the harvesting rate is faster than natural stand replacement, it is probably a good idea to focus on the conservation of interior forest species that are likely to best maintain their populations in large forest patches.

Forest management based on NDE has provided insights of how to sustainably manage forests, considering the maintenance of wildlife and ecosystem functions. However in light of recent research, I provide the following suggestions to improve forest management beyond strict emulation of natural disturbance patterns:

1. Large retention patches have better conservation value than small ones (< 1 ha). Although smaller patches emulate historical size distributions of fire skips, their conservation value is limited due to negative edge effects (Lee et al., 2015);
2. More strong connectivity between patches is required to promote original biodiversity. Thus, irregular distribution of retention patches emulating patterns of fire skips may interrupt species' movement between patches if patches are too far apart for species to interact; and
3. Use of dispersed retention that surrounds aggregated retention patches is essential, because it provides a continuous supply of standing and lying deadwood as time passes (Solarik et al., 2012), and together with living trees in the harvested matrix, these deadwood elements may serve as important stepping stones for various forest species especially for saproxylic organisms.

Mitigation of negative effects on biodiversity and ecosystem functions may be the most important non-timber consideration currently affecting large-scale industrial forestry in Canada. To achieve the best conservation outcomes possible, I suggest that managers should try to emulate the important characteristics of what natural disturbance leaves behind. To be most effective, I believe that this tactic must be informed by data about intervals and severity of natural disturbance, and responses of forest biota at both local and landscape scales instead of strictly emulating shapes and patterns of natural disturbance.

6.2.4. Conservation of saproxylic beetles and importance of deadwood

The greatest presently understood threat to saproxylic organisms is forestry practices that result in habitat loss and fragmentation of forested landscapes (Stokland et al., 2012). Because many of the Earth's original forests have been harvested to meet human needs and desires and this is likely to continue, almost all local biotas dependent on forested habitats suffer some level of extirpation. Clearly, the biodiversity of saproxylic species in northern Europe has dramatically decreased coincident with a long history of extensive resource extraction (Siitonen, 2001; Djupström et al., 2008; Stokland et al., 2012). In Finland, for example, reduction in deadwood volume is the most commonly cited cause of decline for threatened forest species and the second most important cause of extirpation of threatened species (Rassi et al., 2010). In Sweden, the distribution and abundance of CWD has been severely affected by forest harvest, and it is known that 85% of red-listed forest-dwelling beetle species are closely related to deadwood (Jonsell et al., 1998). Thus, retention of deadwood appears to be central to conserving saproxylic biodiversity (Siitonen, 2001; Jonsson et al., 2005; Franc, 2007; Jonsell et al., 2007; Stokland et al., 2012; Bouget et al., 2014).

To better manage deadwood and thereby conserve saproxylic organisms, maintenance of the full decompositional ranges of deadwood is essential because different decay classes are required to maintain the rich saproxylic assemblages that characterize natural forest ecosystems (Langor et al., 2008; Ferro et al., 2012b; Lee et al., 2014). However, this aspect of deadwood management in conjunction with its associated value for biodiversity conservation is not easy to achieve with traditional forestry practices and, in fact, has not been sufficiently studied under the modern context of 'green forestry'. Work presented in this dissertation contributes to filling that gap. For example, results in Chapter 3, showed that variation in quality of CWD of clear-cuts remained incredibly low even 10 years post-harvest, representing mostly a single decay class CWD (i.e., highly dried DC 4), and with the total absence of snags. Although retention patches maintained a greater variety of CWD quality, the surrounding clear-cut matrix was hostile to saproxylic organisms in terms of availability of diverse deadwood habitats (Lee et al., 2015). Thus, success in saproxylic beetle conservation will likely depend on how well we are able to manage the range of deadwood quality in the matrix. Toward this end, my work argues that clear-cut harvesting should be avoided, and suggests that dispersed and aggregated retention together will support diversity of deadwood habitats on harvest blocks to promote conservation and recovery of local saproxylic assemblages.

6.3. Final thoughts and future research

Retention forestry has received significant attention from ecologists during the last two decades as a promising framework for conserving forest biodiversity. Although current retention practices clearly benefit many forest organisms compared to impacts of conventional clear-cut harvesting, large gaps in knowledge remain in need of attention. The next step in development and application of retention forestry is for proponents to provide a framework for guidance about best practices for conservation of biodiversity on managed landscapes as more and more area is harvested with retention. In this context, I underscore the following three points based on the results presented in this dissertation.

1. Conservation of the full decompositional ranges of deadwood is crucial to maintain saproxylic beetle diversity. Thus, retention forestry should include deadwood diversity as an important focus for ensuring persistence of saproxylic organisms associated with different decay classes.
2. Leaving small patches (< 1 ha), as currently justified by the philosophy of fire emulation, is not the best conservation tactic. Based on work in this dissertation, I recommend that many or most retention patches should be relatively large (i.e., 3-4 ha) to minimize negative edge effects on saproxylic beetle assemblages and assist with post-harvest retention across managed landscapes.
3. Finally, my work supports the wisdom of using both aggregated and dispersed retention together on the same blocks. I have shown above that dispersed retention in the harvested matrix supports the long-term function of patches left to lifeboat the saproxylic fauna, and thus management that couples them will better maintain saproxylic biodiversity and support its recovery across harvested landscapes.

Research about retention forestry is becoming increasingly important in my view. Most results published to date about this new conservation-oriented approach to forest harvest have focused on short-term responses of forest organisms; however, future research is likely to reveal significant and interesting medium to long-term findings as matrix quality increases (See Baker et al., 2015). This dissertation that reflects work done 10-13 years post-harvest illustrates how our perceptions may change as we are informed by data reflecting longer time frames. Among important issues related to biodiversity conservation through forest management, I suggest that future research should focus on the following five points:

1. detecting an optimal patch size that satisfies the needs of species characteristic of interior forest habitats, concentrating on patches larger than 1 ha and applying a systematic experimental design (Lee et al., 2015);
2. testing the combined effects of aggregated and dispersed retention, since dispersed retention is thought to be highly beneficial for alleviating negative effects of industrial forestry (Pinzon et al. 2012);
3. investigating variation in deadwood quality among different sizes of retention patches in relation to maintenance and recovery of interior forest species, such as species dependent on CWD in later stages of decomposition (Lee et al. 2014);
4. conducting in-depth study of edge effects and forest influences on biodiversity given a range of retention forestry tactics (Baker et al., 2015); and

5. allocating retention (e.g., shape and distance between patches) to optimally protect and maintain biodiversity and functional ecosystem integrity.

Many researchers have argued that there is no single ‘best’ approach to retention forestry that can be universally applied for satisfying all forest biota (e.g., Serrouya and D’Eon, 2004). In my opinion, however, conservation of all species or maintenance of high species diversity in all sites should not be the main purpose of retention forestry. Retention forestry should aim to support recovery and continuity of the heterogeneity characterizing the original forest structure and composition that maintains native biodiversity and ecological functions on larger forest landscapes (Lindenmayer et al., 2012). This opinion flows from a particular environmental ethic or value system. It is rooted in the concept that conservation of forest biodiversity gives explicit attention to maintenance of the original forest species that are mostly threatened by anthropogenic disturbance (Diamond, 1976), and managing other less sensitive species by promoting a natural range of variation, such as generated by fire history, at both the local and landscape scales. Of course, under climate change, history becomes a less useful guide for setting our targets, emphasizing the first part of the concept promoted above. We cannot count on simple emulation of the past to conserve sensitive species into the future.

I hope that results in this dissertation will help coax policy makers toward operating ground-rules that include leaving larger unharvested aggregated retention mixed with some levels of dispersed retention as a part of the new landscape approach to forest management. Then, we may move closer to a goal of explicitly understanding trade-offs that must be managed to develop retention forestry that satisfies both our economic need for timber production and fiber extraction, and our ecological and ethical focus on biodiversity conservation.

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APPENDICES

Appendix 2-A

Adult saproxylic beetles sampled in different decay classes of white spruce downed coarse woody debris. The numbers represent raw abundances except for the numbers in frequency (Freq), which represent the number of occurrence of each species among fifty-four CWD samples.

Family	Species	FG	DC1	DC	DC	DC	DC	DC	Total	Freq
Carabidae	*Agonum retractum* LeConte	PRE					4	2	6	6
Carabidae	*Calathus advena* (LeConte)	PRE					1		1	1
Carabidae	*Calathus ingratus* Dejean	PRE			1				1	1
Carabidae	*Platynus decentis* (Say)	PRE			1		1		2	2
Carabidae	*Psydrus piceus* LeConte	PRE				2			2	2
Carabidae	*Trechus apicalis* Motschulsky	PRE					2		2	2
Cerambycidae	*Tetropium cinnamopterum* (Kirby)	XYL	3	18					21	3
Colydiidae	*Lasconotus complex* LeConte	PRE	2						2	2
Corylophidae	*Arthrolips* sp.1	MYC	1		1				2	2
Cryptophagidae	*Caenoscelis ferruginea* (Sahlberg)	MYC				1			1	1
Cryptophagidae	*Caenoscelis antennalis* (Casey)	MYC			10	1			11	2
Cryptophagidae	*Cryptophagus pilosus* Gyllenhal	MYC		1					1	1
Cryptophagidae	*Cryptophagus acutangulus* Gyllenhal	MYC				2	4		6	6
Cryptophagidae	*Cryptophagus tuberculosus* Mäklin	MYC	1			1		1	3	3
Curculionidae	*Carphonotus testaceus* Casey	XYL		2	4				6	4
Curculionidae	*Crypturgus borealis* Swaine	PHL	5	1	18				24	6
Curculionidae	*Dendroctonus rufipennis* (Kirby)	PHL	1	1					2	2
Curculionidae	*Dryocoetes affaber* (Mannerheim)	PHL	501	363	8				872	13

Curculionidae	*Dryocoetes autographus* (Ratzeburg)	PHL	3						3	2
Curculionidae	*Ips pini* (Say)	PHL	37						37	3
Curculionidae	*Polygraphus rufipennis* (Kirby)	PHL	112	103					215	7
Curculionidae	*Scierus annectans* LeConte	PHL	4	4					8	4
Curculionidae	*Trypodendron lineatum* (Olivier)	MYC	201						201	3
Curculionidae	*Tychius picirostris* (Fabricius)	UNK	1						1	1
Elateridae	*Ctenicera* sp.2	PRE	1						1	1
Elateridae	*Eanus decoratus* (Mannerheim)	PRE			1				1	1
Elateridae	*Pseudanostirus propolus* (LeConte)	PRE			1				1	1
Latridiidae	*Corticaria ferruginea* Marsham	MYC		1	1				2	2
Latridiidae	*Corticaria rubripes* Mannerheim	MYC	1	4	3		1		9	8
Latridiidae	*Cortinicara gibbosa* (Herbst)	MYC	1						1	1
Latridiidae	*Latridius minutus* (Linnaeus)	MYC	1	4	1				6	3
Latridiidae	*Melanophthalma villosa* Zimmerman	MYC	1						1	1
Leiodidae	*Agathidium depressum* Fall	MYX					1		1	1
Leiodidae	*Agathidium pulchrum* LeConte	MYX				1			1	1
Leiodidae	*Agathidium* sp.1	MYX				1			1	1
Leiodidae	*Anisotoma amica* Brown	MYX			1				1	1
Leiodidae	*Leiodes punctostriata* Kirby	MYC						1	1	1
Melandryidae	*Xylita livida* (Sahlberg)	XYL		5					5	2
Monotomidae	*Rhizophagus dimidiatus* Mannerheim	PRE	1	4					5	2
Nitidulidae	*Colopterus truncates* (Randall)	UNK	10						10	1
Nitidulidae	*Epuraea planulata* Erichson	PRE		1					1	1
Nitidulidae	*Epuraea terminalis* Mannerheim	PRE	19			1			20	4
Ptiliidae	*Acrotrichis* sp.1	MYC		1		1	1		3	3
Ptiliidae	*Pteryx* sp.1	MYC			1	3	2	3	9	5
Ptiliidae	*Ptinella* sp.1	MYC			1				1	1
Scraptiidae	*Anaspis rufa* Say	MYC			1				1	1
Silvanidae	Silvanidae sp.1	MYC	1						1	1
Staphylinidae	*Acidota crenata* (Fabricius)	PRE						2	2	2

Staphylinidae	Aleocharinae sp.1	UNK				1			1	1
Staphylinidae	*Amischa* sp.1	PRE	3	1	2	4	3	1	14	10
Staphylinidae	Anthophagini sp.1	PRE		1					1	1
Staphylinidae	*Atheta klagesi* Bernhauer	PRE				1	1		2	2
Staphylinidae	Athetini sp.1	PRE					3		3	2
Staphylinidae	*Dinothenarus pleuralis* (LeConte)	PRE				1			1	1
Staphylinidae	*Euplectus duryi* Casey	PRE					1		1	1
Staphylinidae	*Gabrius brevipennis* (Horn)	PRE				1		1	2	2
Staphylinidae	*Gnypeta* sp.1	UNK		1					1	1
Staphylinidae	*Ischnosoma fimbriatum* Campbell	PRE					2		2	2
Staphylinidae	*Ischnosoma splendidum* (Gravenhorst)	PRE						1	1	1
Staphylinidae	*Lathrobium fauveli* Duvivier	PRE					1	2	3	2
Staphylinidae	*Lathrobium washingtoni* Casey	PRE				1	7	6	14	9
Staphylinidae	*Liogluta aloconotoides* Lohse	PRE					1	1	2	2
Staphylinidae	*Lordithon bimaculatus* (Schrank)	PRE				1			1	1
Staphylinidae	*Mocyta breviuscula* (Mäklin)	PRE	1	1					2	2
Staphylinidae	*Nudobius cephalus* (Say)	PRE	1	2	1	1			5	5
Staphylinidae	*Olisthaerus megacephalus* (Zetterstedt)	PRE				1	3		4	3
Staphylinidae	*Olisthaerus substriatus* (Paykull)	PRE		1					1	1
Staphylinidae	*Olophrum consimile* (Gyllenhal)	PRE		1					1	1
Staphylinidae	*Oxypoda canadensis* Klimaszewski	PRE					1		1	1
Staphylinidae	*Oxypoda frigida* Bernhauer	PRE			1		7	2	10	5
Staphylinidae	*Oxypoda operta* Sjöberg	PRE					2	1	3	3
Staphylinidae	*Phloeopora* sp.1	PRE		2					2	1
Staphylinidae	*Phloeopora* sp.2	PRE	1						1	1
Staphylinidae	*Phloeostiba lapponicus* (Zetterstedt)	PRE	17						17	3
Staphylinidae	*Placusa tachyporoides* (Waltl)	MYC	89			1			90	3
Staphylinidae	*Placusa tacomae* Casey	MYC	4		1				5	2
Staphylinidae	*Pseudopsis sagittal* Herman	PRE					1		1	1
Staphylinidae	*Quedius caseyi* Scheerpeltz	PRE					2		2	2

Staphylinidae	*Quedius criddlei* (Casey)	PRE					1		1	1
Staphylinidae	*Quedius fulvicollis* (Stephens)	PRE					2	1	3	3
Staphylinidae	*Quedius labradorensis* Smetana	PRE						1	1	1
Staphylinidae	*Quedius mordax* Smetana	PRE			1				1	1
Staphylinidae	*Quedius plagiatus* Mannerheim	PRE		1					1	1
Staphylinidae	*Quedius transparens* Motschulsky	PRE		1					1	1
Staphylinidae	*Quedius velox* Smetana	PRE					4	1	5	2
Staphylinidae	*Seeversiella globicollis* (Bernhauer)	PRE					7	3	10	4
Staphylinidae	*Siagonium punctatum* LeConte	MYC			1				1	1
Staphylinidae	*Stenichnus ovipennis* (Casey)	PRE					1		1	1
Staphylinidae	*Stenus austini* Casey	PRE				2		3	5	5
Staphylinidae	*Tachinus elongates* Gyllenhal	PRE				1			1	1
Staphylinidae	*Tachinus frigidus* Erichson	PRE				1			1	1
Staphylinidae	*Tachinus fumipennis* (Say)	PRE		1					1	1
Staphylinidae	*Tachyporus borealis* Campbell	PRE			1	1	5	9	16	10
Trogossitidae	*Peltis fraterna* (Randall)	MYC		1	5				6	2
Total			1024	527	67	32	72	42	1764	

DC=decay class, FG=feeding guilds, MYC=mycetophagous, MYX=myxomycophagous, PHL=phloeophagous, PRE=predaceous, UNK=unknown, XYL=xylophagous.

Appendix 3-A

Saproxylic beetles sampled using window traps attached to girdled trees and snags of boreal white spruce in the harvested matrix, edges and centers of retention patches of three size classes, and intact forest (control) on a harvested landscape in northwestern Alberta. Nomenclature follows that of Bousquet et al. (2013).

					Small patch[e]		Medium patch[f]		Large patch[g]				
Family	Species[a]	FG[b]	Total[c]	HM[d]	Edge	Center	Edge	Center	Edge	Center	IF[h]	Girdled	Snag
Aderidae	*Vanonus* sp.1	XYL	1	1									
Anthicidae	*Anthicus hastatus* Casey	OMN	2			1				1		2	
Buprestidae	*Agrilus* sp.1	XYL	1							1		1	
	Chrysobothris trinervia (Kirby)	XYL	1		1								1
	Dicerca tenebrosa (Kirby)	XYL	1		1								1
	Phaenops drummondi (Kirby)	XYL	3				3					2	1
	Phaenops fulvoguttata (Harris)	XYL	7		1		4		2			6	1
Cantharidae	*Dichelotarsus laevicollis* (Kirby)	PRE	35	4	1	3	3	6	6	9	3	14	17
	Dichelotarsus piniphilus (Eschscholtz)	PRE	30	2	3	5	6	1	4	4	5	12	16
	Dichelotarsus puberulus (LeConte)	PRE	1							1		1	
	Rhagonycha mandibularis (Kirby)	PRE	1				1						1
Carabidae	*Badister obtusus* LeConte	PRE	1			1							1
	Bradycellus congener (LeConte)	PRE	1				1						1
	Calathus advena (LeConte)	PRE	18			4		2		9	3	12	6
	Calathus ingratus Dejean	PRE	1	1									
	Dicheirotrichus cognatus (Gyllenhal)	PRE	1	1									
	Dromius piceus Dejean	PRE	3		1		1			1		2	1
	Nebria gyllenhali (Kirby)	PRE	1	1									
	Platynus decentis (Say)	PRE	11	1		1	2	1		4	2	5	5

					Small patch[e]		Medium patch[f]		Large patch[g]				
Family	Species[a]	FG[b]	Total[c]	HM[d]	Edge	Center	Edge	Center	Edge	Center	IF[h]	Girdled	Snag
	Stereocerus haematopus (Dejean)	PRE	2			1	1						1
Cerambycidae	*Acmaeops proteus* (Kirby)	XYL	5		3		1			1		1	4
	Anastrangalia sanguinea (LeConte)	XYL	1			1							1
	Callidium cicatricosum Mannerheim	XYL	1		1							1	
	Cortodera coniferae Hopping & Hopping	XYL	4		1				2	1		2	2
	Grammoptera subargentata (Kirby)	XYL	4			1	1		2			1	3
	Judolia montivagans (Couper)	XYL	4		1		2	1				1	3
	Meriellum proteus (Kirby)	XYL	7			4	2			1		3	4
	Monochamus scutellatus (Say)	XYL	3				2				1	1	2
	Neoclytus leucozonus (Laporte & Gory)	XYL	3		1		2					2	1
	Neospondylis upiformis (Mannerheim)	XYL	21			4	2	2	6	6	1	20	1
	Pachyta lamed liturata Kirby	XYL	1						1				1
	Phymatodes dimidiatus (Kirby)	XYL	12		1	2	3		4	2			3
	Phymatodes sp.1	XYL	1			1						1	
	Pogonocherus penicillatus LeConte	XYL	10			1	1	2	2	2	2	10	
	Pygoleptura nigrella (Say)	XYL	8	1	3		1	2	1			2	5
	Rhagium inquisitor (Linnaeus)	XYL	2						1		1	1	1
	Tetropium cinnamopterum Kirby	XYL	37		1	4	10	1	12	4	5	37	
	Tetropium parvulum Casey	XYL	6			2		1	3			5	1
	Trachysida mutabilis (Newman)	XYL	1						1				1
	Xylotrechus undulatus (Say)	XYL	29		6	4	9		9	1		26	3
Cerylonidae	*Cerylon castaneum* Say	MYC	5		1	1	1		1	1		3	2
Ciidae	Ciidae sp.1	MYC	1						1				1
	Cis americanus Mannerheim	MYC	1				1					1	
	Cis angustus Hatch*	MYC	3		3							1	2
	Cis horridulus Casey*	MYC	2			1	1					1	1
	Cis striolatus Casey	MYC	2		1		1					2	
	Dolichocis manitoba Dury	MYC	5		1		1	1	2			1	4

Family	Species[a]	FG[b]	Total[c]	HM[d]	Small patch[e]		Medium patch[f]		Large patch[g]		IF[h]	Girdled	Snag
					Edge	Center	Edge	Center	Edge	Center			
	Octotemnus laevis Casey	MYC	10	2	1	1		1	2	2	1	5	3
	Plesiocis cribrum Casey	MYC	2						2				2
Clambidae	*Calyptomerus oblongulus* (Mannerheim)	MYC	7		1		2	2			2	5	2
	Clambus pubescens Redtenbacher	MYC	3				2				1	1	2
Cleridae	*Thanasimus dubius* (Fabricius)	PRE	7							6	1	7	
	Thanasimus undatulus (Say)	PRE	66		3	3	22	2	9	25	2	55	11
Colydiidae	*Lasconotus complex* LeConte	PRE	23		2	2	3	2	1	10	3	20	3
Corylophidae	*Arthrolips* sp.1	MYC	1			1							1
	Clypastraea sp.1	MYC	13		1	2	9	1				8	5
	Orthoperus scutellaris LeConte	MYC	1								1	1	
Cryptophagidae	*Antherophagus ochraceus* Melsheimer	MYC	2							1	1		2
	Atomaria ephippiata Zimmermann	MYC	2	2									
	Atomaria sp.1	MYC	15	4	1	2	3	2	2		1	8	3
	Atomaria sp.2	MYC	2	1	1							1	
	Atomaria sp.3	MYC	6	1	1		1		2		1	2	3
	Atomaria sp.4	MYC	5		1			3			1	2	3
	Atomaria sp.6	MYC	1				1					1	
	Atomaria sp.7	MYC	1							1		1	
	Caenoscelis antennalis (Casey)	MYC	3		2					1		2	1
	Cryptophagus acutangulus Gyllenhal	MYC	1								1		1
	Cryptophagus tuberculosus Mäklin	MYC	58		1	7	6	12	2	13	17	28	30
	Henoticus serratus (Gyllenhal)	MYC	1				1					1	
	Myrmedophila americana (LeConte)	MYC	2		1		1						2
	Pteryngium crenatum (Gyllenhal)[*]	MYC	7				2	1		2	2	1	6
	Salebius octodentatus (Mäklin)[*]	MYC	11		1	3		1		5	1	7	4
Cucujidae	*Pediacus fuscus* Erichson	PRE	60	3	30	3	12	2	5	3	2	40	17
Curculionidae	*Cryphalus ruficollis* Hopkins	PHL	16		2	2		8	1	2	1	10	6
	Crypturgus borealis Swaine	PHL	904	1	2	4	12	4	98	742	41	795	108

Family	Species[a]	FG[b]	Total[c]	HM[d]	Small patch[e]		Medium patch[f]		Large patch[g]		IF[h]	Girdled	Snag
					Edge	Center	Edge	Center	Edge	Center			
	Dendroctonus ponderosae Hopkins	PHL	20		3	11	1		1	2	2	3	17
	Dendroctonus rufipennis (Kirby)	PHL	139		10	19	28	6	37	13	26	125	14
	Dryocoetes affaber (Mannerheim)	PHL	153		12	15	26	20	21	41	18	94	59
	Dryocoetes autographus (Ratzeburg)	PHL	226	2	20	10	33	14	48	71	28	138	86
	Hylobius pinicola (Couper)	RHI	3	1	2							1	1
	Hylurgops porosus (LeConte)	PHL	8		4				1	2	1	4	4
	Hylurgops rugipennis (Mannerheim)	PHL	1		1								1
	Ips pini (Say)	PHL	1246		3	3	1		2	1229	8	1241	5
	Magdalis subtincta LeConte	XYL	8		1	1	3	2			1	7	1
	Orthotomicus caelatus (Eichhoff)	PHL	24		2	5		2	11	1	3	7	
	Orthotomicus latidens (LeConte)	PHL	38		5	1	6		4	3	19	28	10
	Phloeosinus pini Swaine	PHL	7		1	2	3				1	6	1
	Phloeotribus lecontei Schedl	PHL	3		2					1		3	
	Pissodes fiskei Hopkins	PHL	1							1		1	
	Pissodes rotundatus LeConte	PHL	17		3		7		2	2	3	16	1
	Pityogenes plagiatus knechteli Swaine	PHL	14	1	2	6	1		2	1	1	8	5
	Pityophthorus spp.	PHL	47	1	10	11	7	7	6	2	3	26	20
	Polygraphus rufipennis (Kirby)	PHL	356	2	38	84	45	26	60	48	53	284	70
	Rhyncolus brunneus Mannerheim	XYL	78		12	13	14	13	13	8	5	33	45
	Scierus annectans LeConte	PHL	1536	1	25	44	100	546	185	367	268	1403	132
	Scierus pubescens Swaine	PHL	457		13	119	40	125	66	78	16	394	63
	Scolytus piceae (Swaine)	PHL	15		1	1	5		4	1	3	9	6
	Trypodendron lineatum (Olivier)	MYC	117		1			1	18	81	16	98	19
	Trypodendron rufitarsis (Kirby)	MYC	13		1			1		8	3	4	9
	Xylechinus montanus Blackman	PHL	802		4	87	26	361	16	220	88	718	84
Dermestidae	*Megatoma cylindrica* (Kirby)	SAP	6		2	1			1	1	1	5	1
	Megatoma perversa (Fall)	SAP	1				1						1
Elateridae	*Agriotes ferrugineipennis* (LeConte)	RHI	3		2		1					3	

					Small patch[e]		Medium patch[f]		Large patch[g]				
Family	Species[a]	FG[b]	Total[c]	HM[d]	Edge	Center	Edge	Center	Edge	Center	IF[h]	Girdled	Snag
	Ampedus luctuosus (LeConte)	PRE	3	2					1			1	
	Ampedus nigrinus (Herbst)	PRE	24	3	6	2	3		5	3	2	13	8
	Ctenicera sp.1	PRE	1	1									
	Danosoma brevicorne (LeConte)	PRE	1				1						1
	Eanus decoratus (Mannerheim)	PRE	13		2	2	3	3	1		2	7	6
	Eanus estriatus (LeConte)	PRE	5				1		4			4	1
	Hypnoidus bicolor (Eschscholtz)	RHI	2	2									
	Idolus debilis (LeConte)	RHI	9		3	1	2	1	1	1		6	3
	Nitidolimonius resplendens (Eschscholtz)	PRE	11	6					1	3	1	2	3
	Pseudanostirus ochreipennis (LeConte)	PRE	11	1	1	1	3	2			3	2	8
	Pseudanostirus propolus (LeConte)	PRE	43	2	3	9	2	13	2	6	6	16	25
	Pseudanostirus triundulatus (Randall)	PRE	3	3									
	Sericus incongruuus (LeConte)	RHI	1	1									
	Setasomus nitidulus (LeConte)	PRE	12	6	2		2		1		1	3	3
Erotylidae	*Triplax dissimilator* (Crotch)	MYC	1		1								1
Eucinetidae	*Eucinetus* sp.1	MYC	5	2			1			1	1	1	2
Eucnemidae	*Epiphanis cornutus* Eschscholtz[*]	MYC	8		4		2		1	1		5	3
	Microrhagus pectinatus LeConte[*]	MYC	2	1				1					1
Histeridae	*Paromalus mancus* Casey	PRE	12		1	1	4		3	3		6	6
	Platysoma coarctatum LeConte	PRE	3						3				3
	Teretrius montanus Horn	PRE	1			1						1	
Laemophloeidae	*Leptophloeus* sp.1	MYC	15		7	1	1	2	2	2		11	4
Latridiidae	*Cartodere constricta* (Gyllenhal)	MYC	7		2		2		3			5	2
	Corticaria ferruginea Marsham[*]	MYC	28	5	6	3	3	3	3	3	2	9	14
	Corticaria rubripes Mannerheim[*]	MYC	106	5	3	13	15	27	11	18	14	55	46
	Corticaria sp.3	MYC	3					1		2		3	
	Cortinicara gibbosa (Herbst)	MYC	46	19	4	4	1	3	3	6	6	16	11
	Enicmus fictus Fall	MYC	1						1				1

Family	Species[a]	FG[b]	Total[c]	HM[d]	Small patch[e]		Medium patch[f]		Large patch[g]		IF[h]	Girdled	Snag
					Edge	Center	Edge	Center	Edge	Center			
	Enicmus tenuicornis LeConte[*]	MYC	13		1	1	2	3	4	1	1	1	12
	Latridius hirtus Gyllenhal[*]	MYC	3			1	1		1				3
	Latridius minutus (Linnaeus)	MYC	9		1		2	1	1	2	2	7	2
	Melanophthalma villosa (Zimmermann)	MYC	25	6	2	3	3	1	7	1	2	7	12
Leiodidae	*Agathidium depressum* Fall	MYX	5		1		1		1	2		3	2
	Agathidium pulchrum LeConte	MYX	1						1				1
	Agathidium sp.2	MYX	1					1				1	
	Agathidium sp.3	MYX	1							1			1
	Agathidium sp.4	MYX	1			1							1
	Anisotoma amica Brown[*]	MYX	3	1			1		1				2
	Anisotoma globososa Hatch	MYX	2				1				1		2
	Catops sp.1	SAP	1						1			1	
	Colon sp.1	MYC	2	1						1		1	
	Leiodes sp.2	MYC	1				1					1	
Lycidae	*Dictyoptera aurora* (Herbst)	UNK	3		1			2				1	2
Melandryidae	*Dolotarsus lividus* (Sahlberg)	XYL	24		7	2	4	3	5	2	1	7	17
	Melandrya striata Say	XYL	3				2		1			2	1
	Orchesia castanea Melsheimer[*]	XYL	1				1					1	
	Scotochroa sp.1	XYL	9	7			1		1				2
	Serropalpus substriatus Haldeman	XYL	68		4	6	22	7	15	9	5	63	5
	Xylita laevigata (Hellenius)	XYL	1						1				1
	Zilora hispida LeConte	XYL	4		1		1	1		1		1	3
Melyridae	*Hoppingiana hudsonica* (LeConte)	UNK	3	1	1		1						2
	Melyridae sp.1	UNK	1							1			1
	Trichochrous albertensis Blaisdell	UNK	1		1							1	
Monotomidae	*Rhizophagus brunneus* Horn	PRE	115	1	22	20	13	24	3	14	18	63	51
	Rhizophagus dimidiatus Mannerheim	PRE	129		2	12	3	20	12	53	27	112	17
	Rhizophagus remotus LeConte	PRE	5							4	1		5

Family	Species[a]	FG[b]	Total[c]	HM[d]	Small patch[e]		Medium patch[f]		Large patch[g]		IF[h]	Girdled	Snag
					Edge	Center	Edge	Center	Edge	Center			
Mycetophagidae	*Mycetophagus distinctus* Hatch	MYC	1					1					1
	Mycetophagus serrulatus (Casey)[*]	MYC	6		1	1		2			2	3	3
Nitidulidae	*Colopterus truncatus* (Randall)	UNK	5	1		1		1		2		4	
	Epuraea flavomaculata Mäklin	OMN	1							1		1	
	Epuraea helvola Erichson	OMN	1								1	1	
	Epuraea linearis Mäklin	OMN	40		3	5	1	3	7	9	12	32	8
	Epuraea obliqua Hatch	OMN	19	4	2	4	2	1	3	2	1	12	3
	Epuraea planulata Erichson	OMN	4						1	2	1	3	1
	Epuraea rufa (Say)[*]	OMN	1					1				1	
	Epuraea truncatella (Mannerheim)	OMN	30			3	1	6	3	8	9	26	4
	Epuraea sp. 5	OMN	8			1			1	5	1	8	
	Epuraea spp. (*E. avara* & *E. terminalis*)[i]	OMN	75		7	7	2	25	5	22	7	74	1
	Glischrochilus sanguinolentus (Olivier)	OMN	8					1	1	1	5	4	4
	Glischrochilus siepmanni Brown	OMN	7			3	1	2			1	2	5
	Glischrochilus vittatus (Say)	OMN	7				1		4		2	3	4
	Meligethes canadensis Easton	UNK	4		2	1	1					2	2
Ptiliidae	*Acrotrichis* sp.1	MYC	5	1			2		1		1	2	2
	Pteryx sp.1	MYC	1				1					1	
Ptinidae	*Caenocara scymnoides* LeConte	UNK	1	1									
	Desmatogaster subconnata (Fall)	UNK	1		1							1	
	Dorcatoma moderata White[*]	XYL	1						1				1
	Ernobius gentilis Fall[*]	XYL	2			2							2
	Hemicoelus carinatus (Say)	XYL	21		3	1		1	4	8	4	4	17
	Microbregma emarginatum (Duftschmid)	XYL	21				3		4	13	1	4	17
	Ptilinus lobatus Casey	XYL	1			1	1						2
	Utobium elegans (Horn)	XYL	12		4			1	3	4		2	10
Pythidae	*Pytho americanus* Kirby	PHL	2								2	2	
Salpingidae	*Sphaeriestes virescens* (LeConte)	UNK	2		1						1	1	1

					Small patch[e]		Medium patch[f]		Large patch[g]				
Family	Species[a]	FG[b]	Total[c]	HM[d]	Edge	Center	Edge	Center	Edge	Center	IF[h]	Girdled	Snag
Scirtidae	*Cyphon variabilis* (Thunberg)	OMN	5	4				1					1
Scraptiidae	*Anaspis atrata* Champion	UNK	9	1	4		3			1		3	5
	Anaspis rufa Say	UNK	25	3	7	5	2		3	3	2	10	12
	Canifa pallipes (Melsheimer)*	UNK	2				1			1			2
Silvanidae	*Dendrophagus cygnaei* Mannerheim	MYC	1				1					1	
	Silvanus bidentatus (Fabricius)*	MYC	11					4	3		4	11	
Sphindidae	*Odontosphindus clavicornis* Casey	MYX	1							1		1	
Staphylinidae	*Acidota crenata* (Fabricius)	PRE	69		55	1	4	1	8			58	11
	Amischa sp.1	PRE	4	2	1		1					2	
	Anotylus sobrinus (LeConte)	PRE	2	1				1					1
	Atheta pseudosubtilis Klimaszewski & Langor	PRE	1						1				1
	Atheta sp.1	PRE	2										2
	Atheta graminicola (Gravenhorst)	PRE	8		2	1	2		3			1	7
	Atheta remulsa Casey	PRE	1				1						1
	Athetini sp.1	PRE	5	1	2	1		1				3	1
	Boreophilia davidgei Klimaszewski & Godin	UNK	4				1	1		1	1	1	3
	Carcinocephalus sp.1	UNK	1							1		1	
	Carpelimus sp.1	UNK	4	2		1	1					1	1
	Carphacis nepigonensis (Bernhauer)	PRE	8						8				8
	Dalotia coriaria (Kraatz)	UNK	1								1	1	
	Dinaraea worki Klimaszewski & Jacobs	PRE	2		1				1			2	
	Dinothenarus pleuralis (LeConte)	PRE	2				2						2
	Euplectus duryi Casey*	PRE	6	1		3	1			1		2	3
	Gabrius brevipennis (Horn)	PRE	4	1		2					1	1	2
	Gyrophaena sp.1	MYC	2				1		1			1	1
	Homalota plana (Gyllenhal)	UNK	6	1							5	5	
	Ischnosoma splendidum (Gravenhorst)	PRE	5			1	3				1		5
	Leptacinus intermedius Donisthorpe	UNK	1			1							1

Family	Species[a]	FG[b]	Total[c]	HM[d]	Small patch[e]		Medium patch[f]		Large patch[g]		IF[h]	Girdled	Snag
					Edge	Center	Edge	Center	Edge	Center			
	Lordithon fungicola Campbell	PRE	2						1	1		1	1
	Lordithon kelleyi (Malkin)	PRE	1					1				1	
	Lordithon longiceps (LeConte)	PRE	4		1			1		1	1	1	3
	Megarthrus angulicollis Mäklin	PRE	1			1							1
	Micropeplus laticollis Mäklin	PRE	12		1		1	4	2	2	2	8	4
	Mocyta breviuscula (Mäklin)	PRE	2	1						1			1
	Mycetoporus americanus Erichson	PRE	4		2	1	1					2	2
	Nudobius cephalus (Say)	PRE	3	1					1	1		1	1
	Olisthaerus megacephalus (Zetterstedt)	PRE	15		4			1	7	2	1	6	9
	Olophrum consimile (Gyllenhal)	PRE	1						1				1
	Oxypoda canadensis Klimaszewski	PRE	2					2					2
	Oxypoda frigida Bernhauer	PRE	5	1				1	2	1		2	2
	Oxypoda lacustris Casey	PRE	4	3			1					1	
	Oxypoda operta Sjöberg	PRE	6				3		2		1	2	4
	Philhygra sp.1	PRE	1	1									
	Philhygra sp.2	PRE	5	1	1		1	1	1			2	2
	Philhygra sp.3	PRE	1			1							1
	Phloeonomus sp.1	PRE	21		1			2	3	15		20	1
	Phloeopora sp.1	PRE	2			1				1		1	1
	Phloeostiba lapponica (Zetterstedt)	PRE	14	1	2	2		1	4		4	8	5
	Placusa spp. (*P. icompleta*, *P. pseudosuecica*, & *P. tachyporoides*)[j]	MYC	45		6	3	6	6	10	8	6	41	4
	Placusa tacomae Casey	MYC	12		1					10	1	12	
	Porrhodites inflatus (Hatch)	UNK	1							1		1	
	Pseudopsis sagitta Herman	PRE	3			1	1			1		2	1
	Quedius plagiatus Mannerheim	PRE	18		1		5		4	3	5	4	14
	Quedius velox Smetana	PRE	15		3	2			6	1	3	7	8
	Schistoglossa hampshirensis Klimaszewski	UNK	1				1					1	

Family	Species[a]	FG[b]	Total[c]	HM[d]	Small patch[e]		Medium patch[f]		Large patch[g]		IF[h]	Girdled	Snag
					Edge	Center	Edge	Center	Edge	Center			
	Siagonium punctatum (LeConte)[*]	MYC	34	2	6	3	8	4	8	2	1	6	26
	Stenichnus ovipennis (Casey)[*]	PRE	3		2			1					3
	Stenichnus sp.2	PRE	3					1	1		1	1	2
	Syntomium confragosum Mäklin	UNK	1				1					1	
	Tachinus elongatus Gyllenhal	PRE	1		1								1
	Tachinus frigidus Erichson	PRE	1				1					1	
	Tachyporus borealis Campbell	PRE	1								1		1
	Trichiusa pilosa Casey	UNK	1	1									
Stenotrachelidae	*Cephaloon tenuicorne* LeConte	OMN	108	75	11	4	5	2	5	5	1	16	17
	Stenotrachelus aeneus (Fabricius)	UNK	3				1		1		1	1	2
Tenebrionidae	*Bius estriatus* (LeConte)	UNK	4			1	1		1	1		1	3
	Corticeus praetermissus (Fall)	PRE	11							10	1	10	1
	Corticeus tenuis (LeConte)	PRE	4			1				1	2	4	
Trogossitidae	*Peltis fraterna* (Randall)	MYC	4				1		1	2			4
	Thymalus marginicollis Chevrolat	MYC	4					3		1		1	3
Total numbers of individuals			8546	221	491	658	672	1389	910	3341	864	6753	1572
Total numbers of species			260	66	118	101	133	90	119	118	107	190	194

[a] Species newly recorded from the province of Alberta are marked with an asterisk.

[b] FG (feeding guild): MYC (mycetophages), MYX (myxomycophages), OMN (omnivores), PHL (phloeophages), PRE (predators), RHI (rhizophages), SAP (saprophages), XYL (xylophages), and UNK (unknown)

[c] Total is a sum of values from HM, small, medium and large patches, and IF.

[d] HM (harvested matrix)

[e] Small patches range from 0.63 to 1.06 ha

[f] Medium patches range from 1.43 to 2.93 ha

[g] Large patches range from 3.34 to 5.93 ha

[h] IF (intact forest)

[i] We likely considered two nitidulid beetle species (*Epuraea avara* and *E. terminalis*) as *Epuraea* spp. because of difficulties in reliably separating these species.

[j] We also considered three possible aleocharine rove beetle species (*Placusa incompleta*, *P. pseudosuecica*, and *P. tachyporoides*) as *Placusa* spp. because of similarities in habitus and high and overlapping variation in male genitalia.

Appendix 4-A

Saproxylic beetles sampled using emergence traps on decays classes 2 and 4 logs (numbers in parenthesis) and window traps attached to girdled trees and snags of boreal white spruce in the harvested matrix (2% retention), aggregated retention patches surrounded by 20% and 50% dispersed retention, and uncut forest (control) on a Ecosystem Management Emulating Natural Disturbance (EMEND) landscape in northwestern Alberta. Nomenclature follows that of Bousquet et al. (2013).

								Window traps		Emergence traps	
Family	Species[a]	FG[b]	Total[c]	HM[d]	20%[e]	50%[f]	CT[g]	Girdled	Snag	DC[h] 2	DC 4
Anthicidae	*Anthicus hastatus* Casey	OMN	1(1)	1(1)				1			(1)
Buprestidae	*Anthaxia inornata* (Randall)	XYL	7(1)	4	2	1(1)		3	4	(1)	
	Buprestis maculativentris Say	XYL	2	2				2			
	Chrysobothris trinervia (Kirby)	XYL	11	11				3	8		
	Dicerca tenebrica (Kirby)	XYL	1		1				1		
	Dicerca tenebrosa (Kirby)	XYL	21	15	2	4		11	10		
	Phaenops fulvoguttata (Harris)	XYL	42(1)	26	14	2(1)		40	2	(1)	
Cantharidae	*Dichelotarsus laevicollis* (Kirby)	PRE	24(3)	4(1)	9(2)	8	3	13	11	(1)	(2)
	Dichelotarsus piniphilus (Eschscholtz)	PRE	21(2)	6	4	5	6(2)	8	13	(2)	
	Rhagonycha fraxini (Say)	PRE	2	2				1	1		
	Rhagonycha mandibularis (Kirby)	PRE	2(1)	2(1)				1	1		(1)
	Silis difficilis LeConte	UNK	1	1				1			
Carabidae	*Agonum consimile* (Gyllenhal<)	PRE	1				1		1		
	Agonum thoreyi Dejean	PRE	1	1				1			
	Bembidion sp.1	PRE	(3)	(2)	(1)					(2)	(1)
	Calathus advena (LeConte)	PRE	12(16)		7(11)	1(5)	4	8	4	(13)	(3)
	Calathus ingratus Dejean	PRE	(1)			(1)				(1)	
	Platynus decentis (Say)	PRE	36(16)	1(2)	20(10)	10(4)	5	20	16	(11)	(5)

Appendix 4-A (continued)

								Window traps		Emergence traps	
Family	Species[a]	FG[b]	Total[c]	HM[d]	20%[e]	50%[f]	CT[g]	Girdled	Snag	DC[h] 2	DC 4
	Stereocerus haematopus (Dejean)	PRE	(4)		(3)		(1)			(1)	(3)
	Tachyta angulata Casey	PRE	(1)	(1)							(1)
	Trechus apicalis Motschulsky	PRE	(1)			(1)				(1)	
Cerambycidae	*Acanthocinus pusillus* (Kirby)	XYL	18	13	4	1		13	5		
	Acmaeops proteus (Kirby)	XYL	27(4)	16	7(2)	4(2)		19	8	(4)	
	Anastrangalia sanguinea (LeConte)	XYL	1		1			1			
	Asemum striatum (Linnaeus)	XYL	5	2	2	1		4	1		
	Callidium cicatricosum Mannerheim	XYL	2	1	1			1	1		
	Cortodera coniferae Hopping & Hopping	XYL	4	2		1	1		4		
	Grammoptera subargentata (Kirby)	XYL	7	1	3	1	2	1	6		
	Judolia montivagans (Couper)	XYL	1		1			1			
	Meriellum proteus (Kirby)	XYL	6(1)	3	1(1)	2		4	2		(1)
	Monochamus scutellatus (Say)	XYL	12	8	3	1		11	1		
	Neoclytus leucozonus (Laporte & Gory)	XYL	23(1)	18(1)	4		1	14	9	(1)	
	Neospondylis upiformis (Mannerheim)	XYL	45	4	16	22	3	37	8		
	Pachyta lamed liturata Kirby	XYL	2	2				1	1		
	Phymatodes dimidiatus (Kirby)	XYL	113(1)	13	88(1)	8	4	107	6	(1)	
	Pogonocherus penicillatus LeConte	XYL	52(5)	10	16	12(5)	14	46	6	(5)	
	Pygoleptura nigrella (Say)	XYL	10	7		3		3	7		
	Rhagium inquisitor (Linnaeus)	XYL	5	1	1	3		4	1		
	Semanotus sp.1	XYL	1				1	1			
	Tetropium cinnamopterum Kirby	XYL	72(13)	11	12(1)	38(9)	11(3)	69	3	(12)	(1)
	Tetropium parvulum Casey	XYL	19(1)	4(1)	4	9	2	13	6	(1)	
	Trachysida mutabilis (Newman)	XYL	4	2	2				4		
	Xylotrechus undulatus (Say)	XYL	82	58	10	8	6	77	5		
Cerylonidae	*Cerylon castaneum* Say	MYC	12(1)	5(1)	3	3	1	5	7	(1)	
Ciidae	Ciidae sp.1	MYC	2(6)		1(2)	1(4)		2		(1)	(5)

Appendix 4-A (continued)

Family	Species[a]	FG[b]	Total[c]	HM[d]	20%[e]	50%[f]	CT[g]	Window traps		Emergence traps	
								Girdled	Snag	DC[h] 2	DC 4
	Cis americanus Mannerheim	MYC	13(4)	10	1(4)	2			13	(2)	(2)
	Cis angustus Hatch*	MYC	6(2)	1	1	3(2)	1	1	5		(2)
	Cis fuscipes Mellié<	MYC	2	1		1		1	1		
	Cis horridulus Casey*	MYC	2	2					2		
	Cis striolatus Casey	MYC	10	9		1		5	5		
	Dolichocis manitoba Dury	MYC	11(8)	3(3)	3(1)	2(3)	3(1)	1	10	(1)	(7)
	Octotemnus laevis Casey	MYC	1	1					1		
	Plesiocis cribrum Casey	MYC	2(2)	2	(2)				2	(2)	
Clambidae	*Calyptomerus oblongulus* (Mannerheim)	MYC	4		1		3	3	1		
	Clambus pubescens Redtenbacher	MYC	4(1)		2		2(1)	2	2		(1)
Cleridae	*Madoniella dislocata* (Say)*	PRE	5(1)	5(1)				3	2	(1)	
	Thanasimus dubius (Fabricius)	PRE	77	27	11	38	1	75	2		
	Thanasimus undatulus (Say)	PRE	232(8)	81	56(2)	61(6)	34	186	46	(8)	
Colydiidae	*Lasconotus complex* LeConte	PRE	236(48)	35	65(8)	70(38)	66(2)	202	34	(47)	(1)
Corylophidae	*Clypastraea* sp.1	MYC	32(5)	24	2(1)	6(4)		24	8	(5)	
	Orthoperus scutellaris LeConte	MYC	4	2		1	1	1	3		
Cryptophagidae	*Antherophagus ochraceus* Melsheimer	DET	1			1			1		
	Atomaria sp.1	MYC	20(2)	10(1)	3(1)	4	3	9	11	(2)	
	Atomaria sp.2	MYC	2(2)	1		(2)	1		2	(1)	(1)
	Atomaria sp.3	MYC	4	1		2	1	2	2		
	Atomaria sp.4	MYC	2(1)	(1)	1	1		1	1	(1)	
	Atomaria sp.5	MYC	1				1	1			
	Caenoscelis antennalis (Casey)	MYC	2(1)		1	(1)	1	1	1	(1)	
	Cryptophagus acutangulus Gyllenhal<	MYC	(18)	(2)	(10)	(4)	(2)			(11)	(7)
	Cryptophagus tuberculosus Mäklin	MYC	51(5)	5	13(2)	21(3)	12	35	16	(3)	(2)
	Myrmedophila americana (LeConte)	MYC	2(3)	2	(1)	(2)		1	1	(1)	(2)
	Pteryngium crenatum (Gyllenhal)*	MYC	4			3	1		4		

Appendix 4-A (continued)

								Window traps		Emergence traps	
Family	Species[a]	FG[b]	Total[c]	HM[d]	20%[e]	50%[f]	CT[g]	Girdled	Snag	DC[h] 2	DC 4
	Salebius octodentatus (Mäklin)[*]	MYC	1(3)			(3)	1		1		(3)
Cucujidae	*Cucujus clavipes puniceus* Mannerheim	PRE	7	5	1	1		4	3		
	Pediacus fuscus Erichson	PRE	207(3)	190(2)	10(1)	5	2	180	27	(2)	(1)
Curculionidae	*Carphonotus testaceus* Casey	XYL	1(15)	1(3)	(8)	(4)		1		(14)	(1)
	Cossonus quadricollis Van Dyke	XYL	6	3		3		2	4		
	Cryphalus ruficollis Hopkins	PHL	2				2	2			
	Crypturgus borealis Swaine	PHL	20659	11363	2160	6376	760	18436	2223		
			(464)	(6)	(190)	(267)	(1)			(460)	(4)
	Dendroctonus rufipennis (Kirby)	PHL	322(13)	94	53(9)	127(4)	48	287	35	(13)	
	Dryocoetes affaber (Mannerheim)	PHL	4868	286	1699	1222	1661	3912	956		
			(2214)	(1)	(1225)	(902)	(86)			(2211)	(3)
	Dryocoetes autographus (Ratzeburg)	PHL	370(23)	200	48(9)	98(11)	24(3)	292	78	(20)	(3)
	Hylobius pinicola (Couper)	RHI	6	2	1	3		2	4		
	Hylurgops rugipennis (Mannerheim)	PHL	1	1				1			
	Ips pini (Say)	PHL	2097(9)	1260(1)	216(5)	598(3)	23	2056	41	(9)	
	Magdalis sp.1	XYL	1				1	1			
	Magdalis subtincta LeConte	XYL	12	4	2	3	3	8	4		
	Orthotomicus caelatus (Eichhoff)	PHL	9(1)	8	1	(1)		2	7	(1)	
	Orthotomicus latidens (LeConte)	PHL	4(12)	2	1	1(12)		4		(12)	
	Phloeosinus pini Swaine	PHL	10	1	2	3	4	5	5		
	Phloeotribus lecontei Schedl	PHL	2	2				2			
	Pissodes rotundatus LeConte	PHL	32(55)	1(1)	8(1)	15(32)	8(21)	30	2	(55)	
	Pityogenes plagiatus knechteli Swaine	PHL	6	4	2			3	3		
	Pityophthorus spp.	PHL	356(53)	213(35)	42(1)	83(17)	18	221	135	(51)	(2)
	Polygraphus rufipennis (Kirby)	PHL	1605	353	549	362	341	1543	62		
			(584)	(5)	(393)	(148)	(38)			(581)	(3)
	Rhyncolus brunneus Mannerheim	XYL	74(38)	30(17)	21(6)	19(14)	4(1)	48	26	(19)	(19)

Appendix 4-A (continued)

								Window traps		Emergence traps	
Family	Species[a]	FG[b]	Total[c]	HM[d]	20%[e]	50%[f]	CT[g]	Girdled	Snag	DC[h] 2	DC 4
	Scierus annectans LeConte	PHL	2552	66	950	575	961	2121	431		
			(21)	(2)	(3)	(14)	(2)			(18)	(3)
	Scierus pubescens Swaine	PHL	431(6)	63	155(6)	100	113	349	82	(6)	
	Scolytus piceae (Swaine)	PHL	75	30	29	16		63	12		
	Trypodendron lineatum (Olivier)	MYC	2777	794	524	1205	254	2358	419		
			(215)		(88)	(39)	(88)			(211)	(4)
	Trypodendron retusum (LeConte)	MYC	2			1	1	2			
	Trypodendron rufitarsis (Kirby)	MYC	1				1	1			
	Xylechinus montanus Blackman	PHL	537(20)	79(4)	99(11)	50(5)	309	479	58	(20)	
Dermestidae	*Megatoma cylindrica* (Kirby)	DET	10(2)	5(2)	1	1	3	6	4	(1)	(1)
	Megatoma perversa (Fall)	DET	5(2)	3(2)		2		2	3	(2)	
Elateridae	*Ampedus apicatus* (Say)	PRE	6(1)	5(1)			1	3	3	(1)	
	Ampedus luctuosus (LeConte)	PRE	18	16		2		5	13		
	Ampedus nigrinus (Herbst)	PRE	37(5)	25(3)	5(1)	4	3(1)	15	22	(4)	(1)
	Ctenicera kendalli Kirby	PRE	1	1					1		
	Danosoma brevicorne (LeConte)	PRE	8(2)	5	2(2)	1		4	4	(2)	
	Denticollis denticornis (Kirby)	PRE	2			1	1		2		
	Eanus decorates (Mannerheim)	PRE	18(4)	4	4(1)	6(2)	4(1)	9	9	(1)	(3)
	Eanus estriatus (LeConte)	PRE	2	1	1			1	1		
	Harminius triundulatus (Mannerheim)	PRE	1(1)			1(1)			1		(1)
	Hypnoidus bicolor (Eschscholtz)	RHI	1	1				1			
	Idolus debilis (LeConte)	RHI	6	2	4			4	2		
	Liotrichus stricklandi (Brown)	PRE	2		2			1	1		
	Nitidolimonius resplendens (Eschscholtz)	PRE	9	4	4	1		4	5		
	Pseudanostirus nigricollis (Bland)	PRE	1		1			1			
	Pseudanostirus ochreipennis (LeConte)	PRE	7	3	3	1		3	4		
	Pseudanostirus propolus (LeConte)	PRE	41(5)	1(1)	17	13(4)	10	19	22	(2)	(3)

Appendix 4-A (continued)

								Window traps		Emergence traps	
Family	Species[a]	FG[b]	Total[c]	HM[d]	20%[e]	50%[f]	CT[g]	Girdled	Snag	DC[h] 2	DC 4
	Pseudanostirus triundulatus (Randall)	PRE	6	5	1			2	4		
	Sericus incongruuus (LeConte)	RHI	3	2	1			1	2		
	Setasomus nitidulus (LeConte)	PRE	7(1)	7(1)				5	2		(1)
Erotylidae	*Triplax californica* LeConte	MYC	2	1		1			2		
	Triplax dissimilator (Crotch)	MYC	1		1				1		
Eucinetidae	*Eucinetus* sp.1	MYC	1(3)		(1)	(2)	1	1			(3)
Eucnemidae	*Epiphanis cornutus* Eschscholtz*	MYC	4(3)	1		2(2)	1(1)	1	3	(1)	(2)
	Microrhagus pectinatus LeConte*	MYC	3	2			1	1	2		
Histeridae	*Hister* sp.3	PRE	2	2				1	1		
	Paromalus mancus Casey	PRE	48(7)	11	14(7)	8	15	34	14	(7)	
	Platysoma coarctatum LeConte	PRE	8	7		1		4	4		
	Teretrius montanus Horn	PRE	2	2					2		
Laemophloeidae	*Leptophloeus* sp.1	MYC	16(5)	4	5(3)	3(2)	4	14	2	(5)	
Latridiidae	*Cartodere constricta* (Gyllenhal)	MYC	27(1)	9(1)	15	3		22	5		(1)
	Corticaria ferruginea Marsham*	MYC	11	3	2	3	3	9	2		
	Corticaria rubripes Mannerheim*	MYC	131(31)	24(10)	38(10)	38(9)	31(2)	65	66	(16)	(15)
	Corticaria sp.2	MYC	(4)		(1)	(3)				(2)	(2)
	Corticaria sp.3	MYC	(1)		(1)					(1)	
	Cortinicara gibbosa (Herbst)	MYC	90(2)	30	18	35(2)	7	56	34	(2)	
	Enicmus tenuicornis LeConte*	MYC	2(2)	1(2)			1	1	1	(2)	
	Latridius hirtus Gyllenhal*	MYC	4			4		1	3		
	Latridius minutus (Linnaeus)	MYC	12	2	3	5	2	8	4		
	Melanophthalma pumila (LeConte)	MYC	1			1			1		
	Melanophthalma villosa (Zimmermann)	MYC	53(2)	28	14(2)	7	4	29	24	(1)	(1)
	Stephostethus breviclavis (Fall)*	MYC	1		1				1		
	Stephostethus liratus (LeConte)	MYC	4(1)		2	2	(1)	2	2		(1)
Leiodidae	*Agathidium depressum* Fall	MYX	4(1)	(1)	2	1	1	1	3		(1)

Appendix 4-A (continued)

								Window traps		Emergence traps	
Family	Species[a]	FG[b]	Total[c]	HM[d]	20%[e]	50%[f]	CT[g]	Girdled	Snag	DC[h] 2	DC 4
	Agathidium pulchrum LeConte	MYX	1(1)			1(1)		1			(1)
	Agathidium sp.1	MYX	1		1			1			
	Agathidium sp.2	MYX	1			1		1			
	Agathidium sp.5	MYX	2			2			2		
	Agathidium sp.6	MYX	2	2				2			
	Anisotoma amica Brown*	MYX	1			1		1			
	Anisotoma globososa Hatch	MYX	4(2)	1		(2)	3	1	3		(2)
	Catops basilaris Say	DET	1		1				1		
	Colon magnicolle Mannerheim	MYC	1	1					1		
	Colon sp.1	MYC	1	1					1		
Lycidae	*Dictyoptera aurora* (Herbst)	UNK	1		1				1		
	Greenarus thoracicus (Randall)	UNK	1		1				1		
Melandryidae	*Dolotarsus lividus* (Sahlberg)	XYL	33	19	2	9	3	5	28		
	Melandrya striata Say	XYL	7	2	2	3			7		
	Orchesia castanea Melsheimer*	XYL	2(1)	(1)		1	1		2		(1)
	Scotochroa sp.1	XYL	3(2)	1	(1)	2(1)		3		(1)	(1)
	Serropalpus substriatus Haldeman	XYL	85(8)	24(2)	20(3)	32(1)	9(2)	77	8	(5)	(3)
	Xylita laevigata (Hellenius)	XYL	2(1)	(1)		2			2		(1)
	Xylita livida (Sahlberg)	XYL	(22)	(3)	(8)	(6)	(5)			(20)	(2)
	Zilora hispida LeConte	XYL	1			1			1		
Monotomidae	*Rhizophagus brunneus* Horn	PRE	167	43	28	77	19	98	69		
	Rhizophagus dimidiatus Mannerheim	PRE	282(33)	12	110(19)	81(13)	79(1)	233	49	(33)	
	Rhizophagus remotus LeConte	PRE	6	2	2	2		5	1		
Mordellidae	*Mordellaria borealis* (LeConte)	OMN	4(2)	2(2)	1	1		1	3	(2)	
Nitidulidae	*Colopterus truncatus* (Randall)	UNK	1	1				1			
	Epuraea flavomaculata Mäklin	OMN	2			2		1	1		
	Epuraea linearis Mäklin	OMN	245(17)	10	61(2)	35(12)	139(3)	201	44	(17)	

Appendix 4-A (continued)

								Window traps		Emergence traps	
Family	Species[a]	FG[b]	Total[c]	HM[d]	20%[e]	50%[f]	CT[g]	Girdled	Snag	DC[h] 2	DC 4
	Epuraea obliqua Hatch	OMN	16(6)	3	4(2)	6(4)	3	13	3	(6)	
	Epuraea planulata Erichson	OMN	3	2		1		1	2		
	Epuraea rufomarginata (Stephens)*	OMN	2(5)		1	1(5)		1	1	(5)	
	Epuraea sp.1	OMN	17	5		7	5	12	5		
	Epuraea spp. (*E. avara* & *E. terminalis*)	OMN	29	5	3	17	4	18	11		
	Epuraea truncatella (Mannerheim)	OMN	75(4)	5	14(4)	19	37	42	33	(4)	
	Glischrochilus sanguinolentus (Olivier)	OMN	12	1		4	7	2	10		
	Glischrochilus siepmanni Brown	OMN	5		3	1	1	2	3		
	Glischrochilus vittatus (Say)	OMN	1(1)	1		(1)		1		(1)	
	Meligethes canadensis Easton	UNK	2	1		1			2		
Ptiliidae	*Acrotrichis* sp.1	MYC	10(1)	1	3(1)	6		10			(1)
	Pteryx sp.1	MYC	1(1)	1		(1)		1		(1)	
Ptinidae	*Caenocara scymnoides* LeConte	UNK	1		1				1		
	Desmatogaster subconnata (Fall)	UNK	5(2)	2	(2)	3		1	4		(2)
	Dorcatoma moderata White*	XYL	7	2	3	2		2	5		
	Ernobius gentilis Fall*	XYL	2			1	1	1	1		
	Hemicoelus carinatus (Say)	XYL	25(4)	6(1)	9(2)	9	1(1)	10	15		(4)
	Microbregma emarginatum (Duftschmid)	XYL	54(2)	4	23	21(2)	6	15	39	(2)	
	Ptilinus lobatus Casey	XYL	6	3	1	1	1		6		
	Ptinus sexpunctatus Panzer	PRE	1	1					1		
	Utobium elegans (Horn)	XYL	24(1)	6	9(1)	7	2	6	18	(1)	
Pyrochroidae	*Schizotus cervicalis* Newman	MYC	(1)		(1)						(1)
Pythidae	*Priognathus monilicornis* (Randall)	XYL	(1)			(1)					(1)
	Pytho niger Kirby	PHL	(7)		(2)	(2)	(3)			(7)	
	Pytho planus (Olivier)	PHL	1	1					1		
Scirtidae	*Cyphon variabilis* (Thunberg)	OMN	8(2)	1	3	3(2)	1	2	6		(2)
Scraptiidae	*Anaspis atrata* Champion	UNK	5	2	1	2		2	3		

Appendix 4-A (continued)

Family	Species[a]	FG[b]	Total[c]	HM[d]	20%[e]	50%[f]	CT[g]	Window traps		Emergence traps	
								Girdled	Snag	DC[h] 2	DC 4
	Anaspis rufa Say	UNK	1		1			1			
	Canifa pallipes (Melsheimer)*	UNK	4(3)	4(1)	(2)			1	3	(2)	(1)
Silvanidae	*Dendrophagus cygnaei* Mannerheim	MYC	2		2			1	1		
	Silvanus bidentatus (Fabricius)*	MYC	7		2	2	3	7			
Sphindidae	*Odontosphindus clavicornis* Casey	MYX	2		1	1		1	1		
Staphylinidae	*Acidota crenata* (Fabricius)	PRE	40	39		1		24	16		
	Acidota quadrata (Zetterstedt)	PRE	1	1				1			
	Aleocharinae sp.23	UNK	(1)			(1)				(1)	
	Anotylus sobrinus (LeConte)	PRE	1				1		1		
	Atheta klagesi Bernhauer	PRE	1(2)		(2)	1		1			(2)
	Bolitobius sp.1	UNK	(2)			(1)	(1)			(1)	(1)
	Bolitobius sp.2	UNK	(1)	(1)							(1)
	Bolitopunctus muricatulus (Hatch)	UNK	2			2		1	1		
	Boreophilia davidgei Klimaszewski &	UNK	1		1				1		
	Boreophilia islandica (Kraatz)*	UNK	(1)		(1)						(1)
	Carphacis nepigonensis (Bernhauer)	PRE	3	2	1				3		
	Dalotia coriaria (Kraatz)	UNK	1	1				1			
	Deinopteroloma subcostatum (Mäklin)	UNK	1		1			1			
	Dinaraea worki Klimaszewski & Jacobs*	PRE	1(1)	1			(1)	1			(1)
	Dinothenarus pleuralis (LeConte)	PRE	1			1		1			
	Eucnecosum brunnescens (Sahlberg)	UNK	(1)		(1)					(1)	
	Eucnecosum tenue (LeConte)	UNK	1		1			1			
	Euplectus duryi Casey*	PRE	9	3		4	2	2	7		
	Gyrophaena sp.1	MYC	1			1			1		
	Heterothops minor Smetana	PRE	1	1				1			
	Homalota plana (Gyllenhal)*	UNK	3	1	1	1		2	1		
	Ischnosoma fimbriatum Campbell	PRE	(1)	(1)						(1)	

Appendix 4-A (continued)

								Window traps		Emergence traps	
Family	Species[a]	FG[b]	Total[c]	HM[d]	20%[e]	50%[f]	CT[g]	Girdled	Snag	DC[h] 2	DC 4
	Ischnosoma pictum (Horn)	PRE	(1)	(1)						(1)	
	Ischnosoma splendidum (Gravenhorst)	PRE	3(1)	1		2	(1)	1	2	(1)	
	Lathrobium washingtoni Casey	PRE	2	1	1			1	1		
	Leptusa gatineauensis Klimaszewski &	PRE	(1)	(1)						(1)	
	Liogluta aloconotoides Lohse*	PRE	(1)		(1)					(1)	
	Lordithon fungicola Campbell	PRE	8		3	4	1	5	3		
	Lordithon kelleyi (Malkin)	PRE	7			4	3	1	6		
	Lordithon longiceps (LeConte)	PRE	4	1	1	1	1	1	3		
	Lordithon thoracicus (Fabricius)	PRE	1	1				1			
	Megarthrus angulicollis Mäklin	PRE	1			1		1			
	Micropeplus laticollis Mäklin	PRE	10	3	1	4	2	8	2		
	Mocyta breviuscula (Mäklin)	PRE	4(2)	2	1(1)	1(1)		2	2		(2)
	Mycetoporus americanus Erichson	PRE	2(1)	(1)	1	1		1	1		(1)
	Nudobius cephalus (Say)	PRE	3(5)	2(1)	(3)	1(1)		2	1	(5)	
	Oligota sp.1	PRE	4(4)	2	(1)	2(2)	(1)	2	2	(1)	(3)
	Olisthaerus megacephalus (Zetterstedt)	PRE	16(1)	4	4(1)	3	5	7	9		(1)
	Olophrum consimile (Gyllenhal)	PRE	4(2)	3(2)		1			4	(1)	(1)
	Oxypoda canadensis Klimaszewski	PRE	(2)			(2)				(2)	
	Oxypoda frigida Bernhauer	PRE	2	1		1		1	1		
	Oxypoda hiemalis Casey*	PRE	1				1	1			
	Oxypoda lacustris Casey	PRE	3	2			1	1	2		
	Oxypodini sp.1	PRE	(4)	(4)							(4)
	Philonthus caeruleipennis (Mannerheim)	PRE	1			1			1		
	Philonthus varians (Paykull)	PRE	1	1				1			
	Phloeonomus sp.1	PRE	29	2	7	4	16	16	13		
	Phloeopora spp.	PRE	9	2	1	2	4	4	5		
	Phloeostiba lapponica (Zetterstedt)	PRE	13(1)	5	2(1)	2	4	10	3	(1)	

Appendix 4-A (continued)

Family	Species[a]	FG[b]	Total[c]	HM[d]	20%[e]	50%[f]	CT[g]	Window traps		Emergence traps	
								Girdled	Snag	DC[h] 2	DC 4
	Phyllodrepa humerosa (Fauvel)	PRE	(3)		(2)		(1)			(2)	(1)
	Placusa spp. (*P. icompleta**, *P.* & *P. tachyporoides**)	MYC	29(5)	6	6(2)	6(3)	11	18	11	(5)	
	Placusa tacomae Casey	MYC	35(2)	22	7(2)	4	2	35		(2)	
	Porrhodites inflatus (Hatch)	UNK	2		1	1		2			
	Pseudopsis sagitta Herman	PRE	4	1		2	1	1	3		
	Pycnoglypta aptera* Campbell<	PRE	(2)	(1)		(1)				(2)	
	Quedius criddlei (Casey)	PRE	4(4)		1(1)	2(3)	1	1	3	(1)	(3)
	Quedius erythrogaster Mannerheim	PRE	1				1	1			
	Quedius plagiatus Mannerheim	PRE	10(3)		2(1)	3(1)	5(1)	2	8	(3)	
	Quedius rusticus Smetana	PRE	9(1)	1	5	2(1)	1	4	5		(1)
	Quedius velox Smetana	PRE	58(8)	7	15(1)	28(3)	8(4)	28	30	(6)	(2)
	Scaphium castanipes Kirby	MYC	1		1				1		
	Schistoglossa campbelli*□ Klimaszewski	UNK	2	1	1			1	1		
	Seeversiella globicollis (Bernhauer)	PRE	3	2		1			3		
	Sepedophilus wickhami* Campbell	MYC	1	1					1		
	Siagonium punctatum (LeConte)*	MYC	32(2)	17	10(1)	5(1)		15	17	(1)	(1)
	Stenichnus ovipennis (Casey)*	PRE	5(2)	1(2)	1	1	2	3	2	(1)	(1)
	Stenus austini Casey	PRE	(2)	(2)						(2)	
	Tachinus basalis Erichson	PRE	1				1		1		
	Tachinus elongatus Gyllenhal	PRE	6	2	3		1	2	4		
	Tachinus fumipennis (Say)	PRE	(1)		(1)					(1)	
	Tachyporus borealis Campbell	PRE	(2)	(1)		(1)				(1)	(1)
Stenotrachelidae	*Cephaloon tenuicorne* LeConte	OMN	28	4	5	14	5	17	11		
Tenebrionidae	*Bius estriatus* (LeConte)	UNK	8	5	1	2		1	7		
	Corticeus praetermissus (Fall)	PRE	65	53	5	7		64	1		
	Corticeus tenuis (LeConte)	PRE	6(1)	5		1(1)		4	2	(1)	

Appendix 4-A (continued)

								Window traps		Emergence traps	
Family	Species[a]	FG[b]	Total[c]	HM[d]	20%[e]	50%[f]	CT[g]	Girdled	Snag	DC[h] 2	DC 4
	Scaphidema aeneolum (LeConte)	MYC	1	1					1		
	Upis ceramboides (Linnaeus)	OMN	1	1					1		
Trogossitidae	*Calitys scabra* (Thunberg)	MYC	1	1					1		
	Peltis fraterna (Randall)	MYC	4(12)	1	2(2)	(6)	1(4)		4		(12)
	Thymalus marginicollis Chevrolat	MYC	2(4)		(2)	2	(2)	1	1	(2)	(2)
Total number of individuals using window traps			40791	16143	7540	11874	5234	34919	5872		
Total number of individuals using emergence traps			(4251)	(150)	(2128)	(1684)	(289)			(4055)	(196)

[a] Species new to the province of Alberta are marked with an asterisk.

[b] FG (feeding guild): DET (detritivorous), MYC (mycetophagous), MYX (myxomycophagous), OMN (omnivorous), PHL (phloeophagous), PRE (predaceous), RHI (rhizophagous), UNK (unknown), and XYL (xylophagous)

[c] Total is a sum of values from HM, 20%, 50%, and CT.

[d] HM (harvested matrix, 2% retention)

[e] 20% (0.2 ha and 0.46 ha aggregated retention patches surrounded by 20% dispersed retention)

[f] 50% (0.2 ha and 0.46 ha aggregated retention patches surrounded by 50% dispersed retention)

[g] CT (control, 10 ha uncut forest)

[h] DC (decay class)

Appendix 5-A

Adult saproxylic beetles sampled from two types of white spruce CWD (i.e., logs and snags) in large aggregated retention patches (0.46 ha) surrounded by 2% retention and two sizes of aggregated retention patches (0.20 and 0.46 ha) surrounded by 20% and 50% dispersed retention, and in unharvested control on the Ecosystem Management Emulating Natural Disturbance (EMEND) experimental landscape in northwestern Alberta. Nomenclature follows Bousquet et al. (2013).

Family	Species	FG[a]	Total[b]	2%-L[c]	20%-S[d]	20%-L[e]	50%-S[f]	50%-L[g]	CT[h]	Logs	Snags
Cantharidae	*Dichelotarsus laevicollis* (Kirby)	PRE	1						1	1	
Carabidae	*Agonum consimile* (Gyllenhal<)	PRE	2				2			2	
	Platynus decentis (Say)	PRE	6	2			3		1	3	3
Cerambycidae	*Tetropium cinnamopterum* Kirby	XYL	77	9	31	11	8	15	3	63	14
Clambidae	*Clambus pubescens* Redtenbacher	MYC	9	4	1	3	1			7	2
Cleridae	*Thanasimus undatulus* (Say)	PRE	5	1	1	3				3	2
Colydiidae	*Lasconotus complex* LeConte	PRE	115	43	4	32	21	10	5	28	87
Corylophidae	*Arthrolips* sp.1	MYC	11		1			10		11	
	Clypastraea sp.1	MYC	19	19							19
	Orthoperus scutellaris LeConte	MYC	1		1					1	
Cryptophagidae	*Atomaria* sp.3	MYC	2				1		1		2
	Caenoscelis antennalis (Casey)	MYC	1	1							1
	Cryptophagus acutangulus Gyllenhal	MYC	6	4					2	6	
	Cryptophagus tuberculosus Mäklin	MYC	1						1	1	
Curculionidae	*Carphonotus testaceus* Casey	XYL	11		6	2	3			7	4
	Crypturgus borealis Swaine	PHL	1414	125	81	528	288	17	375	96	1318
	Dendroctonus rufipennis (Kirby)	PHL	84		3		8	15	58	57	27
	Dryocoetes affaber (Mannerheim)	PHL	9631	881	668	1672	1171	1313	3926	2906	6725
	Dryocoetes autographus (Ratzeburg)	PHL	1231	430	61	144	214	98	284	1162	69

Appendix 5-A (continued)

Family	Species	FG[a]	Total[b]	2%-L[c]	20%-S[d]	20%-L[e]	50%-S[f]	50%-L[g]	CT[h]	Logs	Snags
	Hylurgops porosus (LeConte)	PHL	3					1	2	2	1
	Ips pini (Say)	PHL	15	15							15
	Orthotomicus caelatus (Eichhoff)	PHL	201	129	47	4	17	4		110	91
	Pissodes rotundatus LeConte	PHL	9		1	2	5		1		9
	Polygraphus rufipennis (Kirby)	PHL	2136	1105	315	316	280	28	92	874	1262
	Scierus annectans LeConte	PHL	221	24	2	89	33	22	51	131	90
	Trypodendron lineatum (Olivier)	MYC	3691	301	63	490	501	657	1679	722	2969
	Xylechinus montanus Blackman	PHL	21	3	3	2	13			3	18
Elateridae	*Idolus debilis* (LeConte)	RHI	1			1					1
	Pseudanostirus propolus (LeConte)	PRE	1	1						1	
Histeridae	*Paromalus mancus* Casey	PRE	10	1	1	2		3	3	1	9
Latridiidae	*Cartodere constricta* (Gyllenhal)	MYC	3	1		1	1			1	2
	Corticaria rubripes Mannerheim	MYC	15	2	2	3	3	3	2	6	9
	Corticaria sp.4	MYC	1			1				1	
	Latridius minutus (Linnaeus)	MYC	3				2		1	3	
Leiodidae	Leiodidae sp.1	UNK	2		1					1	1
Melandryidae	*Serropalpus substriatus* Haldeman	XYL	56		28		9		19	30	26
Monotomidae	*Rhizophagus dimidiatus* Mannerheim	PRE	235	15	4	13	8	48	147	107	128
	Rhizophagus remotus LeConte	PRE	1					1		1	
Nitidulidae	*Colopterus truncatus* (Randall)	UNK	2					1	1	2	
	Epuraea linearis Mäklin	OMN	3	2				1		1	2
	Epuraea obliqua Hatch	OMN	6	3		1		2		3	3
	Epuraea planulata Erichson	OMN	12					6	6	6	6
	Glischrochilus vittatus (Say)	OMN	1		1					1	
Ptiliidae	*Acrotrichis* sp.1	MYC	16	2				6	8	14	2
	Pteryx sp.1	MYC	1				1			1	
	Ptiliolum sp.1	MYC	1	1						1	
	Ptinella sp.1	MYC	1				1			1	

Appendix 5-A (continued)

Family	Species	FG[a]	Total[b]	2%-L[c]	20%-S[d]	20%-L[e]	50%-S[f]	50%-L[g]	CT[h]	Logs	Snags
Ptinidae	*Hemicoelus carinatus* (Say)	XYL	22				1	3	18	1	21
	Microbregma emarginatum	XYL	4			1	2		1	1	3
Pyrochroidae	*Schizotus cervicalis* Newman	MYC	1				1			1	
Pythidae	*Pytho seidlitzi* Blair<	PHL	2	1			1			2	
Scirtidae	*Cyphon variabilis* (Thunberg)	OMN	8	1	1	2			4	5	3
Silvanidae	*Silvanus bidentatus* (Fabricius)	MYC	3			1		1	1	2	1
Staphylinidae	*Acidota crenata* (Fabricius)	PRE	1	1						1	
	Aleocharinae sp.41	UNK	2		1		1			1	1
	Aleocharinae spp.	UNK	12		1	4	5		2	8	4
	Anotylus sobrinus (LeConte)	PRE	2			1		1		2	
	Atheta fanatica Casey	PRE	1					1		1	
	Atheta klagesi Bernhauer	PRE	1			1				1	
	Athetini sp.2	PRE	3	1	2					2	1
	Dinaraea worki Klimaszewski & Jacobs	PRE	2				1	1		1	1
	Euplectus duryi Casey	PRE	1						1		1
	Ischnosoma splendidum (Gravenhorst)	PRE	1	1						1	
	Nudobius cephalus (Say)	PRE	16		1		6	6	3	12	4
	Oligota sp.1	PRE	2	1	1						2
	Oxypoda frigida Bernhauer	PRE	9				3	2	4	6	3
	Oxypoda sp.2	PRE	1						1	1	
	Phloeonomus sp.1	PRE	100	16	7	12	16	16	33	44	56
	Phloeopora spp.	PRE	128	19	16	9	16	6	62	56	72
	Phloeostiba lapponica (Zetterstedt)	PRE	18	2	3	1	5	3	4	9	9
	Placusa spp. (*P. icompleta*, *P.* *& P. tachyporoides*)[i]	MYC	722	42	45	56	65	260	254	266	456
	Placusa tacomae Casey	MYC	1	1							1
	Pseudopsis sagitta Herman	PRE	2						2	2	
	Quedius plagiatus Mannerheim	PRE	1						1		1

Appendix 5-A (continued)

Family	Species	FG[a]	Total[b]	2%-L[c]	20%-S[d]	20%-L[e]	50%-S[f]	50%-L[g]	CT[h]	Logs	Snags
	Siagonium punctatum (LeConte)	MYC	1					1			1
	Stenichnus ovipennis (Casey)	PRE	1		1					1	
	Tachyporus borealis Campbell	PRE	3			1	1		1	3	
Tenebrionidae	*Corticeus praetermissus* (Fall)	PRE	1	1							1
Total			20367	3211	1405	3409	2718	2563	7061	6808	13559

[a] FG (feeding guild): MYC (mycetophagous), OMN (omnivorous), PHL (phloeophagous), PRE (predaceous), RHI (rhizophagous), UNK (unknown), and XYL (xylophagous)

[b] Total is a sum of values from 2%, 20%, 50%, and CT.

[c] 2%-L (0.46 ha aggregated retention patches surrounded by 2% retention (standard clear-cut))

[d] 20%-S (0.20 ha aggregated retention patches surrounded by 20% dispersed retention)

[e] 20%-L (0.46 ha aggregated retention patches surrounded by 20% dispersed retention)

[f] 50%-S (0.20 ha aggregated retention patches surrounded by 50% dispersed retention)

[g] 50%-L (0.46 ha aggregated retention patches surrounded by 50% dispersed retention)

[h] CT (unharvested control that is 10 ha uncut forest)

[i] We also considered three possible aleocharine rove beetle species (*Placusa incompleta*, *P. pseudosuecica*, and *P. tachyporoides*) as *Placusa* spp. because of similarities in habitus and high and overlapping variation in male genitalia.

Appendix 5-B

Saproxylic beetle larvae (LV) sampled from two types of white spruce CWD (i.e., logs and snags) in large aggregated retention patches (0.46 ha) surrounded by 2% retention and two sizes of aggregated retention patches (0.20 and 0.46 ha) surrounded by 20% and 50% dispersed retention, and in unharvested control on the Ecosystem Management Emulating Natural Disturbance (EMEND) experimental landscape in northwestern Alberta. Nomenclature follows Bousquet et al. (2013).

Family	Species	FG[a]	Total[b]	2%-L[c]	20%-S[d]	20%-L[e]	50%-S[f]	50%-L[g]	CT[h]	Logs	Snags
Cantharidae	Cantharidae LV sp.1	PRE	2				2			2	
Carabidae	Carabidae LV sp.2	PRE	1					1			1
	Carabidae LV sp.3	PRE	1		1						1
Cerambycidae	Cerambycidae LV sp.1	XYL	112	7	9	2	75	15	4	93	19
Cleridae	*Thanasimus* LV sp.1	PRE	37	8	3	11	8	2	5	15	22
Colydiidae	Colydiidae LV sp.1	PRE	2		1	1					2
Corylophidae	Corylophidae LV sp.1	MYC	4	2	2					2	2
Cryptophagidae	Cryptophagidae LV sp.1	MYC	1			1				1	
Cucujidae	Cucujidae LV sp.1	PRE	3		2	1					3
	Pediacus fuscus Erichson LV	PRE	2	2						2	
Elateridae	Elateridae LV sp.2	UNK	15	4	2	3	1	4	1	13	2
	Elateridae LV sp.4	UNK	1						1		1
Eucinetidae	*Eucinetus* LV sp.1	MYC	13	1		3	3	6		4	9
Melyridae	Melyridae LV sp.1	UNK	4	3			1			1	3
Monotomidae	*Rhizophagus* LV sp.1	PRE	462	36	8	21	14	185	198	225	237
Nitidulidae	Nitidulidae LV sp.2	OMN	417	10	1	33	63	182	128	135	282
	Nitidulidae LV sp.4	OMN	48	1		2	7	31	7	2	46
Ptinidae	Ptinidae LV sp.1	XYL	4		1		3			4	
Pythidae	*Pytho planus* (Olivier) LV	PHL	4		1	1		2			4

Appendix 5-B (continued)

Family	Species	FG[a]	Total[b]	2%-L[c]	20%-S[d]	20%-L[e]	50%-S[f]	50%-L[g]	CT[h]	Logs	Snags
	Pytho seidlitzi Blair< LV	PHL	40		4	2	20	1	13	24	16
Silvanidae	*Dendrophagus cygnaei* Mannerheim LV	MYC	2					2		2	
Staphylinidae	*Quedius* LV sp.1	PRE	1						1	1	
	Quedius LV sp.2	PRE	1						1	1	
	Staphylinidae LV sp.2	UNK	594	47	27	59	75	172	214	219	375
	Staphylinidae LV sp.6	UNK	13	2	2		5		4	8	5
	Staphylinidae LV sp.7	UNK	10						10	10	
	Staphylinidae LV sp.9	UNK	335	29	11	4	6	151	134	152	183
	Staphylinidae LV sp.10	UNK	1			1					1
	Staphylinidae LV sp.11	UNK	7				1	6		1	6
	Staphylinidae LV sp.12	UNK	1					1		1	
	Staphylinidae LV sp.13	UNK	3					1	2	3	
Unknown	Coleoptera LV sp.8	UNK	32		1			30	1	1	31
	Coleoptera LV sp.10	UNK	1		1					1	
	Coleoptera LV sp.11	UNK	2				2			2	
Total			2176	152	77	145	286	792	724	925	1251

[a] FG (feeding guild): MYC (mycetophagous), OMN (omnivorous), PHL (phloeophagous), PRE (predaceous), UNK (unknown), and XYL (xylophagous)

[b] Total is a sum of values from 2%, 20%, 50%, and CT.

[c] 2%-L (0.46 ha aggregated retention patches surrounded by 2% retention (standard clear-cut))

[d] 20%-S (0.20 ha aggregated retention patches surrounded by 20% dispersed retention)

[e] 20%-L (0.46 ha aggregated retention patches surrounded by 20% dispersed retention)

[f] 50%-S (0.20 ha aggregated retention patches surrounded by 50% dispersed retention)

[g] 50%-L (0.46 ha aggregated retention patches surrounded by 50% dispersed retention)

[h] CT (unharvested control that is 10 ha uncut forest)

Appendix 6-A

Total species list of saproxylic beetles collected in white spruce stands and mixed stands from EMEND and nearby industrial harvest blocks during 2009-2013.

Family	Species	FG[a]	Abundance	Methods[b]
Aderidae	*Vanonus* sp.1	XYL	1	WT
Anthicidae	*Anthicus hastatus* Casey	OMN	4	WT, RD
Buprestidae	*Agrilus* sp.1	XYL	1	WT
	Anthaxia inornata (Randall)	XYL	8	WT
	Buprestis maculativentris Say	XYL	2	WT
	Chrysobothris trinervia (Kirby)	XYL	12	WT
	Dicerca tenebrica (Kirby)	XYL	1	WT
	Dicerca tenebrosa (Kirby)	XYL	22	WT
	Phaenops drummondi (Kirby)	XYL	3	WT
	Phaenops fulvoguttata (Harris)	XYL	50	WT, RD
Cantharidae	*Dichelotarsus laevicollis* (Kirby)	PRE	63	WT, RD
	Dichelotarsus piniphilus (Eschscholtz)	PRE	53	WT, RD
	Dichelotarsus puberulus (LeConte)	PRE	1	WT
	Rhagonycha fraxini (Say)	PRE	2	WT
	Rhagonycha mandibularis (Kirby)	PRE	4	WT, RD
	Silis difficilis LeConte	UNK	1	WT
Carabidae	*Agonum consimile* (Gyllenhal)	PRE	3	WT, RD
	Agonum retractum LeConte	PRE	6	RD
	Agonum thoreyi Dejean	PRE	1	WT
	Badister obtusus LeConte	PRE	1	WT
	Bembidion sp.1	PRE	3	RD
	Bradycellus congener (LeConte)	PRE	1	WT

Appendix 6-A (continued)

Family	Species	FG[a]	Abundance	Methods[b]
	Calathus advena (LeConte)	PRE	47	WT, RD
	Calathus ingratus Dejean	PRE	3	WT, RD
	Dicheirotrichus cognatus (LeConte)	PRE	1	WT
	Dromius piceus Dejean	PRE	3	WT
	Nebria gyllenhali (Kirby)	PRE	1	WT
	Platynus decentis (Say)	PRE	71	WT, RD
	Psydrus piceus LeConte	PRE	2	RD
	Stereocerus haematopus (Dejean)	PRE	6	WT, RD
	Tachyta angulata Casey	PRE	1	RD
	Trechus apicalis Motschulsky	PRE	3	RD
Cerambycidae	*Acanthocinus pusillus* (Kirby)	XYL	18	WT
	Acmaeops proteus (Kirby)	XYL	36	WT, RD
	Anastrangalia sanguinea (LeConte)	XYL	2	WT
	Asemum striatum (Linnaeus)	XYL	5	WT
	Callidium cicatricosum Mannerheim	XYL	3	WT
	Cortodera coniferae Hopping & Hopping	XYL	8	WT
	Grammoptera subargentata (Kirby)	XYL	11	WT
	Judolia montivagans (Couper)	XYL	5	WT
	Meriellum proteus (Kirby)	XYL	14	WT, RD
	Monochamus scutellatus (Say)	XYL	15	WT
	Neoclytus leucozonus (Laporte & Gory)	XYL	27	WT, RD
	Neospondylis upiformis (Mannerheim)	XYL	66	WT
	Pachyta lamed liturata Kirby	XYL	3	WT
	Phymatodes dimidiatus (Kirby)	XYL	126	WT, RD
	Phymatodes sp.1	XYL	1	WT
	Pogonocherus penicillatus LeConte	XYL	67	WT, RD

Appendix 6-A (continued)

Family	Species	FG[a]	Abundance	Methods[b]
	Pygoleptura nigrella (Say)	XYL	18	WT
	Rhagium inquisitor (Linnaeus)	XYL	7	WT
	Semanotus sp.1	XYL	1	WT
	Tetropium cinnamopterum Kirby	XYL	220	WT, RD
	Tetropium parvulum Casey	XYL	26	WT, RD
	Trachysida mutabilis (Newman)	XYL	5	WT
	Xylotrechus undulatus (Say)	XYL	111	WT
Cerylonidae	*Cerylon castaneum* Say	MYC	18	WT, RD
Ciidae	Ciidae sp.1	MYC	9	WT, RD
	Cis americanus Mannerheim	MYC	18	WT, RD
	Cis angustus Hatch	MYC	11	WT, RD
	Cis fuscipes Mellié	MYC	2	WT
	Cis horridulus Casey	MYC	4	WT
	Cis striolatus Casey	MYC	12	WT
	Dolichocis Manitoba Dury	MYC	24	WT, RD
	Octotemnus laevis Casey	MYC	11	WT
	Plesiocis cribrum Casey	MYC	6	WT, RD
Clambidae	*Calyptomerus oblongulus* (Mannerheim)	MYC	11	WT
	Clambus pubescens Redtenbacher	MYC	17	WT, RD
Cleridae	*Madoniella dislocata* (Say)	PRE	6	WT, RD
	Thanasimus dubius (Fabricius)	PRE	84	WT
	Thanasimus undatulus (say)	PRE	311	WT, RD
Colydiidae	*Lasconotus complex* LeConte	PRE	424	WT, RD
Corylophidae	*Arthrolips* sp.1	MYC	12	WT, RD
	Clypastraea sp.1	MYC	69	WT, RD
	Corylophidae sp.1	MYC	2	RD

Appendix 6-A (continued)

Family	Species	FG[a]	Abundance	Methods[b]
	Orthoperus scutellaris	MYC	6	WT, RD
Cryptophagidae	*Antherophagus ochraceus* Melsheimer	DET	3	WT
	Atomaria ephippiata Zimmermann	MYC	2	WT
	Atomaria sp.1	MYC	37	WT, RD
	Atomaria sp.2	MYC	6	WT, RD
	Atomaria sp.3	MYC	12	WT, RD
	Atomaria sp.4	MYC	8	WT, RD
	Atomaria sp.5	MYC	1	WT
	Atomaria sp.6	MYC	1	WT
	Atomaria sp.7	MYC	1	WT
	Caenoscelis antennalis (Casey)	MYC	8	WT, RD
	Cryptophagidae sp.1	MYC	11	RD
	Cryptophagus acutangulus Gyllenhal	MYC	31	WT, RD
	Cryptophagus pilosus Gyllenhal	MYC	1	RD
	Cryptophagus tuberculosus Mäklin	MYC	118	WT, RD
	Henoticus serratus (Gyllenhal)	MYC	1	WT
	Myrmedophila americana (LeConte)	MYC	7	WT, RD
	Pteryngium crenatum (Gyllenhal)	MYC	11	WT
	Salebius octodentatus (Mäklin)	MYC	15	WT, RD
Cucujidae	*Cucujus clavipes puniceus* Mannerheim	PRE	7	WT
	Pediacus fuscus Erichson	PRE	270	WT, RD
Curculionidae	*Carphonotus testaceus* Casey	XYL	33	WT, RD
	Cossonus quadricollis Van Dyke	XYL	6	WT
	Cryphalus ruficollis Hopkins	PHL	18	WT
	Crypturgus borealis Swaine	PHL	23465	WT, RD
	Dendroctonus ponderosae Hopkins	PHL	20	WT

Appendix 6-A (continued)

Family	Species	FG[a]	Abundance	Methods[b]
	Dendroctonus rufipennis (Kirby)	PHL	560	WT, RD
	Dryocoetes affaber (Mannerheim)	PHL	17738	WT, RD
	Dryocoetes autographus (Ratzeburg)	PHL	1853	WT, RD
	Hylobius pinicola (Couper)	RHI	9	WT
	Hylurgops porosus (LeConte)	PHL	11	WT, RD
	Hylurgops rugipennis (Mannerheim)	PHL	2	WT
	Ips pini (Say)	PHL	3404	WT, RD
	Magdalis sp.1	XYL	1	WT
	Magdalis subtincta LeConte	XYL	20	WT
	Orthotomicus caelatus (Eichhoff)	PHL	235	WT, RD
	Orthotomicus latidens (LeConte)	PHL	54	WT, RD
	Phloeosinus pini Swaine	PHL	17	WT
	Phloeotribus lecontei Schedl	PHL	5	WT
	Pissodes fiskei Hopkins	PHL	1	WT
	Pissodes rotundatus LeConte	PHL	113	WT, RD
	Pityogenes plagiatus knechteli Swaine	PHL	20	WT
	Pityophthorus spp.	PHL	456	WT, RD
	Polygraphus rufipennis (Kirby)	PHL	4896	WT, RD
	Rhyncolus brunneus Mannerheim	XYL	190	WT, RD
	Scierus annectans LeConte	PHL	4338	WT, RD
	Scierus pubescens Swaine	PHL	894	WT, RD
	Scolytus piceae (Swaine)	PHL	90	WT
	Trypodendron lineatum (Olivier)	MYC	7001	WT, RD
	Trypodendron retusum (LeConte)	MYC	2	WT
	Trypodendron rufitarsis (Kirby)	MYC	14	WT
	Tychius picirostris (Fabricius)	UNK	1	RD

Appendix 6-A (continued)

Family	Species	FG[a]	Abundance	Methods[b]
	Xylechinus montanus Blackman	PHL	1380	WT, RD
Dermestidae	*Megatoma cylindrica* (Kirby)	DET	18	WT, RD
	Megatoma perversa (Fall)	DET	8	WT, RD
Elateridae	*Agriotes ferrugineipennis* (LeConte)	RHI	3	WT
	Ampedus apicatus (Say)	PRE	7	WT, RD
	Ampedus luctuosus (LeConte)	PRE	21	WT
	Ampedus nigrinus (Herbst)	PRE	66	WT, RD
	Ctenicera kendalli Kirby	PRE	1	WT
	Ctenicera sp.1	PRE	1	WT
	Ctenicera sp.2	PRE	1	RD
	Danosoma brevicorne (LeConte)	PRE	11	WT, RD
	Denticollis denticornis (Kirby)	PRE	2	WT
	Eanus decoratus (Mannerheim)	PRE	36	WT, RD
	Eanus estriatus (LeConte)	PRE	7	WT
	Harminius triundulatus (Mannerheim)	PRE	2	WT, RD
	Hypnoidus bicolor (Eschscholtz)	RHI	3	WT
	Idolus debilis (LeConte)	RHI	16	WT, RD
	Liotrichus stricklandi (Brown)	PRE	2	WT
	Nitidolimonius resplendens (Eschscholtz)	PRE	20	WT
	Pseudanostirus nigricollis (Bland)	PRE	1	WT
	Pseudanostirus ochreipennis (LeConte)	PRE	18	WT
	Pseudanostirus propolus (LeConte)	PRE	91	WT, RD
	Pseudanostirus triundulatus (Randall)	PRE	9	WT
	Sericus incongruus (LeConte)	RHI	4	WT
	Setasomus nitidulus (LeConte)	PRE	20	WT, RD
Erotylidae	*Triplax californica* LeConte	MYC	2	WT

Appendix 6-A (continued)

Family	Species	FG[a]	Abundance	Methods[b]
	Triplax dissimilator (Crotch)	MYC	2	WT
Eucinetidae	*Eucinetus* sp.1	MYC	9	WT, RD
Eucnemidae	*Epiphanis cornutus* Eschscholtz	MYC	15	WT, RD
	Microrhagus pectinatus LeConte	MYC	5	WT
Histeridae	*Hister* sp.3	PRE	2	WT
	Paromalus mancus Casey	PRE	77	WT, RD
	Platysoma coarctatum LeConte	PRE	11	WT
	Teretrius montanus Horn	PRE	3	WT
Laemophloeidae	*Leptophloeus* sp.1	MYC	36	WT, RD
Latridiidae	*Cartodere constricta* (Gyllenhal)	MYC	38	WT, RD
	Corticaria ferruginea Marsham	MYC	41	WT, RD
	Corticaria rubripes Mannerheim	MYC	292	WT, RD
	Corticaria sp.2	MYC	4	RD
	Corticaria sp.3	MYC	4	WT, RD
	Corticaria sp.4	MYC	1	RD
	Cortinicara gibbosa (Herbst)	MYC	139	WT, RD
	Enicmus fictus Fall	MYC	1	WT
	Enicmus tenuicornis LeConte	MYC	17	WT, RD
	Latridius hirtus Gyllenhal	MYC	7	WT
	Latridius minutus (Linnaeus)	MYC	30	WT, RD
	Melanophthalma pumila (LeConte)	MYC	1	WT
	Melanophthalma villosa (Zimmermann)	MYC	81	WT, RD
	Stephostethus breviclavis (Fall)	MYC	1	WT
	Stephostethus liratus (LeConte)	MYC	5	WT, RD
Leiodidae	*Agathidium depressum* Fall	MYX	11	WT, RD
	Agathidium pulchrum LeConte	MYX	4	WT, RD

Appendix 6-A (continued)

Family	Species	FG[a]	Abundance	Methods[b]
	Agathidium sp.1	MYX	2	WT, RD
	Agathidium sp.2	MYX	2	WT
	Agathidium sp.3	MYX	1	WT
	Agathidium sp.4	MYX	1	WT
	Agathidium sp.5	MYX	2	WT
	Agathidium sp.6	MYX	2	WT
	Anisotoma amica Brown	MYX	5	WT, RD
	Anisotoma globososa Hatch	MYX	8	WT, RD
	Catops basilaris Say	DET	1	WT
	Catops sp.1	DET	1	WT
	Colon magnicolle Mannerheim	MYC	1	WT
	Colon sp.1	MYC	3	WT
	Leiodes punctostriata Kirby	MYC	1	RD
	Leiodes sp.2	MYC	1	WT
	Leiodidae sp.1	UNK	2	RD
Lycidae	*Dictyopterus aurora* (Herbst)	UNK	4	WT
	Greenarus thoracicus (Randall)	UNK	1	WT
Melandryidae	*Dolotarsus lividus* (Sahlberg)	XYL	33	WT
	Melandrya striata Say	XYL	10	WT
	Orchesia castanea Melsheimer	XYL	4	WT, RD
	Scotochroa sp.1	XYL	14	WT, RD
	Serropalpus substriatus Haldeman	XYL	217	WT, RD
	Xylita laevigata (Hellenius)	XYL	4	WT, RD
	Xylita livida (Sahlberg)	XYL	51	WT, RD
	Zilora hispida LeConte	XYL	6	WT, RD
Melyridae	*Hoppingiana hudsonica* (LeConte)	UNK	3	WT

Appendix 6-A (continued)

Family	Species	FG[a]	Abundance	Methods[b]
	Melyridae sp.1	UNK	1	WT
	Trichochrous albertensis Blaisdell	UNK	1	WT
Monotomidae	*Rhizophagus brunneus* Horn	PRE	282	WT
	Rhizophagus dimidiatus Mannerheim	PRE	684	WT, RD
	Rhizophagus remotus LeConte	PRE	12	WT, RD
Mordellidae	*Mordellaria borealis* (LeConte)	OMN	6	WT, RD
Mycetophagidae	*Mycetophagus distinctus* Hatch	MYC	1	WT
	Mycetophagus serrulatus (Casey)	MYC	6	WT
Nitidulidae	*Colopterus truncatus* Randall	UNK	18	WT, RD
	Epuraea flavomaculata Mäklin	OMN	3	WT
	Epuraea helvola Erichson	OMN	1	WT
	Epuraea linearis Mäklin	OMN	305	WT, RD
	Epuraea obliqua Hatch	OMN	47	WT, RD
	Epuraea planulata Erichson	OMN	46	WT, RD
	Epuraea rufomarginata (Stephens)	OMN	7	WT, RD
	Epuraea sp.1	OMN	17	WT
	Epuraea sp.4	OMN	4	WT
	Epuraea sp.5	OMN	8	WT
	Epuraea sp.6	OMN	1	WT
	Epuraea spp.	OMN	29	WT
	Epuraea terminalis Mannerheim	OMN	95	WT, RD
	Epuraea truncatella (Mannerheim)	OMN	79	WT, RD
	Glischrochilus sanguinolentus (Olivier)	OMN	20	WT
	Glischrochilus siepmanni Brown	OMN	12	WT
	Glischrochilus vittatus (Say)	OMN	10	WT, RD
	Meligethes canadensis Easton	UNK	6	WT

Appendix 6-A (continued)

Family	Species	FG[a]	Abundance	Methods[b]
Ptiliidae	*Acrotrichis* sp.1	MYC	35	WT, RD
	Pteryx sp.1	MYC	13	WT, RD
	Ptiliolum sp.1	MYC	1	RD
	Ptinella sp.1	MYC	2	RD
Ptinidae	*Caenocara scymnoides* LeConte	UNK	2	WT
	Desmatogaster subconnata (Fall)	UNK	8	WT, RD
	Dorcatoma moderata White	XYL	8	WT
	Ernobius gentilis Fall	XYL	4	WT
	Hemicoelus carinatus (Say)	XYL	72	WT, RD
	Microbregma emarginatum (Duftschmid)	XYL	81	WT, RD
	Ptilinus lobatus Casey	XYL	8	WT
	Ptinus sexpunctatus Panzer	PRE	1	WT
	Utobium elegans (Horn)	XYL	37	WT, RD
Pyrochroidae	*Schizotus cervicalis* Newman	MYC	2	RD
Pythidae	*Priognathus monilicornis* (Randall)	XYL	1	RD
	Pytho niger Kirby	PHL	7	RD
	Pytho planus (Olivier)	PHL	3	WT
	Pytho seidlitzi Blair	PHL	2	RD
Salpingidae	*Sphaeriestes virescens* (LeConte)	UNK	2	WT
Scirtidae	*Cyphon variabilis* (Thunberg)	OMN	23	WT, RD
Scraptiidae	*Anaspis atrata* Champion	UNK	14	WT
	Anaspis rufa Say	UNK	27	WT, RD
	Canifa pallipes (Melsheimer)	UNK	9	WT, RD
Silvanidae	*Dendrophagus cygnaei* Mannerheim	MYC	3	WT
	Silvanus bidentatus (Fabricius)	MYC	22	WT, RD
Sphindidae	*Odontosphindus clavicornis* Casey	MYX	3	WT

Appendix 6-A (continued)

Family	Species	FG[a]	Abundance	Methods[b]
Staphylinidae	*Acidota crenata* (Fabricius)	PRE	112	WT, RD
	Acidota quadrata (Zetterstedt)	PRE	1	WT
	Aleocharinae sp.1	UNK	1	RD
	Aleocharinae sp.23	UNK	1	RD
	Aleocharinae sp.41	UNK	2	RD
	Aleocharinae spp.	UNK	12	RD
	Amischa sp.1	PRE	18	WT, RD
	Anotylus sobrinus (LeConte)	PRE	5	WT, RD
	Anthophagini sp.1	PRE	1	RD
	Atheta (Microdota) pseudosubtilis Klimaszewski & Langor<	PRE	1	WT
	Atheta (Microdota) sp.	PRE	2	WT
	Atheta fanatica Casey	PRE	1	RD
	Atheta graminicola (Gravenhorst)<	PRE	8	WT
	Atheta klagesi Bernhauer	PRE	6	WT, RD
	Atheta remulsa Casey	PRE	1	WT
	Athetini sp.1	PRE	3	RD
	Athetini sp.2	PRE	3	RD
	Athetini spp.	PRE	5	WT
	Bolitobius sp.1	UNK	2	RD
	Bolitobius sp.2	UNK	1	RD
	Bolitopunctus muricatulus (Hatch)	UNK	2	WT
	Boreophilia davidgei Klimaszewski & Godin	UNK	5	WT
	Boreophilia islandica (Kraatz)	UNK	1	RD
	Carcinocephalus sp.1	UNK	1	WT
	Carpelimus sp.1	UNK	4	WT

Appendix 6-A (continued)

Family	Species	FG[a]	Abundance	Methods[b]
	Carphacis nepigonensis (Bernhauer)	PRE	11	WT
	Dalotia coriaria (Kraatz)	UNK	2	WT
	Deinopteroloma subcostatum (Mäklin)	UNK	1	WT
	Dinaraea worki Klimaszewski & Jacobs	PRE	6	WT, RD
	Dinothenarus pleuralis (LeConte)	PRE	4	WT, RD
	Eucnecosum brunnescens (Sahlberg)	UNK	1	RD
	Eucnecosum tenue (LeConte)	UNK	1	WT
	Euplectus duryi Casey	PRE	17	WT, RD
	Gabrius brevipennis (Horn)	PRE	6	WT, RD
	Gnypeta sp.1	UNK	1	RD
	Gyrophaena sp.	MYC	3	WT
	Heterothops minor Smetana	PRE	1	WT
	Homalota plana (Gyllenhal)	UNK	9	WT
	Ischnosoma fimbriatum Campbell	PRE	3	RD
	Ischnosoma pictum (Horn)	PRE	1	RD
	Ischnosoma splendidum (Gravenhorst)	PRE	11	WT, RD
	Lathrobium fauveli Duvivier	PRE	3	RD
	Lathrobium washingtoni Casey	PRE	16	WT, RD
	Leptacinus intermedius Donisthorpe	UNK	1	WT
	Leptusa gatineauensis Klimaszewski & Pelletier	PRE	1	RD
	Liogluta aloconotoides Lohse	PRE	3	RD
	Lordithon bimaculatus (Schrank)	PRE	2	WT, RD
	Lordithon fungicola Campbell	PRE	10	WT
	Lordithon kelleyi (Malkin)	PRE	7	WT
	Lordithon longiceps (LeConte)	PRE	8	WT
	Lordithon thoracicus (Fabricius)	PRE	1	WT

Appendix 6-A (continued)

Family	Species	FG[a]	Abundance	Methods[b]
	Megarthrus angulicollis Mäklin	PRE	2	WT
	Micropeplus laticollis Mäklin	PRE	22	WT
	Mocyta breviuscula (Mäklin)	PRE	10	WT, RD
	Mycetoporus americanus Erichson	PRE	7	WT, RD
	Nudobius cephalus (Say)	PRE	32	WT, RD
	Oligota sp.1	PRE	10	WT, RD
	Olisthaerus megacephalus (Zetterstedt)	PRE	36	WT, RD
	Olisthaerus substriatus (Paykull)	PRE	1	RD
	Olophrum consimile (Gyllenhal)	PRE	8	WT, RD
	Oxypoda canadensis Klimaszewski	PRE	5	WT, RD
	Oxypoda frigida Bernhauer	PRE	26	WT, RD
	Oxypoda hiemalis Casey	PRE	1	WT
	Oxypoda lacustris Casey	PRE	7	WT
	Oxypoda operta Sjöberg	PRE	9	WT, RD
	Oxypoda sp.2	PRE	1	RD
	Oxypodini sp.1	PRE	4	RD
	Philhygra sp.1	PRE	1	WT
	Philhygra sp.2	PRE	5	WT
	Philhygra sp.3	PRE	1	WT
	Philonthus caeruleipennis (Mannerheim)	PRE	1	WT
	Philonthus varians (Paykull)	PRE	1	WT
	Phloeonomus sp.1	PRE	150	WT, RD
	Phloeopora sp.1	PRE	2	RD
	Phloeopora sp.2	PRE	1	RD
	Phloeopora spp.	PRE	139	WT, RD
	Phloeostiba lapponica (Zetterstedt)	PRE	63	WT, RD

Appendix 6-A (continued)

Family	Species	FG[a]	Abundance	Methods[b]
	Phyllodrepa humerosa (Fauvel)	PRE	3	RD
	Placusa spp. (*P. icompleta*, *P. pseudosuecica,* & *P. tachyporoides*)	MYC	756	WT, RD
	Placusa tachyporoides (Waltl)	MYC	135	WT, RD
	Placusa tacomae Casey	MYC	55	WT, RD
	Porrhodites inflatus (Hatch)	UNK	3	WT
	Pseudopsis sagitta Herman	PRE	10	WT, RD
	Pycnoglypta aptera Campbell	PRE	2	RD
	Quedius caseyi Scheerpeltz	PRE	2	RD
	Quedius criddlei (Casey)	PRE	9	WT, RD
	Quedius erythrogaster Mannerheim	PRE	1	WT
	Quedius fulvicollis (Stephens)	PRE	3	RD
	Quedius labradorensis Smetana	PRE	1	RD
	Quedius mordax Smetana	PRE	1	RD
	Quedius plagiatus Mannerheim	PRE	33	WT, RD
	Quedius rusticus Smetana	PRE	10	WT, RD
	Quedius transparens Motschulsky	PRE	1	RD
	Quedius velox Smetana	PRE	86	WT, RD
	Scaphium castanipes Kirby	MYC	1	WT
	Schistoglossa campbelli Klimaszewski	UNK	2	WT
	Schistoglossa hampshirensis Klimaszewski	UNK	1	WT
	Seeversiella globicollis (Bernhauer)	PRE	13	WT, RD
	Sepedophilus wickhami Campbell	MYC	1	WT
	Siagonium punctatum (LeConte)	MYC	70	WT, RD
	Stenichnus ovipennis (Casey)	PRE	12	WT, RD
	Stenichnus sp.2	PRE	3	WT
	Stenus austini Casey	PRE	7	RD

Appendix 6-A (continued)

Family	Species	FG[a]	Abundance	Methods[b]
	Syntomium confragosum Mäklin	UNK	1	WT
	Tachinus basalis Erichson	PRE	1	WT
	Tachinus elongatus Gyllenhal	PRE	8	WT, RD
	Tachinus frigidus Erichson	PRE	2	WT, RD
	Tachinus fumipennis (Say)	PRE	2	RD
	Tachyporus borealis Campbell	PRE	22	WT, RD
	Trichiusa pilosa Casey	UNK	1	WT
Stenotrachelidae	*Cephaloon tenuicorne* LeConte	OMN	136	WT
	Stenotrachelus aeneus (Fabricius)	UNK	3	WT
Tenebrionidae	*Bius estriatus* (LeConte)	UNK	12	WT
	Corticeus praetermissus (Fall)	PRE	77	WT, RD
	Corticeus tenuis (LeConte)	PRE	11	WT, RD
	Scaphidema aeneolum (LeConte)	MYC	1	WT
	Upis ceramboides (Linnaeus)	OMN	1	WT
Trogossitidae	*Calitys scabra* (Thunberg)	MYC	1	WT
	Peltis fraterna (Randall)	MYC	26	WT, RD
	Thymalus marginicollis Chevrolat	MYC	10	WT, RD
Total	377 species		75719	

[a] FG (feeding guild): DET (detritivorous), MYC (mycetophagous), MYX (myxomycophagous), OMN (omnivorous), PHL (phloeophagous), PRE (predaceous), RHI (rhizophagous), UNK (unknown), and XYL (xylophagous)

[b] WT (window traps), RD (rearing drums or emergence trap)