"*Cucujus clavipes* Fabricius, 1781 (Coleoptera: Cucujidae) word cloud"

"Dead wood is anything but dead. It is the lifeblood of an intricate web of life in which insects figure prominently."

~ Grove and Hanula, 2006

University of Alberta

Saproxylic Beetles (Coleoptera) Associated With Aspen Deadwood in Broad-Leaved Boreal Mixedwood Stands

by

Charlene Meridith Wood

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of

Master of Science
in
Conservation Biology

Department of Renewable Resources

Fall 2012
Edmonton, Alberta

Abstract

I assessed deadwood-associated (i.e., ‘saproxylic’) beetles (Coleoptera) along a decay gradient of trembling aspen in mature deciduous stands of the boreal mixedwood forest in NW Alberta. Various collection methods were employed to sample saproxylic beetle species. Assemblages differed between host substrate types and decay classes. Many species were also associated with moss presence and percent bark cover. Although small (7 to 15.9 cm) diameter logs were most abundant in the stands, most indicator species were associated with logs ≥25 cm in diameter. Samples of saproxylic beetles varied greatly depending on collection method; however window trap captures were compositionally similar regardless of their placement (on snags or freely-hanging). This suggests that window traps are less appropriate for assessing small-scale habitat associations. Deadwood associations revealed here indicate that a wide range of substrate types, decay classes, and sizes are important features of saproxylic beetle habitats that should be retained for biodiversity conservation.

Acknowledgements

This adventure would not be possible without the support and encouragement of my family (Dad, Mom, Bryan, Grace, Alan, Jayne, and Lachlan) and friends. Thanks especially to Zaid Jumean, for his love, patience, and various contributions to the production of this thesis. I would like to thank my supervisors John Spence and David Langor for giving me the opportunity to carry out this study and suggestions on this thesis. I would also like to thank my committee, Ellen Macdonald, Nadir Erbilgin, and Maya Evenden for comments on the final thesis.

Best wishes go to the Spence Lab members that I have had the pleasure to know. Your support has been integral to the production of this thesis, and your friendship has made the ride enjoyable! Much appreciation also goes out to my fellow 'EMENDers', especially Jason Edwards and Charlene Hahn, for creating a 'home away from home' for my two summers at camp. The striking Northern skies, campfires, and cribbage tournaments will not soon be forgotten. Finally, those years at EMEND are filled with lasting memories of Suzanne Abele – my "fast friend."

Statistical guidance was provided by Jaime Pinzón, Guillaume Blanchet, Stéphane Bourassa, Evan Esch, and Anne Oxbrough. Additionally, thanks to Zaid, Stéphane and Anne for useful suggestions on my chapters. I would also like to thank the many people at the Northern Forestry Centre (Canadian Forest Service) that helped with aspects of field work, species identification, and construction of collection devices (Daryl Williams, Colin Myrholm, Greg Pohl). In particular, thanks to Jim Hammond for guidance in the early stages of my project and 'showing me the ropes' with saproxylic beetles. I would also like to thank Daishowa Marubeni International Limited (DMI) for allowing sampling on their forest management area and Jim Witiw and Florence Niemi (DMI) for helpful discussion. Amy Jimmo, Emily Turton, Melanie von Engelhardt, Philip Hoffman, Kimberly Stang, and Tory Cullen assisted with fieldwork and/or sample processing. Additional thanks to Dustin Hartley and Stéphane for help with rove beetle and ground beetle identifications as well as Danny Shpeley, Dr. Ball, and the UASM collection. I would like to acknowledge the many editors and contributors to the online taxonomic website 'BugGuide', through which I was able to ask advice of many experts in various groups. Particular thanks go to Wolfgang Rücker, Andreas Herrmann, Yves Bousquet, Colin Johnson, Donald Chandler, Paul Johnson, Andrew Cline, and Vasilli Belov. Brewing support and general merriment were provided by Stéphane and Colin Bergeron.

Financial support was given by a Natural Sciences and Engineering Research Council of Canada (NSERC) Postgraduate Scholarship and Queen Elizabeth II Scholarship, Alberta Conservation Association (ACA) Grants in Biodiversity, Natural Resources Canada (NRCan), Alberta Sustainable Resource Development (SRD), the Forest Resource Improvement Association of Alberta (FRIAA) through DMI and Canadian Forest Products (CANFOR), the Manning Forestry Research Fund, the Sustainable Forest Management Network, and the DMI grant held by David Langor (NRCan) for downed woody debris management and measurement research.

Table of Contents

List of Tables

List of Figures

1. INTRODUCTION

In much of the boreal forest region, clear-cutting and fire suppression practices have drastically reduced the amount and heterogeneity of deadwood habitats (Esseen et al. 1997; Siitonen 2001), seriously impacting the saproxylic fauna (species associated with deadwood). Thus, the conservation of saproxylic biodiversity has become a major concern, particularly in Europe (Nieto and Alexander 2010). However, for much of North America, little is known of saproxylic communities and their required habitats, even from unmanaged forests. Avoiding depletion of this important component of forest biodiversity requires data that delimits the saproxylic assemblages of various deadwood habitats, their responses to disturbances, and the particular conditions that should be conserved to maintain local populations. Because many species are often rare, occurring in low population sizes or infrequently distributed across the landscape, it is also important to develop appropriate methods for quantitative assessments of the saproxylic community. In this thesis, I assessed the performance of various collection methods and the particular substrate requirements of saproxylic beetles inhabiting various decay states of aspen in mature broad-leaved stands of the boreal mixedwood forest. Studies of saproxylic assemblages applied across a broad range of deadwood qualities are needed to better identify critical habitats for conservation.

1.1. Boreal Forest Landscapes

1.1.1. The Boreal Mixedwood Forest

The boreal forest, largely dominated by coniferous tree species, is circumpolar in distribution covering the northern extents of North America and Eurasia. This large northern forest accounts for about one third of global forested area and 77% of Canadian forests (Stelfox 1995). Although characterized by a predominance of mature coniferous trees, the boreal landscape is a mosaic of stands varying in canopy composition, age, size, and shape (Peterson and Peterson 1992). In Canada, the more southern part of the boreal forest, extending from northeastern British Columbia, through the north and central prairie regions, to southwestern Manitoba (Stelfox 1995), comprises a patchwork of broadleaf, conifer, and mixedwood stands, known as the boreal mixedwood ecoregion.

The boreal mixedwood ecoregion of Canada is mainly delimited by altitudinal and climatic factors, which generate forests with distinctive vegetation communities, site characteristics, disturbance regimes, and successional pathways. Trembling aspen (*Populus tremuloides* Michaux) and white spruce (*Picea glauca* [Moench] Voss) are dominant tree species, though black spruce (*Picea mariana* [Miller] Britton, Sterns, & Poggenburg), balsam fir (*Abies balsamea* [Linnaeus] Miller), tamarack (*Larix laricina* [Du Roi] Koch), white birch (*Betula papyrifera* Marshall),

balsam poplar (*Populus balsamifera* Linnaeus), lodgepole pine (*Pinus contorta* Douglas), and jack pine (*Pinus banksiana* Lambert) commonly occur. Understory vegetation consists of various shrubs and forbs, with typical sites consisting of low-bush cranberry (*Viburnum edule* [Michaux] Rafinesque), prickly rose (*Rosa acicularis* Lindley), beaked hazelnut (*Corylus cornuta* Marshall), Saskatoon berry (*Amelanchier alnifolia* [Nuttall] Nuttall), Canada buffalo-berry (*Shepherdia canadensis* [Linnaeus] Nuttall), twinflower (*Linnaea borealis* Linnaeus), green alder (*Alnus crispa* [Aiton]), bunchberry (*Cornus canadensis* Linnaeus), wild sarsaparilla (*Aralia nudicaulis* Linnaeus), and dewberry (*Rubus pubescens* Rafinesque) (Beckingham and Archibald 1996).

Site physiography varies considerably throughout the boreal mixedwood and includes flat-topped hills, rolling uplands, undulating and flat lowlands, and lowlands dominated by shallow lakes (Beckingham and Archibald 1996). The dominant soils are organic, grey luvisols, brunisols, and gleysols (Beckingham and Archibald 1996). Fire intervals largely control stand composition and structure (Bergeron 2000; Bergeron and Debuc 1989). Mixedwood forests may follow various successional pathways following fire, in part due to fire intensity and initial colonization history (Bergeron and Debuc 1989).

1.1.2. Broad-leaved Stands

A characteristic feature of early to intermediate post-fire succession is the presence of pioneer broad-leaved stands, dominated by aspen. Because aspen can rapidly regenerate after fire events by suckering from clonal rhizomes (Mittion and Grant 1996), this is usually the species to most quickly form a canopy in early seral stages. Young aspen stands often act as a “nurse crop” that facilitates growth of coniferous tree species which eventually replace the aspen forest (Farrar 1995). However, sometimes aspen forms the climax species (Cumming et al. 2000).

Broad-leaved stands are generally the most species rich forests of the boreal region, surpassed only by riparian forests (DeByle et al. 1985; Finch and Ruggiero 1993; Mitton and Grant 1996). In western North America, aspen is considered a keystone species (Oaten and Larsen 2008b), with these broad-leaved stands forming biodiversity “hotspots” (Oaten and Larsen 2008a, b; Simonson et al. 2001). Aspen stands favour soil macrofauna diversity, which in turn increases the rate of soil processes (Laganiere et al. 2009). Aspen also has higher aboveground net primary productivity and litterfall nitrogen than either black spruce or jack pine stands (Reich et al. 2001). Aspen supports a high species richness of understory plants (Berger and Puettmann 2000; Hart and Chen 2008; MacDonald and Fenniak 2007; Reich et al. 2001), birds (Griffis-Kyle and Beier 2003; Hobson and Bayne 2000a, b; Hollenbeck and

Ripple 2007), lichens (Hedenas and Hedstrom 2007), and invertebrates (Chong et al. 2001; Hammond 1997; Langor et al. 2008).

1.2. Deadwood as Critical Habitat

1.2.1. Definition of Deadwood

For the purpose of this thesis, deadwood is considered as the dead tissue of standing, leaning, and fallen trees, including the bark and wood. Deadwood will be herein used as a general term to encompass the terms “dead wood”, “woody debris”, “woody material”, “snag”, “log”, and similarly related terms.

1.2.2. Deadwood Habitats

Deadwood is an important natural component of forest ecosystems. Huston (1996), for example, stated that deadwood has a greater impact on biodiversity than any other manageable component of forest ecosystems. Deadwood plays a substantial role in many ecosystem processes, including: carbon and nutrient cycling, geomorphology of slopes and waterways, stand hydrological balance, soil formation, germination and regeneration, and providing habitat and structure for a large diversity of biota (Franklin et al. 1987; Harmon et al. 1986; Stevens 1997). Contribution of deadwood to each of these roles varies by ecosystem, natural disturbance type and regime, and nutrient and

moisture regimes (Stevens 1997). Through these ecological roles, deadwood contributes significantly to overall forest productivity and biodiversity.

Deadwood and its various attributes are critical to maintaining biodiversity, particularly of sensitive species (e.g., Berg et al. 1994; Grove 2002a; Jonsell 2008; Tikkanen et al. 2006). The large amount of variation in deadwood substrates (e.g., species, orientation, diameter, microclimate, extent of decay) creates numerous heterogeneous microsites, which can support a high diversity of species. All main organismal groups are represented in deadwood habitats, most notably, fungi (Heilmann-Clausen and Christensen 2005; Junninen et al. 2006), bryophytes (Ődor et al. 2006), lichens (Ulikzka and Angelstam 2000), beetles and other insects (Gibb et al. 2008; Grove 2002a; Martikainen et al. 2000; Rotheray et al. 2001), arachnids (Pinzon and Spence 2010; Skubala and Duras 2008), birds (Martin and Eadie 1999; Hunter 1990), small mammals (Sullivan and Sullivan 2001), and amphibians (DeMaynadier and Hunter 1995). A key source of the high diversity in deadwood arises from the decay process because this reflects a succession of insect (Esseen et al. 1997; Hammond et al. 2001) and fungal (Jonsell et al. 1998) communities.

The importance of deadwood size is becoming well known. Although small pieces of wood (<10cm diameter) are important for fungal

diversity (Heilmann-Clausen and Christensen 2004; Norden et al. 2003), large diameter wood often supports higher overall numbers of fungus, bryophyte and invertebrate species (Andersson and Hytteborn 1991; Bader et al. 1995; Soderstrom 1988), including rare, threatened, and endangered species (Kruys et al. 1999; Jonsell et al. 1998). Large diameter wood provides more substrate for habitat, has a greater capacity to hold moisture (Harmon et al. 1986), has more stable microclimatic conditions (Boddy, 1983), different wood-decay dynamics (Yee et al. 2006), and a longer persistence on the landscape (Holeksa et al. 2008). The value of large diameter wood is particularly great and given that harvesting causes dramatic losses to large diameter deadwood (Siitonen, 2001), forest managers have been challenged to develop prescriptions for retaining this vital resource.

Fire history and self-thinning (senescence of large trees) create a high diversity of deadwood sizes and decay states in mature aspen stands (Lee et al. 1997). This large amount of structural heterogeneity no doubt contributes greatly to the biodiversity of these stands, which support many cryptogam species (Crites and Dale 1998) and beetles (Hammond et al. 2004) specializing on various decay states of deadwood. Although few studies are available from aspen deadwood in western Canada, at least 300 species of beetles (Hammond 1996), 33 mosses, 32 lichens, 24 macrofungi, and 7 liverworts (Crites and Dale 1998) use dead aspen

habitats. An additional 1500 saproxylic arthropods (Diptera, Hymenoptera, Heteroptera, Lepidoptera, Thysanoptera, Collembola, Acari, Pseudoscorpiones, Araneae, Opiliones) have been collected, but not identified to species (Hammond, 1997).

Conservation is a key concept in most approaches to Sustainable Forest Management, and conservation of deadwood has become an important issue in forests worldwide. Under most harvesting regimes key structural features and processes may be lost or reduced on boreal landscapes, thus impacting associated fauna and likely having implications for the productivity of these ecosystems.

1.3. Study organisms in focus

1.3.1. Definition of 'Saproxylic'

The word 'saproxylic' was first coined by Dajoz (1966) for insects living in decaying wood, and is derived from the Greek words *sapros* and *xylon*, meaning 'decayed' and 'wood'. The most widely accepted definition of saproxylic invertebrates are those that are "dependent, during some part of their life cycle, upon the dead or dying wood of moribund or dead trees (standing or fallen), or upon wood-inhabiting fungi, or upon the presence of other saproxylics" (Speight 1989). Several others have discussed alternate definitions and have extended the use of the term to

species occurring in microhabitats of healthy trees (Alexander 2008, Schmidl and Bussler 2004, Stokland et al. 2012), since live trees may contain many of the habitats (e.g., loose bark, decomposed wood, rot-holes, wood-decay fungi) important for saproxylic organisms (Speight 1989).

In this thesis I adopt the broad definition of saproxylic proposed 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”, which includes bark and sap in addition to wood, at any stage of decay of trees (standing or fallen). This definition thus supports species living in microsites of living trees (wounds, dead branches, cavities, sap runs), but excludes phytophagous species, feeding exclusively on living tissue.

It may become difficult to draw the line between saproxylic and non-saproxylic species, as decayed wood becomes increasingly incorporated into the forest floor as humus. Members of the soil community may become frequent residents of these well-decayed woody substrates, without having a true affinity for saproxylic habitats. As a result, some reviewers have questioned the validity of including non-rhysodine beetles in the families Carabidae and to a lesser extent, Staphylinidae, in the saproxylic community (J. Spence, pers. comm.). To

address this concern, I have reviewed the habitat and feeding ecology of the taxa collected in this thesis, and assigned them to three levels of saproxylic association consistent with the terminology of Dahlberg and Stokland (2004) and Grove and Forster (2011). ‘Obligate saproxylic’ species are considered to only live, breed, feed, and/or overwinter in deadwood habitats (wood, bark, or wood-decaying fungi), and are thus dependent on deadwood for survival and reproduction. ‘Facultative saproxylic’ species may partially depend on deadwood or be opportunistically associated with deadwood habitats, but are also found in other habitats, and are thus not completely dependent on deadwood for persistence. And ‘non-saproxylic’ species are those not thought to have any association with deadwood. In this thesis, the term saproxylic will refer to both obligate and facultative saproxylics, together.

Some support exists for saproxylic associations in the Carabidae, such as in the genera *Platynus* and *Pterostichus*, whose larvae have been associated with loose bark, dead branches, and decaying wood (Dahlberg and Stockland 2004; Goulet 1974; Hamilton 1884; Work et al. 2004). To be conservative, given the controversy of defining saproxylic associations in the Carabidae, these species were deemed ‘facultative saproxylic’ in this thesis. Saproxylic associations can be particularly strong for some rove beetles. For instance, *Atrecus* species are known to be obligate saproxylics, occurring under bark of especially brown-rotted wood of old

trunks / stumps in Europe (Dahlberg and Stockland 2004), and in North America, under bark and in scolytine galleries (Arnett and Thomas 2000). Of course, the precision of these designations will be improved with future data that contributes to our understanding of species' natural history.

Some species may be collected by chance in deadwood habitats, but were deemed 'non-saproxylic' if their known ecology did not suggest associations with deadwood. These included, e.g., the Carabidae genera *Amara, Calathus, Calosoma, Diacheila*, all Coccinellidae except *Didion*, Chrysomelidae, Orsodacnidae, Scarabaeidae, Silphidae, and the Staphylinidae genera *Acidota, Carpelimus, Eusphalerum*, and *Ontholestes*.

1.3.2. Saproxylic Beetles

In terms of described species, beetles (Coleoptera) are the most species-rich order of insects (Gaston 1991), and they are relatively well studied, in terms of taxonomy and ecology, relative to other insect groups. This order comprises a major proportion of the insect fauna associated with old trees and deadwood in boreal forests (Jonsell and Weslien 2003; Jonsell et al. 1998; Martikainen et al. 2000; Siitonen 2001). For instance, Siitonen (2001) considered some 800 beetle species as saproxylic in forests of Fennoscandia, but 900 beetle species were deemed saproxylic from Norway alone (Økland et al. 1996). Forty-two percent of all beetle

species collected from old growth spruce forests and aspen trees were saproxylic in Finland (Martikainen et al. 2000; Martikainen 2001), whereas 25 to 56% of all beetle species were saproxylic in Germany (Blab et al. 1994; Köhler 2000).

Saproxylic beetles are vital to forest ecosystems, especially through their roles in decomposition cycles. Bore holes and colonization of freshly dead trees by bark- and wood-boring beetles facilitate initial colonization of deadwood by speciose cryptogam (fungus, lichen, and bryophyte) and vascular plant communities thus contributing to nutrient and energy cycling that drive forest regeneration and primary productivity. In addition to feeding on wood and bark, saproxylic beetles may also be fungus feeders, scavengers, and predators, exhibiting a characteristic and functionally important succession in deadwood over time (Esseen et al. 1997). Deadwood-associated insects are also an important food source for many forest organisms, including other arthropods, birds (especially woodpeckers) and numerous other vertebrates.

Many saproxylic species have shown negative responses to forest fragmentation and clear-cut harvesting (Siitonen 2001), making saproxylic beetles an important focal group. The International Union for the Conservation of Nature (IUCN) recently assessed the status of Europe's saproxylic beetles, and has included 436 species on the European Red-

List (Nieto and Alexander 2010). In total, 29 species of saproxylic beetles at risk of global extinction, 46 species at risk of extinction from Europe, and an additional 56 species threatened or “near threatened”. Unfortunately, for most species, there is still not enough data to determine conservation status.

Knowledge is currently even more limited for North America, and studies that have been conducted are spread quite unevenly across forest types and saproxylic taxa. Compared to coniferous forests, there is a much less known about saproxylic beetle communities in aspen. This is surprising, particularly given the wide geographical range of this species in North America and that the closely related European aspen (*P. tremula* Linné) is among the most important tree species for saproxylic beetle diversity in European forests (Martikainen 2001; Jonsell 2007; Lindhe and Lindelow 2004; Sverdrup-Thygeson and Ims 2002; Tikkanen et al. 2006; Ahnlund 1996; Sahlin and Schroeder 2010). As well, wood consumer species are better known than those of other functional guilds (Stokland et al. 2012). Few studies have examined the entire saproxylic beetle community associated with *P. tremuloides* (Hammond et al. 2001, 2004; Hammond, 1997; Jacobs et al. 2007). Others have focused on phloeophagous and xylophagous beetles (Saint-Germain et al. 2006, 2007; Webb et al. 2008; Petty, 1977) or click-beetles (Thomas et al.

2009). In short, little is known about the North American fauna and the particular microhabitats they require.

There are significant knowledge gaps with respect to saproxylic beetles and other scarcely known groups (lichens, microfungi, mites, etc.) on the boreal mixedwood landscape. Baseline faunistic studies are needed across much of this region. Some authors are highlighting the importance of this little known fauna through synthesis of saproxylic literature (Langor et al. 2006, 2008) and taxonomic reviews (Majka and Cline, 2006; Majka and Pollock, 2006; Majka, 2007; Majka et al. 2008; Majka et al. 2009; Majka and Langor, 2010; Majka et al. 2010). The importance of further species-level work has been emphasized (Spence et al. 2008) in order to improve understanding of species requirements and develop meaningful conservation strategies. Therefore, beetles were a highly suitable choice to study in assessing assemblages across a wide range of saproxylic habitats provided by aspen, including live trees, dead trees (i.e., ‘snags’) and fallen trees (i.e., ‘logs’), in stands dominated by broadleaf trees in the boreal mixedwood forest of northwest Alberta, Canada.

1.4. Thesis structure

1.4.1. Overall Objectives

To maintain saproxylic diversity and the valuable ecosystem services they provide we need to ensure that suitable habitats and ecological conditions are preserved across managed forest landscapes. Studies of saproxylic beetles applied across a broad range of deadwood substrates are needed to better identify, delimit, and classify critical habitats for saproxylic organisms. To optimize monitoring programs, it is also important to determine appropriate methods for sampling the saproxylic community. Based on this information, conservation strategies can be developed to best manage this sensitive community, and mitigate potential biodiversity losses. Overall, by investigating the saproxylic beetle community across a diversity of aspen habitats, I seek to improve our understanding of the beetle assemblages (and the species comprising them) in particular substrate types and qualities of aspen deadwood in unmanaged boreal broad-leaved forests. In the following chapters I consecutively address three main questions:

1) What collection method or combination of methods is most suitable to provide a robust sample of saproxylic beetles and/or to assess substrate-associations?

2) How do saproxylic species and assemblages vary across different diameter classes of logs?

3) What are the habitat types and deadwood attributes associated with saproxylic beetles and how do assemblages vary across different substrates?

1.4.2. Thesis Chapters

I have divided my thesis into 5 chapters, each addressing a specific objective. Here, in Chapter 1, I establish the focused rationale and context for my study, including definitions of terms used throughout the thesis, and outline the thesis structure.

In Chapter 2, I explain various collection methods used for sampling saproxylic beetles in the thesis. I use these data to assess efficiency and biases of each collection method and determine the utility of each method for determining substrate associations. Such a comparison was necessary, as past studies were largely dominated by the use of one collection method (window traps), which may limit the scope of our understanding in the saproxylic fauna. The aim of this chapter was ascertain which collection methods are appropriate for future assessments of saproxylic beetle diversity.

Chapter 3 is focused on the relationship between saproxylic beetles and deadwood diameter, in relation to predefined size classes of aspen deadwood that occurs naturally in old growth broad-leaved stands across

the study area. As there is much evidence from studies the world over to show that deadwood diameter is a major factor influencing saproxylic diversity, and no such assessments have been made for aspen logs in North America, it was important to consider these relationships in this study. In this chapter, I describe species richness, assemblage composition, and habitat use by saproxylic beetles across each size class. I broadly discuss the possible context for the observed associations, touching on particular deadwood qualities that differ between these habitats and the ecology of related species.

In Chapter 4 I assess saproxylic beetles across various substrate types and attributes, with a focus on decay classes. Previous studies have been largely biased towards early successional taxa (bark and wood boring beetles) and freshly dead wood, and thus the full community of saproxylic beetles is not well known from a wide range of aspen deadwood decay classes in standing and fallen wood (although, see Hammond et al. 2004). Such an assessment of the saproxylic community is needed to fully understand our fauna and the habitat associations of North American taxa. This information will be useful for predicting species responses to alterations in the distribution and abundance of deadwood qualities across managed landscapes, and to maintain particular deadwood habitats for biodiversity conservation.

In the last chapter of my thesis (Chapter 5) I synthesize the major findings from the preceding chapters in order to summarize the ecology of saproxylic beetles using aspen habitats. Using the information about efficiencies and biases of collection methods, habitat associations, and new species records, I discuss important considerations for future research, conservation schemes, and management of deadwood.

Lastly, in Appendix 5-A, I provide the overall data for all saproxylic beetle taxa in relation to the main factors examined in Chapters 2, 3, and 4. This table also distinguishes new species records for Alberta and new species to science found during this study. It should be noted that the functional guilds and saproxylic classifications given in this compilation should be considered a starting point, as many species associations are still uncertain.

1.5. Literature Cited

Alexander, K.N.A. 2008. Tree biology and saproxylic Coleoptera: issues of definitions and conservation language. In: Vignon, V. and Asmodé J.F. (eds) Proceedings of the 4th Symposium and Workshop on the Conservation of Saproxylic Beetles, held in Vivoin, Sarthe Department – France 27-29 June 2006. Revue d'Écologie (Terre Vie), supplement 10: pp 9-13.

Ahnlund, H. 1996. Saproxylic insects on a Swedish dead aspen. Entomologisk Tidskrift. 117:137-144.

Anderson, L.I. and H. Hytteborn. 1991. Bryophytes and decaying wood — a comparison between managed and natural forest. Holarctic Ecology 14: 121–130.

Arnett, R.H. and M.C. Thomas. 2001. American Beetles, Volume 1. CRC Press. 464pp.

Bader, P., S. Jansson and B.G. Jonsson. 1995. Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. Biological Conservation 72(3): 355-362.

Beckingham, J. and J. H. Archibald. 1996. Field guide to ecosites of Northern Alberta. Special Report 5. Natural Resources Canada, Canadian Forest Service. Northwest Region. Edmonton, AB.

Berg, A., U. Gärdenfors, T. Hallingbäck and M. Norén. 2002. Habitat preferences of red-listed fungi and bryophytes in woodland key habitats in southern Sweden – analyses of data from a national survey, Biodiversity and Conservation 11: 1479–1503.

Berger, A. and K. J. Puettmann. 2000. Overstory composition and stand structure influence herbaceous plant diversity in the mixed aspen forest of northern Minnesota. American Midland Naturalist. 143(1): 111-125.

Bergeron, Y. 2000. Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. Ecology 81(6): 1500-1516.

Bergeron, Y. and M. Dubuc.1989. Succession in the southern part on the Canadian boreal forest, Vegetatio 79: 51–63.

Blab, J., E. Nowak, W. Trautmann and H. Sukopp. 1994. Rote Liste der gefahrdeten Tiere und pflanzen in der Bundesrepublik Deutschland. Greven, Ger: Kilda.

Boddy, L. 1983. The effect of temperature and water potential on the growth rate of wood-rotting basidiomycetes. Transactions of the British Mycological Society 80: 141-149.

Caners, R.T., S.E. Macdonald and R.J. Belland. 2010. Responses of boreal epiphytic bryophytes to different levels of partial canopy harvest. Botany 88: 315-328.

Chong, G.W., S.E. Simonson, T.J. Stohlgren and M.A. Kalkhan. 2001. Biodiversity: Aspen Stands Have the Lead, But Will Nonnative Species Take Over? In: Shepperd, W.D., D. Binkley, D.L. Bartos, T.J. Stohlgren, L.G. Eskew. Sustaining aspen in western landscapes. United States Department of Agriculture Forest Service Proceedings, Rocky Mountain Research Station RMRS-P-18: 261-271.

Crites, S., and M.R.T. Dale. 1998. Diversity and abundance of bryophytes, lichens, and fungi in relation to woody substrate and successional stage in aspen mixedwood boreal forests. Canadian Journal of Botany 76: 641-651.

Cumming, S.G., F.K.A. Schmiegelow, and P.J. Burton. 2000. Gap dynamics in Boreal aspen stands: is the forest older than we think? Ecological Applications 10(3): 744-759.

Dahlberg, A. and J. Stokland. 2004. Vedlevande arters krav pa substrat - sammanställning och analys av 3600 arter. Skogsstyrelsen, Report No. 7: 70 pp.

Dajoz, R. 1966. Ecologie et biologie des coléoptères xylophages de la hêtraie. [Ecology and biology of xylophagous beetles of the beechwood] Vie Milieu 17: 525-636.

DeByle, N.V. and R.P Winokur. (eds.). 1985. Aspen: ecology and management in the western United States. USDA Forest Service General Technical Report. RM-119. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, 283 pp.

DeMaynadier P.G. and M.L. Hunter. 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. Environmental Reviews 3:230–261

Esseen, P. A., B. Ehnström, L. Ericson and K. Sjöberg. 1997. Boreal forests. Ecological Bulletins 46:16–47.

Finch, D.M. and L.F. Ruggiero. 1993. Wildlife habitats and biological diversity in the Rocky Mountains and Northern Great Plains. Natural Areas Journal 12:191-203.

Franklin, J.F., H.H. Shugart and M.E. Harmon. 1987. Tree Death as an Ecological Process. BioScience 37(8): 550-556.

Gaston, K.J. 1991. Body size and probability of description: the beetle fauna of Britain. Ecological Entomology 16: 505-508.

Gibb, H., J. Hilszczajski, J. Hjältén, K. Danell, J.P. Ball, R.B. Pettersson and O. Alinvi. 2008. Responses of parasitoids to saproxylic hosts and habitat: a multi-scale study using experimental logs. Oecologia 155(1): 63-74.

Goulet, H. 1974. Biology and relationships of *Pterostichus adstrictus* Eschscholtz and *Pterostichus pensylvanicus* LeConte (Coleoptera: Carabidae). Quaestionnes Entomologicae 10: 3-33.

Griffis-Kyle, K.L. and P. Beier. 2003. Small isolated aspen stands enrich bird communities in southwestern ponderosa pine forests. Biological Conservation 110 (3): 375-385.

Grove, S.J. 2002a. Saproxylic insect ecology and the sustainable management of forests. Annual Review of Ecology and Systematics 33:1–23.

Grove, S.J. 2002b. The influence of forest management history on the integrity of the saproxylic beetle fauna in an Australian lowland tropical rainforest. Biological Conservation 104: 149–171.

Grove, S.J. and L. Forster. 2011. A decade of change in the saproxylic beetle fauna of eucalypt logs in the Warra long-term log-decay experiment, Tasmania. Division of

Forest Research and Development Technical Report 10/2011, Forestry Tasmania, Hobart, 70pp.

Hamilton, J. 1884. The survival of the fittest among certain species of *Pterostichus* as deduced from their habits. The Canadian Entomologist 16: 73-77.

Hammond, H.E.J. 1996. Arthropod biodiversity of *Populus* spp. coarse woody material in north-central Alberta. M.Sc. Thesis. University of Alberta, Canada.

Hammond, H. E. J. 1997. Arthropod biodiversity from *Populus* coarse woody material in north-central Alberta: A review of taxa and collection methods. The Canadian Entomologist 129:1009-1033.

Hammond, H. E. J., D. W. Langor and J. R. Spence. 2001. Early colonization of *Populus* wood by saproxylic beetles (Coleoptera). Canadian Journal of Forest Research 31: 1175–1183.

Hammond, H.E.J., D.W. Langor and J.R. Spence. 2004. Saproxylic beetles (Coleoptera) using *Populus* in boreal aspen stands of western Canada: spatiotemporal variation and conservation of assemblages. Canadian Journal of Forest Research 34: 1-19.

Harmon, M.E., J.F. Franklin, F.J. Swanson, P.Sollins , S.V. Gregory, J.D. Lattin, N.H. Anderson, S.P. Cline, N.G. Aumen, J.R. Sedell, G.W. Lienkaenper, K.J. Cromack and K.W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15: 133–302.

Hart, S. A. and H.Y.H. Chen. 2006. Understory vegetation dynamics of North American boreal forests. Critical Reviews in Plant Sciences 25:381–397.

Hedenas, H. and P. Hedstrom. 2007. Conservation of epiphytic lichens: Significance of remnant aspen (*Populus tremula*) trees in clear-cuts. Biological Conservation 135: 388-395.

Heilmann-Clausen, J. and M. Christensen. 2004. Does size matter? On the importance of various dead wood fractions for fungal diversity in Danish beech forests. Forest Ecology and Management 201 (2004) 105–117.

Heilmann-Clausen J., E. Aude and M. Christensen. 2005. Cryptogam communities on decaying deciduous wood—does tree species diversity matter? Biodiversity Conservation 14: 2061–2078.

Hobson, K. A. and E. Bayne. 2000a. Breeding bird communities in boreal forest of western Canada: consequences of “unmixing” the mixedwoods. Condor 102: 759–769.

Hobson, K. A., and Bayne, E. 2000b. The effects of stand age on avian communities in aspen-dominated forests of central Saskatchewan, Canada. Forest Ecology and Management 136:121–134.

Hollenbeck, J. P. and Ripple, W. J. 2007. Aspen and conifer heterogeneity effects on bird diversity in the northern Yellowstone ecosystem. Western North American Naturalist 67(1): 92-101.

Hunter, M. L., Jr. 1990. Wildlife, forests, and forestry. Principles of managing forests for biological diversity, pp. 370.

Huston M.A. 1996. Models and management implications of coarse woody debris impacts on biodiversity. In: Mcminn J.W. and D.A. Crossley. (eds.). Proceedings of the Workshop on Coarse Woody Debris in Southern Forests: Effects on Biodiversity. Asheville, USDA Forest Service: 139–143.

Jacobs, J.M., J.R. Spence and D.W. Langor. 2007. Influence of boreal forest succession and dead wood qualities on saproxylic beetles. Agricultural and Forest Entomology 9: 3–16.

Jonsell, M., K. Nitterus and K. Stighall. 2004. Saproxylic beetles in natural and man-made deciduous high stumps retained for conservation. Biological Conservation 118: 163-173.

Jonsell, M. 2007. Effects on biodiversity of forest fuel extraction, governed by processes working on a large scale. Biomass and Bioenergy 31: 726–732.

Jonsell, M. 2008. Saproxylic beetle species in logging residues: which are they and which residues do they use? Norwegian Journal of Entomology 55: 109-122.

Jonsell, M. and J. Weslien. 2003. Felled or standing retained wood- it makes a difference for saproxylic beetles. Forest Ecology and Management 175: 425-435.

Jonsell, M., J. Weslien and B. Ehnström. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodiversity and Conservation 7: 749–764.

Junninen K., M. Similä, J. Kouki and H. Kotiranta. 2006. Assemblages of wood-inhabiting fungi along the gradients of succession and naturalness in boreal pine-dominated forests in Fennoscandia. Ecography 29:75–83.

Kaila, L., Martikainen, P, and Punttila, P. 1997. Dead trees left in clear-cuts benefit saproxylic Coleoptera adapted to natural disturbances in boreal forest. Biodiversity and Conservation 6: 1-18.

Köhler, F. 2000. Totholzkafer in Naturwaldzellen des nördlichen Rheinlandes. Vergeleichende Studien zur Totholzkäferfauna Deutschlands und deutschen Naturwaldforschung [Saproxylic Beetles in Nature Forests of the Norther Rhineland. Comparative Studies on the Saproxylic Beetles of Germany and Contributions to German Nature Forest Research]. Recklinghausen: Landesamt Agrarordnung NRW. 351pp. In German.

Kruys, N., C. Fries, B.G. Jonsson, T. Lämås and G. Ståhl. 1999. Wood-inhabiting cryptogams on dead Norway spruce (*Picea abies*) trees in managed Swedish boreal forests. Canadian Journal Forest Research 29: 178–186.

Laganière, J., D. Paré and R.L. Bradley. 2009. Linking the abundance of aspen with soil faunal communities and rates of belowground processes within single stands of mixed aspen–black spruce. Applied Soil Ecology 41 (1): 19-28.

Langor, D.W., J.R. Spence, H.E.J. Hammond, J. Jacobs and T.P. Cobb. 2006. Maintaining Saproxylic Insects in Canada's Extensively Managed Boreal Forests: a Review. In: Grove, S.J. and J.L. Hanula. (eds.). 2006. Insect biodiversity and dead wood: proceedings of a symposium for the 22nd International Congress of Entomology. General Technical Report SRS-93. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 109 p.

Langor, D.W., H.E.J. Hammond, J.R. Spence, J. Jacobs and T.P. Cobb. 2008. Saproxylic insect assemblages in Canadian forests: diversity, ecology, and conservation. The Canadian Entomologist 140: 453–474.

Lee, P. C., S. Crites, M. Nietfeld, H.V. Nguyen and J.B. Stelfox. 1997. Characteristics and origins of deadwood material in aspen dominated boreal forests. Ecological Applications 7: 691-701.

Lindhe, A. and A. Lindelow. 2004. Cut high stumps of spruce, birch, aspen and oak as breeding substrates for saproxylic beetles. Forest Ecology and Management 203: 1-20.

Macdonald, S.E. and T.E. Fenniak. 2007. Understory plant communities of boreal mixedwood forests in western Canada: Natural patterns and response to variable-retention harvesting. Forest Ecology and Management 242: 34–48.

Majka, C.G. 2010. The Mycetophagidae (Coleoptera) of the Maritime Provinces of Canada. ZooKeys 64: 9-23.

Majka, C.G., C. Johnson and D.W. Langor. 2010. Contributions towards an understanding of the Atomariinae (Coleoptera, Cryptophagidae) of Atlantic Canada. ZooKeys 35: 37-63.

Majka, C.G. and D.W. Langor. 2010. Contributions towards an understanding of the Cryptophaginae (Coleoptera, Cryptophagidae) of Atlantic Canada. ZooKeys 35: 13-35.

Majka, C.G., D.W. Langor and W.H. Rücker. 2009. Latridiidae (Coleoptera) of Atlantic Canada: new records, keys to identification, new synonyms, distribution, and zoogeography. The Canadian Entomologist 141: 317-370.

Martikainen, P. 2001. Conservation of threatened saproxylic beetles: significance of retained aspen *Populus tremula* on clearcut areas. Ecological Bulletin 49:205- 218.

Martikainen P., J. Siitonen, P. Punttila, L. Kaila and J. Rauh. 2000. Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biological Conservation 94: 199–209.

Martin K. and J.M. Eadie. 1999. Nest webs: a community-wide approach to the management and conservation of cavity-nesting forest birds. Forest Ecology and Management 115: 243–257.

Mitton, J.B. and M.C. Grant. 1996. Genetic Variation and the Natural History of Quaking Aspen. BioScience 46(1): 25-31.

Nieto, A. and K.N.A. Alexander. 2010. European Red List of Saproxylic Beetles. Luxembourg: Publications Office of the European Union.

Nordén, B., M. Ryberg, F. Götmark and B. Olausson. 2003. Relative importance of coarse and fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests. Biological Conservation 117(1): 1-10.

Oaten, D. K. and K.W. Larsen. 2008a. Aspen stands as small mammal “hotspots” within dry forest ecosystems of British Columbia. Northwest Science 82(4): 276-285.

Oaten, D.K. and K.W. Larsen. 2008b. Stand characteristics of three forest types within the dry interior forests of British Columbia, Canada: Implications for biodiversity. Forest Ecology and Management 256: 114-120.

Odor P., J. Heilmann-Clausen, M. Christensen, E. Aude, K.W. Dort, A. Piltaver, I. Siller, M.T. Veerkamp, T. Standovár, A.F.M. Hees, J. Kosec, N. Matocec, H. Kraigher and T. Grebenc. 2006. Diversity of dead wood inhabiting fungi and bryophytes in semi-natural beech forests in Europe. Biological Conservation 131: 58–71.

Økland, B., A. Bakke, S. Hagvar and T. Kvamme. 1996. What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. Biodiversity and Conservation 5: 75-100.

Peterson, E.B. and N.M. Peterson. 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces. Forestry Canada, Special Report 1, Edmonton, AB.

Petty, J.L. 1977. Bionomics of two aspen bark beetles *Trypophloeus populi* and *Procryphalus mucronatus* (Coleoptera: Scolytidae). Great Basin Naturalist 37(1): 105-127.

Pinzon, J. and J.R. Spence. 2010. Bark-dwelling spider assemblages (Araneae) in the boreal forest: dominance, diversity, composition and life-histories. Journal of Insect Conservation 14: 439-458.

Reich, P.B., P. Bakken, D. Carlson, L.E. Frelich, S.K. Friedman and D.F. Grigal. 2001. Influence of logging, fire, and forest type on biodiversity and productivity in Southern Boreal forests. Ecology 82 (10): 2731-2748.

Rotheray, G., G. Hancock, S. Hewitt, D. Horsfield, I. MacGowan, D. Robertson and K. Watt. 2001. The biodiversity and conservation of saproxylic Diptera in Scotland. Journal of Insect Conservation 5: 77-85.

Sahlin, E. and L.M. Schroeder. 2010. Importance of habitat patch size for occupancy and density of aspen-associated saproxylic beetles. Biodiversity and Conservation 19: 1325–1339.

Saint-Germain, M., C.M. Buddle and P. Drapeau. 2006. Sampling saproxylic Coleoptera: scale issues and the importance of behavior. Environmental Entomology 35 (2): 478–487.

Saint-Germain, M., P. Drapeau and C.M. Buddle. 2007. Occurrence patterns of aspen-feeding wood-borers (Coleoptera: Cerambycidae) along the wood decay gradient: active selection for specific host types or neutral mechanisms? Ecological Entomology 32: 712-721.

Schmidl, J. and H. Bussler. 2004. Ecological guilds of xylobiontic beetles in Germany. Use in landscape ecological surveys - a methodological standard. Naturschutz und Landschaftsplanung 36(7): 202-218.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins 49: 11–41.

Siitonen, J. and L. Saaristo. 2000. Habitat requirements and conservation of *Pytho kolwensis*, a beetle species of old-growth boreal forest. Biological Conservation 94: 211-220.

Simonson, S.E., P.A. Opler, T.J. Stohlgren and G.W. Chong. 2001. Rapid assessment of butterfly diversity in a montane landscape. Biodiversity and Conservation 10: 1369–1386.

Skubala, P. and M. Duras. 2008. Do decaying logs represent habitat islands? Orbatid mite communities in dead wood. Annales Zoologici (Warszawa) 58(2): 454-466.

Speight, M.C.D. 1989. Saproxylic invertebrates and their conservation. Nature and Environment Series 42 Council of Europe. Strasbourg, France. 81 pp.

Spence, J.R., D.W. Langor, J.M. Jacobs, T.T. Work and W.J.A. Volney. 2008. Conservation of forest-dwelling arthropod species: simultaneous management of many small and heterogeneous risks. The Canadian Entomologist 140(4): 510-525.

Söderström, L. 1988. Sequence of bryophytes and lichens in relation to substrate variables of decaying coniferous wood in northern Sweden. Nordic Journal of Botany 8: 89–97.

Stelfox, J.B. (ed.). 1995. Relationship Between Stand Age, Stand Structure, and Biodiversity in Aspen Mixedwood Forests in Alberta. Jointly published by Alberta Environmental Centre (AECV95-R1), Vegreville, Alberta, and Canadian Forest Service (Project No. 0001A), Edmonton, Alberta, 308 pp.

Stevens, V. 1997. The ecological role of coarse woody debris: an overview of the ecological importance of CWD in B.C. forests. Research Branch, British Columbia Ministry of Forests, Victoria, B.C. Working Paper. 30.

Stokland, J.N., J. Siitonen and B.G. Jonsson. 2012. Biodiversity in Dead Wood. Cambridge University Press, Cambridge, New York, xiv, 509pp.

Sullivan T.P. and D.S. Sullivan. 2001. Influence of variable retention harvest on forest ecosystems. II Diversity and population dynamics of small mammals. Journal of Applied Ecology 38: 1234–1252

Sverdrup-Thygeson, A. and R.A. Ims. 2002. The effect of forest clearcutting in Norway on the community of saproxylic beetles on aspen. Biological Conservation 106: 347-357.

Thomas, S.L., R.G. Wagner and W.A. Halteman. 2009. Influence of harvest gaps and coarse woody material on click beetles (Coleoptera: Elateridae) in Maine's Acadian forest. Biodiversity and Conservation 18: 2405-2419.

Tikkanen, O.-P., P. Martikainen, E. Hyvarinen, K. Junninen and J. Kouki. 2006. Red-listed boreal forest species of Finland: associations with forest structure, tree species, and decaying wood. Annales Zoologici Fennici 43: 373-383.

Ulikzka H. and P. Angelstam. 2000. Assessing conservation values of forest stands based on specialised lichens and birds. Biological Conservation 95: 343–351

Webb, A., C.M. Buddle, P. Drapeau and M. Saint-Germain. 2008. Use of remnant boreal forest habitats by saproxylic beetle assemblages in even-aged managed landscapes. Biological Conservation 141: 815-826.

Work, T.T., D.P. Shorthouse, J.R. Spence, W.J.A. Volney and D.W. Langor. 2004. Stand composition and structure of the boreal mixedwood and epigaeic arthropods of the Ecosystem Management Emulating Natural Disturbance (EMEND) landbase in northwestern Alberta. Canadian Journal of Forest Research 34: 417-430.

Yee, M., S.J. Grove, A.M.M. Richardson and C.L. Mohammed. 2006. Brown rot in inner heartwood: Why large logs support characteristic saproxylic beetle assemblages of conservation concern. In Grove, S.J. and J.L. Hanula. (eds.) 2006. Insect biodiversity and deadwood: proceedings of a symposium for the 22nd International Congress of Entomology. General Technical Report. SRS-93. Asheville, NC: US Department of Agriculture Forest Service, Southern Research Station. 109 p.

2. A COMPARISON OF COLLECTION METHODS FOR MEASUREMENT OF SAPROXYLIC BEETLE SPECIES RICHNESS AND ASSEMBLAGE COMPOSITION

2.1. Introduction

Saproxylic insects (i.e., insects associated with dead and dying wood) and deadwood habitats are recognized as critical components of forest ecosystems, and therefore many programs to assess deadwood qualities and dynamics and associated saproxylic insect biodiversity have been implemented in forests around the world (see reviews by Siitonen 2001, Grove 2002a, and Langor et al. 2008 and references therein). Saproxylic insect communities are taxonomically rich, and many species are sensitive to forest management (Siitonen 2001; Grove 2002b; Similä et al. 2002; Langor et al. 2008). In Europe, where knowledge of saproxylic insect faunas, especially beetles, is well developed, nearly 11% of all saproxylic beetles are listed as threatened, with an additional 13% of species listed as “Near Threatened” (Nieto and Alexander 2010). Elsewhere, knowledge of the saproxylic insect fauna is too limited to support equivalent assessments. Nonetheless, saproxylic Coleoptera are an ideal target group for examinations of the effects of forest management on forest biodiversity. Saproxylic beetles are among the most taxonomically diverse and abundant forest organisms, fill a multitude of trophic roles under a wide array of ecological conditions, and are taxonomically better known than other groups of saproxylic insects.

Comprehensive surveys of saproxylic beetles can be difficult to achieve as many species are small, cryptic, and highly microhabitat-specific. A variety of sampling techniques have been employed globally to assess saproxylic beetle assemblages. Emergence traps enclose deadwood *in situ* (Bashford et al. 2001; Økland 1996; Lindhe and Lindelow 2004; Owen 1989) or cut pieces of dead wood *ex situ* (Grove 2000; Wikars 2002; Wikars et al. 2005), and can potentially sample all insects emerging from the enclosed wood microhabitats. Likewise, placement of pieces of deadwood in rearing cages removed from the site of collection, samples the enclosed substrate and yields rich samples, easily associated with particular wood qualities (Hammond et al. 2001; Hammond 1997; Hammond et al. 2004). Although time consuming, collecting beetles by hand through careful dissection of portions of deadwood has been used effectively in European studies (Wikars et al. 2005; Martikainen and Kouki 2003; Vaisanen et al. 1993; Siitonen 1994; Ranius and Jansson 2002) and can be used to generate valuable natural history information, including microhabitat associations. Window (flight-intercept) traps are highly efficient for collecting flight-active saproxylic beetles and can be applied to a variety of substrates, particularly to the trunks of dead trees or hung freely in forest stands (Grove 2002a, Økland 1996; Ranius and Jansson 2002; Martikainen et al. 2000; Hammond 1997; Kaila 1993; Jonsell and Nordlander 1995); However, the association of captured insects with particular deadwood qualities is highly uncertain.

Most studies in North America that have aimed to sample the saproxylic beetle community have exclusively used window-style flight-intercept traps (Jacobs et al. 2007a, b; Hammond et al. 2001; Saint-Germain et al. 2004) or flight-intercept traps in combination with one other collection method such as emergence traps (Webb et al. 2008) and rearing cages (Hammond et al. 2004; Hammond 1997). Although WTs are suggested for saproxylic inventories (Ranius and Jansson 2002), such heavy reliance on largely one type of sampling method may result in incomplete sampling of saproxylic beetle assemblages.

No single collection method provides complete and unbiased samples (Ranius and Jansson 2002), as methods vary considerably in performance, giving rise to functionally distinct samples (Siitonen 1994; Hammond 1997; Hyvarinen et al. 2006). Differences in sample composition originating from different collection techniques reflect species-level likelihoods of being caught by a particular method (Heathcote 1957, Niemelä et al. 1986, Weston and Barney 1998). Although window traps can be used to quickly and easily capture large numbers of individuals and a high diversity of insect species, they are commonly criticized because the catch cannot be associated with certainty with the deadwood to which the trap is attached (Wikars et al. 2005; Saint-Germain et al. 2006; Alinvi et al. 2007). Nonetheless, some studies have employed substrate-attached window traps for relating assemblages to deadwood conditions, and clear logical patterns can usually be detected, despite the sampling ‘noise’ (Økland

1996; Jacobs et al. 2007a; Hammond et al. 2004). Nonetheless, explicit understanding of the efficiency and biases of various collection methods is essential to optimize sampling programs and accurately interpret results from surveys.

Using boreal saproxylic beetles as the focal group, the objectives of this chapter are to examine six commonly employed collection methods in terms of: i) accumulation of species, ii) catch bias, and iii) data gained about assemblage structure. Overall, I evaluate the performance of these collection methods with respect to these results and ease of method setup.

2.2. Methods

2.2.1. Study Area

This study area was located near the Ecosystem Management Emulating Natural Disturbance (EMEND) experimental site in northwest Alberta, Canada (Figure 2.1). The sites were located in the Clear Hills Upland, Lower Foothills Ecoregion in the Boreal Mixedwood Ecological Area (Beckingham and Archibald 1996) of Alberta, approximately 80 km northwest of Peace River. Soils in the area are primarily Luvisolic, well drained and of fine-textured glacial till or glaciolacustrine parent origin (Beckingham and Archibald 1996; Kishchuk 2004). Elevation ranged from 741 to 874 m above sea level.

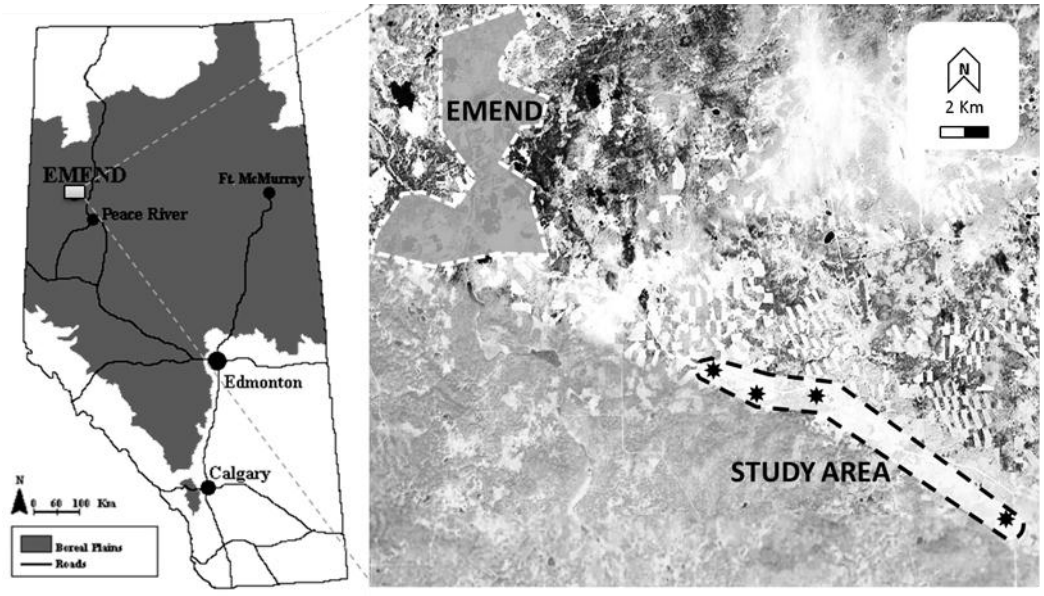

Figure 2.1 Location of the study area (shaded white with black dashed lines) and study sites (black, 8-pointed stars) in relation to the Ecosystem Management Emulating Natural Disturbance (EMEND) experimental site and position in the province of Alberta (displayed by the inset rectangle), within the Boreal Plains ecozone (grey). The surrounding landscape has a history of forest management (as shown by the patches of cut areas), yet all samples were collected from never-harvested, mature aspen stands. Site numbers were based on the distance markers along the DMI P200 logging road. The satellite image was modified from Google Earth (© 2011 Google and third-party suppliers: US Dept of State Geographer, © 2011 TerraMetrics, © 2011 DigitalGlobe, © 2011 Cnes/Spot Image, © 2011 Europa Technologies, © 2011 MapLink/Tele Atlas). The map of Alberta was provided courtesy of EMEND.

I selected four mature, unmanaged stands in a 16.28 km^2 area (site centre: 56°40’39.30" N, 118°06’30.02" W), within a landscape first subjected to commercial harvest over the previous two decades (Figure 2.1). Stand overstory tree composition was dominated by trembling aspen (*Populus tremuloides* Michaux; 85.4%) with minor additions of balsam poplar (*P. balsamifera* Linnaeus; 12.3%), white birch (*Betula papyrifera* Marshall; 1.8%) and white spruce (*Picea glauca* [Moench] Voss; 0.5%). The

understory vegetation cover was mainly (>70%) comprised of prickly rose (*Rosa acicularis* Lindley), low-bush cranberry (*Viburnum edule* [Michaux] Rafinesque), wild sarsaparilla (*Aralia nudicaulis* Linnaeus) and fireweed (*Chamerion angustifolium* [Linnaeus] Holub). Sites were selected based on visual assessments that verified a high density and heterogeneity of deadwood; i.e., they contained both standing and fallen deadwood of various decay states and diameters. Sites were situated adjacent to a logging road to ensure ease of access; however, deadwood samples were taken no closer than 30 m from the nearest road.

2.2.2. Substrate Variables

Deadwood was classified into two substrate types (snags, logs) and six substrate decay classes (1-6), according to position, physical structure, and visual characteristics (Table 2.1). Only deadwood ≥ 7 cm in diameter was sampled. Diameter of trees and snags was measured at breast height (1.3 m), and diameter of logs was measured at the sample center. Surface area and volume were calculated for each sample (except those from window traps) by assuming cylindrical shape. Thus, outer surface area (*SA*), excluding the cut ends of samples, was calculated as $SA = 2 \pi r h$, where r is equal to half of the substrate diameter, and h is the length of the sampled section. Volume (*Vol*) was calculated as $Vol = \pi r^2 h$, where and r and h are defined as above.

2.2.3. Collection Methods

Saproxylic beetles were sampled during summer 2008, using six different collection methods (Figure 2.2a-f). These included two indirect sampling methods [trunk window traps (TWTs), and free-hanging window traps (FWTs)] and four direct habitat sampling methods [hand collections (HCs), funnel extractions (FEs), rearing drums (RDs), and emergence traps (ETs)]. To control for possible vertical stratification of saproxylic beetle assemblages, collections from snags using ET, TWT, and FWT were limited to 1.3-2.3 m above ground level.

Free-Hanging and Trunk Window Traps: Window traps (Kaila 1993; Hammond 1997) were made of a clear plastic pane (1.5 mm x 20 cm x 30 cm) with a cloth funnel underneath attached to a collection jar. One TWT (Figure 2.2e) was placed at breast height on each of 48 snags, representing twelve replicates of each of the four snag decay classes (DC 1-4). TWTs were employed in sites 215 (12 replicates), 219 (24 replicates), and 221 (12 replicates) (refer to Figure 2.1). A total of twelve FWTs (Figure 2.2f) were hung at breast height between two trees at a minimum distance of 2 m from any live or dead stems (three replicates in each of the four stands: 205, 215, 219, 221). Each collection jar for both trap types contained ~30 mL of propylene glycol. Samples were collected and traps were refreshed approximately every 14 days, with beetles subsequently transferred into 70% ethanol for preservation. Traps were run May through August, for an average of 89 and 80 days for TWTs and FWTs, respectively.

Table 2.1 Criteria used to classify live trees, and deadwood (snags and logs) into decay classes (DC). Each criterion was evaluated independently, and the best-fit classification based on the majority of criteria was assigned. Decay characteristics were modified from previously used decay classification schemes (Crites and Dale 1998, McCullough 1948) to better suit the natural range of variation in aspen characteristics observed in the field.

Type	DC	Position	Stability	Wood Texture	Shape	Bark	Branches	Twigs	Stem Condition	Leaves	Plants
Live Tree	0	upright, 90°	very stable	whole, sound, hard wood	round	100%, intact, live, tight	all present, intact	all present, intact	whole, healthy	green leaves present	none (moss in low cover)
Snag	1	≥45°	stable	sound, hard wood	″	100% , intact, no peeling of the outer bark	all present	many fine twigs intact	whole, top present	may be present and brown	″
	2	″	somewhat unstable	″	″	>70%, few vertical cracks, minimal outer bark peeling	many present	few fine twigs	whole, top present	none	″
	3	″	unstable	some soft wood, may be small crevices or pieces lost	round to oval	>50%, loose, vertical cracks and outer bark peeling	may be some	none	broken	″	″
	4	″	very unstable	soft wood, large crevices and fragments lost	round to oval	<50%, very loose, quite fragmented	none	″	″	″	″
Log	1	<45°, elevated on support points	fallen	whole, hard	round	100%, intact, fresh, tight	present, intact	present, intact	″	may be present and brown	″
	2	elevated	″	sound, hard wood	″	>70%, not fresh, mod. tight to loose, outer bark peeling	present	mostly lacking	″	none	″
	3	on ground	″	some soft wood	round	<70%, loose, bark cracked & peeling	some remaining	none	″	″	″
	4	″	″	soft w/ small crevices & pieces lost	round to oval	little to none	none (maybe stubs)	″	″	″	
	5	may be slightly sunken	″	large fragments lost	deformed outline of trunk	none	none	″	″	″	vascular plant colonization
	6	sunken in soil	″	mostly well decayed	flattened or deformed	″	″	″	″	″	moss covered; herbs, shrubs, trees

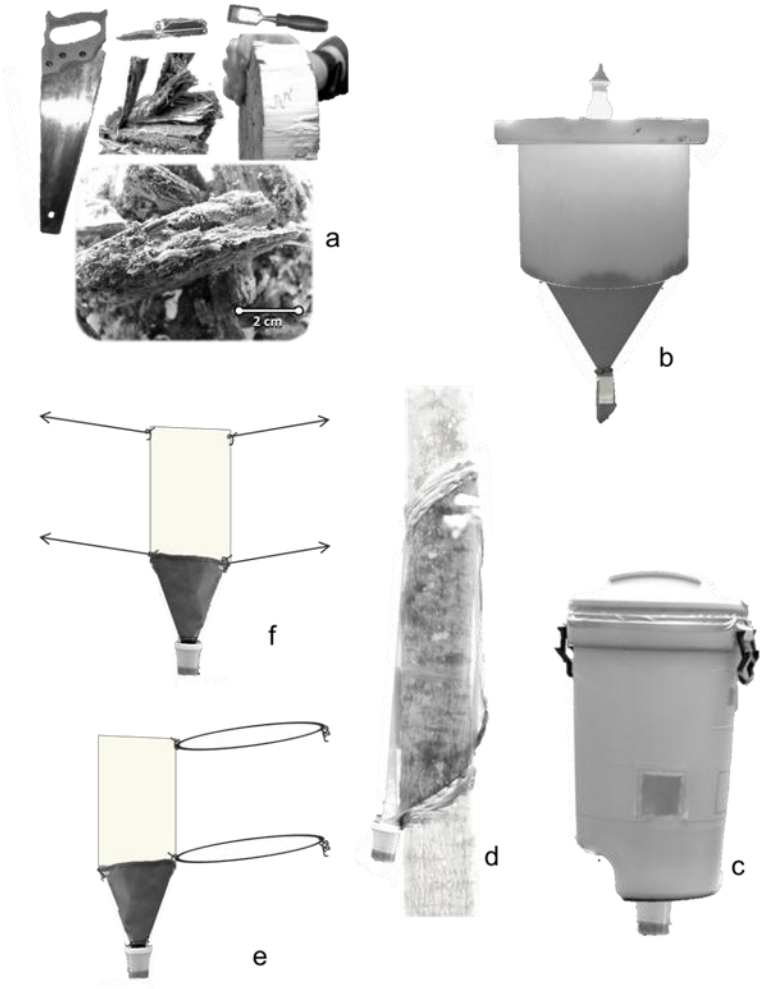

Figure 2.2 Collection methods used to sample saproxylic beetles: a) dissection of logs**,** that involved reducing sections of logs to small fragments and hand-collecting (HC) beetles; b) modified Tullgren funnel extractors (FE), that extracted beetles from wood fragments left over from dissection of logs; c) rearing drums (RD), that allowed beetles to emerge from enclosed wood samples, at ambient outdoor temperature during the course of the study period; d) emergence traps (ET), that covered portions of snag trunks, *in situ*, and collected emerging beetles; e) trunk window traps (TWT), that attached to tree trunks with wire and consisted of clear plastic panes fitted above collection funnels, to catch flying beetles; and f) free window traps (FWT), that were free- hanging and suspended between two trees, to catch flying beetles; Photo c) was provided courtesy of J. Edwards.

Emergence Traps: Emergence traps (ETs; Figure 2.2d) enclosed a 1m section of snags, and were positioned at 1.3 to 2.3m above ground. Grey nylon 'no-see-um' netting (mesh size= 0.6 mm x 0.6mm) was cut in a chevron shape to enclose the sample area. The top and bottom of edges of each trap were underlaid with a strip of foam that, when compressed by the pressure of duct tape wrapped around the edges of the mesh, forced the foam to fill the underlying crevices in the bark, thereby creating a tight seal. The duct tape applied tightly around the circumference of the trap at its top and bottom edges was reinforced by 14 mm staples driven through into the snag to prevent the trap from slipping. The longitudinal edges of the mesh were folded together and stapled, forming a tight seam. A 100 mL plastic jar was attached 10 cm from the mesh edge at the lowest point of the trap, in such a way that the cup sat upright when fitted in place. Each collection jar contained ~30mL of propylene glycol. Samples were collected and preservative refreshed approximately every 14 days, with beetles subsequently transferred into 70% ethanol for storage. A total of 48 ETs were employed, each on one snag of the four snag DCs (DC 1-4), relating to twelve samples of each snag DC. TWTs were employed in sites 215 (12 replicates), 219 (24 replicates), and 221 (12 replicates). Samples varied in diameter from 16.3 cm to 32.7 cm, and averaged 22.3 cm. ETs were run from May through August, for an average of 96 days. The initial study design consisted of ETs employed on both snag and log substrates,

however, log ETs had to be excluded from the analysis, because of a high rate of animal disturbance, which compromised their reliability.

Rearing Drums: A total of 33 samples were reared, each in a separate drum, representing 3 replicates of live trees ('DC 0'), 3 replicates of each of the four snag DCs (DC1-4), and 3 replicates of each of the six log DCs (DC 1-6). Deadwood samples were selected from three of the study sites: 205, 215, and 221, resulting in 11 samples taken from each stand (refer to figure 2.1). Live trees and snags were felled prior to cutting 70 cm long sections of each substrate for RDs. These sections were cut from the portion of the bole at 1.3 to 2 m above ground in order to consistently collect from the same height as sampled by the ETs. Sample diameter ranged from 16 cm to 25.5 cm, with an average diameter of 20.6 cm. Rearing drums (Figure 2.2c) were constructed from 121L Rubbermaid^{TM} garbage bins with a hole drilled through the bottom to allow for collection of beetles in an affixed wide-mouth (9 cm x 9 cm x 12 cm; 760 mL) canning jar. The wood sample was placed on coarse (15 mm x 15 mm) wire-mesh held above the bottom of the drum to prevent the collection device from being blocked. Ventilation holes, 10 cm x 10 cm, were cut on opposing sides of the drum and sealed with fine (~0.8 mm x 0.8 mm) mesh affixed with caulking adhesive. The lid of each drum was fitted with a band of foam and wrapped with duct tape to achieve a tight seal. Rearing drums were set on low plywood tables and kept outdoors in

a forest stand near the EMEND camp for the duration sample collection from May through August (an average of 88 collection days). Beetles were removed from jars every 14 days and transferred into 70% ethanol for storage.

Hand Collections and Funnel Extraction: A total of 70 log samples, each 50 cm long, were subjected to HC from June through August. This included the following replicates of each log DC: ten of DC 1, 14 of DC 2, twelve of DC 3, eleven of DC 4, twelve of DC 5, and eleven of DC 6. Deadwood samples were selected across all study sites (205, 215, 219, and 221), albeit unevenly replicated in each stand. Samples varied in diameter from 8.8 cm to 43 cm, and averaged 23.4 cm. Each sample log section was cut to length and placed on a white tarpaulin for dissection. Dissection and searching for beetle specimens was systematic, progressing from outermost layers of potential habitat (fungi, mosses, bark) to the inner heartwood of the log. Samples were dissected by cutting or breaking them into fine pieces using saws, axes, hatchets, chisels, knives, and fingers (Figure 2.2a). Hand collection time varied from approximately 1 to 4 hours, with an average of 2.7 hours per sample. Beetles that were encountered were immediately preserved in 70% ethanol. In initial HCs, larvae were collected in an attempt to rear them to adults, yet only eleven larvae and two pupae were successfully reared. An addition 149 larvae were thus, not included in the HC dataset.

Subsequent to HC, the dissected wood fragments from 61 of the 70 log samples were placed in modified Tullgren funnel extractors (FE; Figure 2.2b) made from plastic. Each log sample was extracted separately in individual funnels. The cylindrical sample portion of the device (40.6 cm height x 47 cm diameter) was fitted onto the bottom with coarse (2cm x 2cm), metal hardware cloth to hold wood samples above the funnel (29 cm height), whilst allowing passage of beetles downward. The spout (2.5 cm height x 4.6 cm diameter) at the funnel base was fitted with a Whirl-Pak™ bag containing ~50 mL of propylene glycol for killing and preserving beetles. Each FE was sealed on top with a tight lid that consisted of a plastic rim and an open center covered with 2 mm x 2 mm metal mesh. A 100-watt light bulb was suspended above each funnel, about 1-2 cm above the lid, and shone continuously throughout the extraction period. Samples were extracted for an average of 9.9 days, and the captured beetles were transferred into 70% ethanol for storage.

2.3. Analyses

2.3.1. Beetle Determination and Classification

All beetles were identified to species, or to the lowest taxonomic level possible using (and cross-referencing) relevant keys (e.g., Arnett and Thomas 2000; Arnett et al. 2002; Downie and Arnett 1996; Hatch 1962; Lindroth 1961-1969a, b; 1969b; Majka et al. 2009; Smetana 1990).

Specimens that could not be confidently placed to species were excluded from richness and community analyses.

Species were classified into 13 feeding guilds and three categories of saproxylic association (obligate, facultative, and non-saproxylic; Appendix 2-A), based on available literature about larval and adult life histories (e.g., Arnett and Thomas 2000; Arnett et al. 2002; Betz et al 2003; Bousquet 1991; Hammond 1997; Stehr 1991; Wheeler and Blackwell 1984; Wilding et al. 1989). Where information was not available at the species level, I classified the species based on information available at the next closest taxonomic level (e.g., genus).

Feeding guilds were categorised as follows:

- 'phloeophagous' species included beetles that consume phloem tissue (excluding ambrosia beetles)
- 'xylophagous' species included beetles feeding deeper in woody stems, specializing on xylem tissue
- 'mycophagous' species included general fungivores, feeding on macro- and micro-fungi
- ambrosia beetles were isolated from mycophages and phloeophages as a separate group 'ambrosia-feeders', as they are known to be functionally distinct (Gibb et al. 2006)

- slime-mold feeding beetles respond quite distinctly from mycophagous beetles (Siitonen 1994), and thus were placed in a separate group of ‘myxomycetophagous’ beetles
- ‘zoophagous’ species were predators of other live invertebrates
- ‘coprophagous’ species were those known to feed/breed in dung
- ‘detritovorous’ species feed on dead insects and other detritus
- ‘herbivorous’ species feed on live plant tissue, including leaves and non-woody stems
- ‘necrophagous’ species were those known to consume dead mammals
- pollen-feeding species were designated as ‘palynivorous’
- ‘rhizophagous’ species were herbivores specializing on roots of vascular plants
- species that were known to consume a wide range of materials, or unknown feeding habits, were categorized as ‘omnivorous’.

Species were each classified into one of three categories of saproxylic association. ‘Obligately saproxylic’ (Sx^{++}) species are considered to breed/feed only in deadwood or wood-decay fungi, while ‘facultatively saproxylic’ (Sx^{+}) species are known to use habitats other than deadwood or wood-decay fungi. ‘Non-saproxylic’ (Sx^{-}) species are not known to require deadwood or wood-decay fungi at any point in their lifecycle.

2.3.2. Data Manipulation and Analyses

For analyses, replicate samples from each collection method were pooled within DC at each site, resulting in the following sample set, in each collection method group: 4 FWT, 12 TWT, 12 ET, 33 RD, 19 HC, and 22 FE, not including one TWT and one ET that fell about 4 weeks after the start of the study and were not replaced.

Species Richness: To estimate species richness for each collection method, I calculated the number of species expected (with 95% confidence intervals), using a sample-based rarefaction approach. This accounts for sample heterogeneity and avoids overestimates of species richness (Gotelli and Colwell 2001). I chose the incidence-based binomial mixing (Mao-Tau method of moments) approach (Colwell et al. 2004; Mao et al. 2005) as an alternative to resampling to allow for direct statistical comparison of richness among sample sets. The sample axis was rescaled based on average numbers of individuals per sample, as suggested by Gotelli and Colwell (2001) for cases where individual density varies by sample. I compared richness per sample, individuals, sample days, and sample volume. Rarefactions were calculated using all beetle species collected, though patterns were similar when only saproxylic beetles were included. Since FE extractions occurred on wood samples that were previously sampled by HC, I include the combined richness

estimates (“HC+FE”) in comparisons. All rarefactions were performed in EstimateS 8.2 (Colwell 2009).

Assemblage Structure: Multivariate Regression Tree (MRT) analysis (De'Ath 2002) was used to predict which aspects of the collection variables (collection method, substrate decay, substrate type, volume sampled, sampling time, and surface area sampled) were most important in determining saproxylic beetle assemblages. MRT analyses were performed for all collection methods together, with abundances standardized as presence/absence data, using R (R Development Core Team 2009) with the MVPART package (De’Ath 2010) and using the Sorensen distance measure. Using the same model, I performed a Redundancy Analysis (RDA) to assess variation in saproxylic beetle assemblages (excluded Sx^- beetles) in response to various collection variables. I assessed the effect of constraints in the RDA with a permutation test and Type III marginal effects of terms for each factor as appropriate for unbalanced data structures (Legendre and Legendre 1998).

I used Permutational Multivariate Analysis of Variance (Anderson 2001; McArdle and Anderson 2001) to test for differences in composition of saproxylic assemblages of FWTs and TWTs. As PerMANOVA is sensitive to differences in dispersion, I tested the homogeneity of

multivariate dispersions within groups using PERMDISP (Anderson 2006; Anderson et al 2006). Analyses and *post hoc* multiple comparison tests were performed in PERMANOVA version 6.0 (Anderson 2005) and PERMDISP v.2 (Anderson 2006), using Bray-Curtis distance, 3 replicates on each level of substrate (no substrate and Snags DC 1-4), 499 permutations, and excluding non-saproxylic beetles.

Species Associations: I performed two Indicator Species Analyses (ISA) (Dufrêne and Legendre 1997). Firstly, to determine species-selectivity biases for particular collection characteristics, I performed an ISA with saproxylic beetles (excluded Sx^- beetles) grouped according to collection method. As suggested by De Cáceres et al. (2010), I improved upon the standard ISA by considering all possible combinations of groups of collection methods and selecting the combination (or single method) indicated best by particular species. This is a useful practice as species differ in niche breadth, and thus some species may more usefully indicate a combination of conditions, rather than individual conditions (De Caceres et al. 2010).

Secondly, to assess variation in beetle assemblages from each collection method, I performed an ISA on saproxylic beetles with samples grouped according to nodes of the MRT (Figure 2.5). For both ISAs, a species was considered an indicator for a given variable when its indicator

value (IndVal) differed significantly from random (α = 0.05) after a Monte Carlo test based on 2000 and 5000 permutations (for ISA I and ISA II, respectively). I used an IndVal of greater or equal to 25%, as suggested by Dufrêne and Legendre (1997) to designate “useful” indicator species and an IndVal of greater or equal to 60% to designate “strong” indicator species. Species that were strong indicators for a particular collection method were considered as having a collection bias (ISA I). All ISAs were performed using presence-absence transformed species data in PC-ORD version 5.10 (McCune and Mefford 2006).

Collection Method Performance: I compared overall performance of collection methods in terms of their ranks for the following seven variables: adult catch, saproxylic catch, unique saproxylic catch, species accumulation, number of saproxylic feeding guilds, substrate specificity, and ease of setup (summarized in Table 2.4). I then constructed star (radar) plots (Chambers et al. 1983) in Excel 2010 to depict performance (see Figure 2.6). Star plots have been used in a number of disciplines (e.g., business management, chemistry, toxicology, geology, engineering, and medicine) to compare multivariate observations (Agematsu et al. 1993, Halpern 1996, Tughu et al. 2003, Weaver 2000, Saary 2008, Yamaguchi et al. 1998, Kosaka et al. 1995). Each plot consists of a series of rays projecting from a central point, with each ray representing a variable of interest. Ray length is proportional to response for each

variable. Observed values for each variable are connected between rays, forming an enclosed “star” polygon. Area of each polygon was calculated using basic geometry, and used to compare overall rank performance (units of area are a product of all radii units, including ranks).

2.4. Results

Among the total sample of >8000 beetles, 3160 specimens could not be identified to species, including 985 unidentified adults and 2175 immature beetles. Most of the unknown adult beetles belonged to the families Ptiliidae, Staphylinidae (Aleocharinae), and Latridiidae (female Corticariinae). Overall, 5519 beetles were identified, representing 286 species and 50 families. Of these, 33 species (657 specimens) were considered to be not saproxylic (Sx^{-}) and were removed from analyses of saproxylic beetles. The frequency distribution of taxa was highly skewed, with many rare species (88 singletons and 43 doubletons). The most speciose families included Staphylinidae (56 spp., excluding Aleocharinae), Latridiidae (26 spp.), Cryptophagidae (23 spp.), Leiodidae (20 spp.), Carabidae (18 spp.), Elateridae (18 spp.), Curculionidae (17 spp.), and Nitidulidae (17 spp.). The most abundant species collected across all collection methods were: the staphylinid, *Eusphalerum pothos* Mannerheim, (368 individuals); a novel species of monotomid, *Rhizophagus* n.sp. 1, (347 individuals; near *R. pseudobrunneus* Bousquet,

identity confirmed by Y. Bousquet); two latridiid species, *Cortinicara gibbosa* Herbst, (334 individuals), and *Melanophthalma pumila* (LeConte), (278 individuals); a nitidulid, *Epuraea flavomaculata* Mäklin, (242 individuals); and the curculionid ambrosia beetle, *Trypodendron retusum* (LeConte), (229 individuals).

2.4.1. Species Richness

Expected species richness varied greatly according to collection method employed. TWT and HC samples generated the greatest richness according to individual-based rarefactions (Figure 2.3a). Window trap samples (TWT & FWT) yielded the greatest species richness according to sample-based rarefactions (Figure 2.3b). Of the methods sampling a discrete volume of wood, the combination of HC+FE generated the greatest species richness per unit volume, but these estimates did not differ significantly from those based on log RD (Figure 2.3c). According to rarefactions based on sampling time, HC generated the greatest species richness, followed by HC+FE, and RD, and ET had the lowest richness (Figure 2.3d).

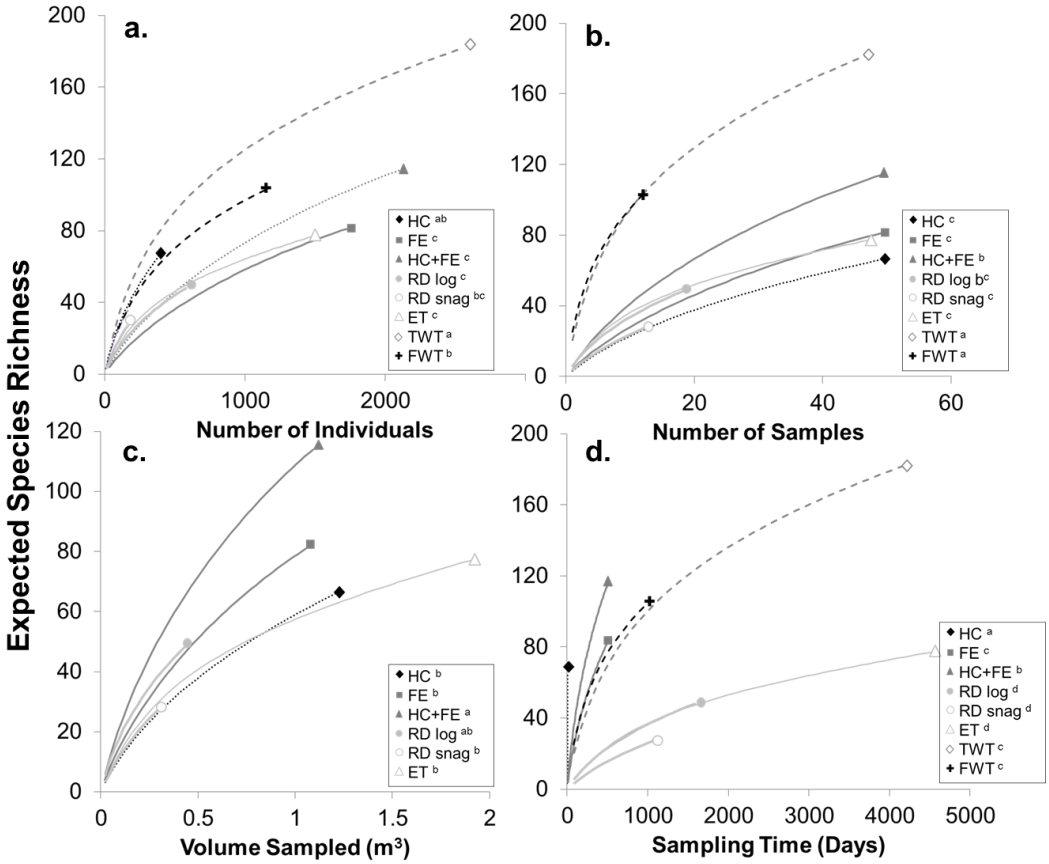

Figure 2.3 Accumulation of saproxylic beetle species with increasing (a) numbers of individuals, (b) deadwood samples, (c) sampled deadwood volume, and (d) sampling time, as given by Mao-Tao interpolations of species density. Significant differences between groups (according to 95% confidence intervals) are provided as superscripts in each legend. Collection methods employed on logs (filled markers) were abbreviated as follows: HC= hand-collection, FE= funnel extraction, HC+FE= pooled sample from HC and FE, and RD log= rearing drum. Collection methods employed on snags (hollow markers) were abbreviated as RD snag= rearing drum, ET= emergence trap, and TWT= trunk window trap. Free hanging window traps (cross marker) were not applied to any deadwood substrates, and were abbreviated as FWT.

2.4.2. Assemblage Structure

Species composition of saproxylic assemblages differed significantly between samples in the overall RDA (Table 2.2, Figure 2.4, *P* = 0.005), with collection method (*P* = 0.005), decay class (*P* = 0.005), substrate type (*P* = 0.0225), and mean number of sampling days (*P* = 0.02875) as significant effects (Table 2.2). Interestingly, neither mean surface area nor mean volume sampled had significant effects (*P* > 0.05).

Table 2.2 Permutation test for RDA under the same model as used in MRT analyses (ModelRDA= presence/absence of saproxlyic beetles ~ Method + Decay Class + Substrate Type + Mean Sampling Time + Mean Surface Area of Sample + Mean Volume of Sample), providing the type III marginal effects of each collection variable on saproxylic beetle assemblages, number of permutations used (n perm), and p-values for tests.

	df	*var*	*F*	*n perm*	*p-value*
Model $_{RDA}$	13	2.28	2.68	199	0.005 **
RDA Axis 1	1	0.77	11.97	199	0.005**
RDA Axis 2	1	0.33	5.16	199	0.005**
Method	3	0.65	2.53	199	0.005 **
Decay Class	6	0.65	1.67	199	0.005 **
Substrate Type	1	0.09	1.42	399	0.023 *
Sampling Time	1	0.10	1.55	799	0.029*
Surface Area	1	0.07	1.13	99	0.26
Volume	1	0.09	1.32	199	0.105
Residual	72	4.71			

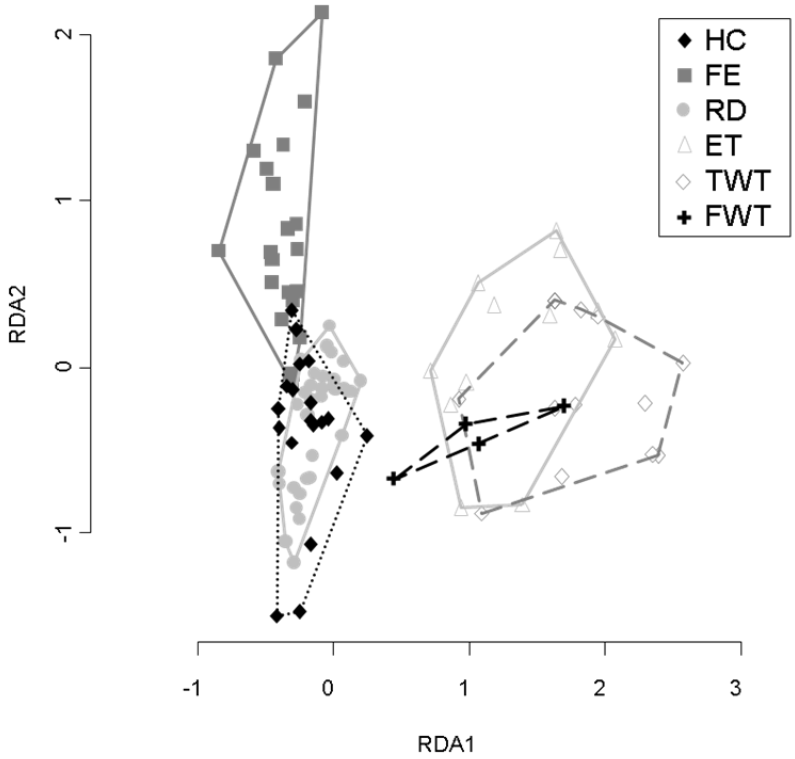

Figure 2.4 Relationship between structure of saproxylic beetle (i.e., Sx++, Sx+ species) assemblages and collection method, as resolved by redundancy analysis ordination (RDA). Polygons enclose all sample points for each collection method (HC= hand-collection, FE= funnel extraction, RD= rearing drum, ET= emergence trap, TWT= trunk window trap, FWT= free-hanging window trap). Axis 1 and axis 2 explained 10.9% and 4.7% of the total variance, respectively.

The most consistent MRT (Figure 2.5) had 13 terminal nodes and identified 24 groups, explaining 57.1% of the variance in the pooled saproxylic beetle catch (1 – Error x 100) with 36.3% predictability (1 – CV Error x 100). Collection method had the largest effect on saproxylic beetle assemblages, explaining the first 3 splits of the MRT (i.e., 61.8% of the explained variance; 35.3% of total variance). All collection method groups

in the MRT diverged into individual components relating to substrate qualities and collection variables, except for window trap methods. The samples from TWT and FWT shared one terminal group (Group III), and are thus, compositionally similar.

Decay Class was the next most important explanatory variable for structuring saproxylic beetle assemblages (Figure 2.5). ET samples (Group IV) were further split into different assemblages based on early (DC 1-2) and late (DC 3-4) decay classes. Likewise, decay class also explained the differences in RD (Group IX) and FE (Group VI) assemblages. FE produced two splits with early to moderately decayed logs (DC 1-4) forming Group XI and late decayed logs (DC 5 -6) forming Group X. RD split based on early decay (live trees, snags DC1-2, logs DC1-3) and late decay (snags DC 3,4 and logs DC4-6) deadwood, forming groups XIII and XIV.

Assemblages were also influenced by collection parameters that researchers can easily control. For instance, the HC (Group X) and FE (VI) methods appear to be influenced by mean sample volume (Figure 2.5). Also, sampling time explained differences within Group XI; assemblages from FE extracted for >10.1 days were distinct from FE extracted for <10.1 days. Thus, protocols using these methods should

ensure that an adequate volume, and surface area of wood is sampled, for a sufficient amount of time (>10.1 day).

No significant differences between assemblages collected in FWTs and TWTs were detected (PERMANOVA: $F= 1.31$, $df= 2$, $p= 0.07$), with all pair-wise comparisons between WT catches on different snag DCs also insignificant (Uncorrected $p\geq 0.1$; $\alpha= 0.05$), thus TWT samples were not sensitive to particular substrate qualities. Multivariate dispersions were not significantly different between TWT and FWT groups (PERMDISP: $F= 2.20$, $df= 2$, $p= 0.14$), therefore the PERMANOVA was not influenced by differences in assemblage homogeneity.

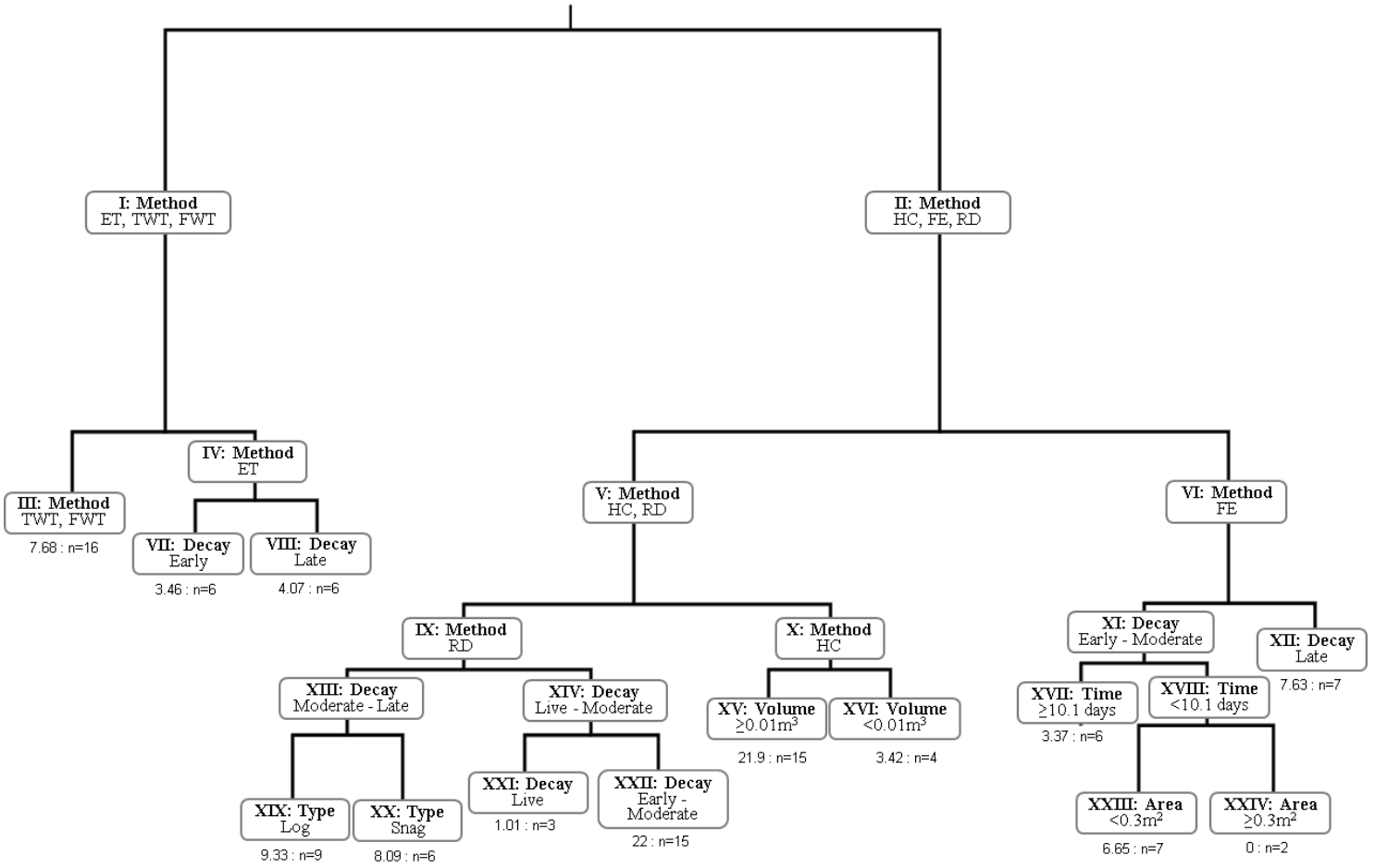

Figure 2.5 Collection variables most important in shaping saproxylic beetle assemblages (i.e., Sx++, Sx+ species) as given by Multivariate Regression Tree (MRT) analysis (Error: 0.429, CV Error: 0.637, SD: 0.037). Volume, surface area, and sampling time given are means calculated for pooled samples. HC= hand-collection, FE= funnel extraction, RD= rearing drum, ET= emergence trap, TWT= trunk window trap, FWT= free-hanging window trap.

2.4.3. Species Associations

Many species were useful indicators for groups identified by the MRT (Table 2.3, groups as in Figure 2.5), showing that method biases are important considerations for studies of saproxylic assemblages. There were more indicator species (54 spp.) for Group III (FWT & TWT) than for any other group. Additional indicator species were associated with particular DCs (e.g., Groups VII, XII, and XIX) within each deadwood substrate. A few species were significant indicators for particular sampling time (Group XVII; Table 2.3) surface area (XXIII, XXIV; Table 2.3) or volume (Group XV, Group XVI; Table 2.3). Most collection methods showed strong biases for particular beetle species (Table 2.3). Window trap samples included the strongest indicator species (13 and 12 spp. for FWT and TWT). In fact, only one other single method (FE) produced a strong indicator species, the 'Plaster Beetle' *Cartodere constrica* (Gyllenhal), (IndVal= 61.8).

Table 2.3 List of saproxylic beetle species that were significant indicator species (IndVal ≥25) for MRT grouping variables (ISA I) and strong indicator species (IndVal ≥ 60) for Collection Method (ISA II). Significance of indicator analyses was determined by a Monte Carlo test with 5000 randomizations (α = 0.05). The functional guild ('Guild') and saproxylic class (Sx: ++= obligate, += facultative) are given for each species. HC= hand collection, FE= funnel extraction, RD= rearing drum, ET= emergence trap, TWT= trunk window trap, FWT= free window trap).

Family *Species*	Guild	Sx	MRT Group	IndVal	Method	IndVal
Anobiidae						
Dorcatoma pallicornis	Myc	++	I, III	39.3, 68.7	TWT	70
Carabidae						
Perigona nigriceps	Zoo	+	XVII	33.3		
Cerambycidae						
Grammoptera subargentata	Xyl	++	I, III	41.5, 73.7	TWT & FWT	70.1
Trachysida aspera aspera	Xyl	++	I, III	28.6, 50	FWT	65.3
Ciidae						
Cis fuscipes	Myc	++	III	25		
Dolichocis manitoba	Myc	++	I	40.3		
Sulcacis curtulus	Myc	++	IV	31.3		
Clambidae						
Clambus pubescens	Myc	+	III	37.5	FWT	68.9
Cryptophagidae						
Antherophagus ochraceus	Det/Pal	+			TWT	64.5
Atomaria ephippiata	Myc	+	XXIII	28.6		
Atomaria sp. 2	Myc	+	XII	28.6		
Cryptophagus sp. 2	Myc	+	I, III	39.2, 71.2	TWT & FWT	63.5
Pteryngium crenatum	Myc	++	III	25		
Curculionidae						
Cossonus pacificus	Xyl	++	I, III	46.4, 55.3	TWT	87.4
Dermestidae						
Megatoma perversa	Det	+	I, IV, VIII	55.8, 37.7, 54	ET & TWT	63.8
Elateridae						
Ampedus nigricans	Omn	++	I, III	50, 61.4	TWT	65.9
Denticollis denticornis	Zoo	+	III	30		
Erotylidae						
Triplax dissimilator	Myc	++	I, III	50, 73.7	TWT	79.7
Eucnemidae						
Epiphanis cornutus	Myc	++	I, III	28.6, 50	FWT	65.3
Latridiidae						
Cartodere constricta	Myc	+	VI, XI, XVII	61.8, 56.2, 49.5	FE	61.8
Corticaria n. sp. 1	Myc	+	I, IV, VII	53.6, 40.3, 56.5	ET & TWT	62.5
Corticaria n. sp. 3	Myc	+	VIII	33.3		
Corticaria serrata	Myc	+	XVII	33.3		
Cortinicara gibbosa	Myc	+	I, III	73.7, 69.9	ET, TWT & FWT	73.7
Enicmus tenuicornis	Myc	+	I, III	32.1, 42.9	TWT	64.5
Melanophthalma helvola	Myc	+	I, III	35.7, 62.5	FWT	88.2
Melanophthalma inermis	Myc	+	XVII	28.1		
Melanophthalma pumila	Myc	+	I, III	60.5, 71.6	TWT &	68.7

Family *Species*	Guild	Sx	MRT Group	IndVal	Method	IndVal
					FWT	
Stephostethus liratus	Myc	+	I, III	36.8, 66.1	FWT	81.8
Leiodidae						
Agathidium cavisternum	Myx	+	III	30		
Anisotoma globososa	Myx	++	III	37.5		
Colon elongatum	Myc	+			FWT	69.5
Monotomidae						
Rhizophagus n. sp. 1	Zoo	++	I, III	57.1, 62.1	TWT	68.8
Mordellidae						
Mycetophagidae						
Typhaea stercorea	Myc	+	XVII	54.9		
Nitidulidae						
Colopterus truncatus	Myc	++	I, III	46.4, 81.2	FWT	83.3
Epuraea flavomaculata	Myc	+	I, III, VII	62.9, 40.5, 50.2	ET, TWT & FWT	62.9
Epuraea sp. 1	Myc	+	XXI	55.6		
Epuraea truncatella	Myc	+	XXI	27.8		
Glischrochilus siepmanni	Myc	+	I, III	39.3, 43.4	FWT	78.3
Glischrochilus vittatus	Myc	+	I	30.8		
Ptiliidae						
Acrotrichis sp. 1	Myc	+	III	41.1		
Pyrochroidae						
Dendroides testacea	Myc	++	III	37.5	FWT	68.9
Scraptiidae						
Anaspis rufa	Omn	++			FWT	73.1
Canifa pallipes	Omn	++	I, III, VIII	77.2, 41.9, 42.9	ET, TWT & FWT	77.2
Silvanidae						
Dendrophagus cygnaei	Myc	++	XVI	39.7		
Staphylinidae						
Atrecus macrocephalus	Zoo	++	XXIV	46.1		
Euplectus duryi	Zoo	+	XII	40.2		
Lathrobium fauveli	Zoo	+	XII	40.2		
Lordithon longiceps	Zoo	+	III	31.2		
Mycetoporus americanus	Myc	+	III	30		
Proteinus limbatus	Myc	+	XII	28.6		
Pseudopsis sagitta	Zoo	+	XII	48.9		
Quedius criddlei	Zoo	+	III	25		
Quedius frigidus	Zoo	+	XII	28.6		
Quedius velox	Zoo	+	I, III	59.4, 78.6	TWT & FWT	76.5
Tachinus fumipennis	Zoo	+	XII	28.9		
Tachyporus borealis	Zoo	+	XII	32.1		
Stenotrachelidae						
Cephaloon tenuicorne	Omn	++	III	37.5	FWT	68.9

2.4.4. Collection Method Performance

Collection methods varied greatly in their rank scores across each performance variable as shown by star plots (Figure 2.6, Table 2.4). Star plots for the HC method had the greatest area and thus had the best

overall performance of the collection methods studied. HC performance was moderate across most variables, but was particularly effective in ease of setup due to minimal cost of materials, no associated construction time, moderate application time in the field, and short sampling period (hours rather than months). HC samples, by their nature, also contain a high proportion of saproxylic individuals and species (98.5%).

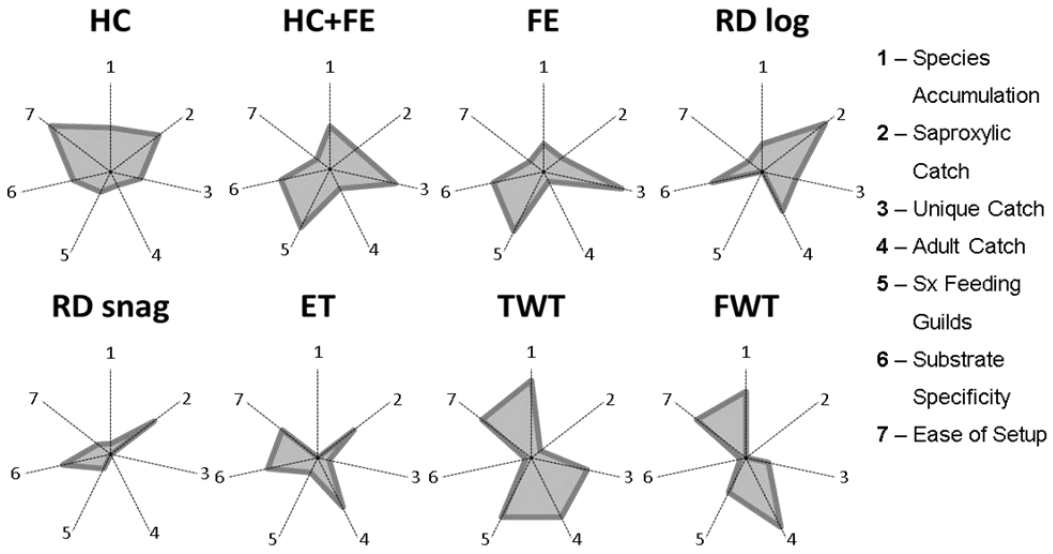

Figure 2.6 Multivariate star (radar) plots for rank performance of each collection method in relation to seven variables. Each variable axis is represented by dashed radial lines, i.e. “rays”, and variable names (right) correspond to each of the seven numbered rays. Observed values of performance (grey) are fractional ranks of observed values (see Table 2.4), with maximum axis lengths scaled to indicate the greatest performance (i.e., lowest rank number) in each variable. Collection methods forming larger polygons (grey area) are thus ranked higher relative to other collection methods in their cumulative performance. Area of each performance polygon was calculated and collection methods rank as follows (with area given in brackets): HC (63), TWT (56), RD log (46), HC+FE (43), FE (32), FWT (25), ET (23), and RD snag (11).

Table 2.4 Observed values (with their associated ranks, where applicable) for each collection method, showing scores for each performance variable used in star plots (bold). Letters for richness parameters are the significance codes between collection method groups (95% CI), and were used as the basis for assigning ranks.

VARIABLE	HC	FE	HC+FE	RD log	RD snag	ET	TWT	FWT
Cumulative richness	67	85	127	49	33	77	182	108
Richness / Individual	ab (2)	c (6.5)	c (6.5)	c (6.5)	bc (4)	c (6.5)	a (1)	b (3)
Richness / Sample	c (6.5)	c (6.5)	b (3)	bc (4)	c (6.5)	c (6.5)	a (1.5)	a (1.5)
Richness / Time	a (1)	c (2)	b (4)	d (7)	d (7)	d (7)	c (4)	c (4)
Richness / Volume	b (4.5)	b (4.5)	a (1)	ab (2)	b (4.5)	b (4.5)		
Species Accumulation†	**3.5 (3)**	**4.88 (5.5)**	**3.63 (4)**	**4.88 (5.5)**	**5.5 (7)**	**6.13 (8)**	**2.17 (1)**	**2.83 (2)**
% Sx Species	98.6%	98%	98.2%	100%	99%	99.3%	87.9%	67.8%
% Sx Individuals	98.5%	92.9%	95.2%	100%	96.9%	96.1%	90.1%	85.1%
Saproxylic Catch‡	**98.5% (2)**	**95.5% (6)**	**96.7% (5)**	**100%% (1)**	**97.9% (3)**	**97.7% (4)**	**89.0% (7)**	**76.5% (8)**
No. of Unique Sx Species	13	28	20.5	7	2	6	47	11
Unique Catch	**19.4% (4)**	**32.9% (1)**	**26.9% (2)**	**14.2% (5)**	**6% (8)**	**7.7% (7)**	**25.8% (3)**	**10.1% (6)**
No. of Adult individuals	237	966	1144	357	125	1110	2382	1148
Adult Catch	**51.5% (5)**	**49.9% (7)**	**50.5% (6)**	**61.5% (4)**	**47.7% (8)**	**69.7% (3)**	**92.8% (2)**	**99.9% (1)**
Sx Feeding Guilds	**87.5% (4.5)**	**100% (2)**	**100% (2)**	**50% (8)**	**75% (6.5)**	**75% (6.5)**	**100% (2)**	**87.5% (4.5)**
Substrate Specificity	**1 (3.5)**	**1 (3.5)**	**1 (3.5)**	**1 (3.5)**	**1 (3.5)**	**1 (3.5)**	**0 (7.5)**	**0 (7.5)**
Materials costs*	1	5	5	4	4	3	2	2
Construction time*	1	5	5	4	4	2	3	3
Application time*	2	4	4	4	4	3	1	1
Duration of Sampling Period*	1	2	2	3	3	3	3	3
Ease of Setup**	**1 (1)**	**4 (6.5)**	**4 (6.5)**	**4 (6.5)**	**4 (6.5)**	**3 (4)**	**2 (2.5)**	**2 (2.5)**
Polygon Area††	62.57 (1)	31.92 (5)	43.05 (4)	43.63 (3)	11.25 (8)	23.30 (7)	56.14 (2)	24.57 (6)

†calculated mean of the above four ranks in species accumulation; ‡calculated mean of the above two proportions; *subjective ranks based on experience from the study; **calculated mean of the above four ranks in collection method materials cost and application effort; ††polygon area refers to the area of each star plot (Figure 2.6); catch rates were given as percentages of total catch for each collection method; fractional ranks of each performance score is given in brackets, calculated where by equal numbers receive the average of their combined ordinal ranks; variables shown in bold are those used in star plots.

TWT were ranked second in overall performance, with a star plot area of 56. While TWTs were not highly ranked in catch of saproxylic beetles or in substrate specificity, they were the most efficient in species accumulation, have a fairly low cost to setup, collect a large proportion of adult beetles (92.8%), and collect all saproxylic functional guilds (Table 2.4). The catch of non-saproxylic beetles (Sx^-) was higher for FWT samples (32.1% of individuals and 14.8% of species) than for TWT samples (12% of individuals and 9.9% of species classified as Sx^-).

Snag RD was the poorest performer (total area ranked last), ranking just below snag ET. Both of these methods showed poor accumulation of species, collected few unique species, and did not collect a large portion of saproxylic functional guilds. The low rank of these methods, however, did not depend on lower abundance of beetles in snags than in logs ($t= 1.27$, $df= 16.85$, $P=0.22$; mean abundance ± 1SE: 1.07 ± 0.26 and 1.43 ± 0.13 for RD snags and logs, respectively).

2.5. Discussion

No other study has compared a similarly wide range of different collection methods for saproxylic beetles, as applied on one landscape over the same time period. I have compared the overall efficiency, function, and limitations of six collection methods and suggest that the results can assist researchers in optimizing collection protocols and

interpreting results of their studies. These results suggest that collection methods for saproxylic beetles should be selected in relation to the specific aims of the study and with an understanding of the particular biases of the collection methods being considered. Most saproxylic beetle studies in North America to date have relied on WTs. Although these generate abundant and diverse samples, WT samples appear to yield less satisfactory ecological data than could be achieved by other methods. In contrast, studies employing direct-habitat sampling methods, such as rearing, emergence trapping, and hand collections are highly regarded for assessing specific substrate relationships, but may be criticized for low return on effort (few individuals and species). Clearly, each study must balance a number of considerations in relation to the aims of the study. In the following discussion I compare groups of similar methods (window traps, rearing methods, and hand collection) and then conclude with overall suggestions for selecting a collection method for sampling saproxylic beetles.

2.5.1. Window Traps

Window traps (WTs) have been popular for assessing saproxylic beetle communities within a particular forest stand. They collect large numbers of flight-mobile adult beetles, in relation to setup effort and cost. However, WT samples are also associated with increased processing time

(Alinvi et al. 2007). Although not formally measured here, WT samples were noticeably larger and required more sorting and processing, due to accumulation of litterfall in samples and the greater proportion of non-target individuals (e.g., zoophagous and palynivorous beetles).

Additionally, there has been debate about the efficacy of WTs for inferring substrate associations (Langor et al. 2008; Ranius and Jansson 2002; Wikars et al. 2005). I found that composition of catches did not differ significantly between window traps affixed to tree trunks (TWTs) and those that were free-hanging (FWTs). Furthermore, assemblages from TWTs were not structured according to snag DCs in the MRT nor in PerMANOVA analyses, and shared only 36% of species found in ETs attached to the same substrate. These findings are consistent with those of Hyvarinen et al. (2006) and Wikars et al. (2005). The two window trap types were also similar in that they collected a high proportion of Sx^{-} beetles (12% and 32% for TWT and FWT, respectively), shared many indicator species in common, and generated similar richness estimates. Assemblages defined by both kinds of window traps had similar functional guild composition and were resolved as one terminal group in MRT analyses.

Use of WTs for monitoring particular beetles may be valid, at least for the 54 saproxylic species from various functional guilds showed strong

collection biases favoring detection in WTs. For example, the latridiid, *Melanophthalma helvola* Motschulsky, was a strong indicator for FWTs. This species has only been recorded from Atlantic Canada and Pennsylvania (Majka et al. 2009). Not much is known about *M. helvola*, but as a fungivore it may be more associated with molds on dead grass, leaf litter, detritus, twigs, canopy, or other habitats not sampled, as it was not even incidentally collected using other methods. Certainly, there were also Sx^{++} indicator species that were collected disproportionately often in WTs. The xylophagous snout beetle, *Cossonus pacificus* Van Dyke (Curculionidae), was a very strong indicator for TWTs (IndVal= 87.4). The large number of strong indicator species for these methods suggests that these species have a very low likelihood of being collected by the other methods, and that WT samples were often dominated by high abundances of certain species. However, it is impossible to relate these species to the stand or substrate being sampled (Wikars et al. 2005), and they may be associated with substrates not sampled here (e.g., non-aspen hosts; limbs, twigs, or roots), thus the ecological value of such monitoring may be problematic.

2.5.2. Rearing Methods: Funnels, Drums, and Emergence Traps

Rearing methods can be particularly valuable for assessing substrate associations and collecting rare species (Langor et al. 2008;

Ranius and Jansson 2002). Compared to WTs, the three rearing techniques examined here (RD, FE, ET) generally yielded relatively low species numbers. The only exception was that FE was very efficient in accumulating species per unit of sampling time. Based on area of the star plot polygons, these methods were ranked in overall performance as follows: RD log, FE, ET, and RD snag. My experience with each method is discussed below, comparing between them where informative.

Funnel extractions are particularly practical for those wishing to expedite sample collection. Funnels generated over three times as many species as other rearing methods, in a fraction of the sampling time. In fact, species richness as estimated from FE samples was comparable to that from window traps when standardized by sampling time, and surpassed only by HC in this respect. Funnels also extracted the largest number of unique saproxylic species, with over 30% of species not found by any other collection method. Similarly, Alinvi et al. (2007) found that Tullgren funnels were much more efficient than traditional bark sieving. Assuming that the specimens removed by HC would have been also extracted in the FE, relative performance of FE may be greater when employed alone. Thus FE would be the best method for studies wishing to explore the completeness of species lists, or for targeting cryptic/uncommon species. I also found that FE was more sensitive than

HC to deadwood substrate qualities, such as decay class, which means that this approach can be effective for studies of habitat associations.

It is important to note that although funnels extracted beetles efficiently, and produced clean samples that were quick to sort, the initial cost of construction is approximately three and four times greater, respectively, than for ETs and RDs. Beetle assemblages from FE are also influenced by sampling time and surface area relationships. For example, detection of *Cryptophagus actangulus* (Cryptophagidae) is strongly associated with FE extraction time ≥ 10.1 days (IndVal= 76). Care should be taken to determine optimal extraction times, as our data show that some beetles will be missed with short extraction times.

Despite earlier suggestions that ETs do not produce enough species and individuals for meaningful ecological analysis (Alinvi et al. 2007, Økland 1996), the results presented here suggest that ETs can yield data suitable for this task. I collected 1592 beetles comprising 77 species from 47 traps, each enclosing a 1 m section of CWD, compared to Økland's (1996) report of 164 beetles of 50 species from 167 *in situ* ETs, each enclosing a 0.75 m section. The catch from these ETs was comparable to that of Wikars et al. (2005), who collected 1400 individuals of 67 species from just 30 *ex situ* ETs, each enclosing a 0.5-1.1m section of CWD. Emergence data have also been successfully used elsewhere to

define assemblages (Yee et al. 2001; Lachat et al. 2006; Bashford et al. 2001; Grove 2000) and my analyses concur that ETs are an appropriate choice for examining substrate relationships.

I expected ET and RD snag methods to sample similar portions of the saproxylic community, yet the assemblages detected diverged from each other in both the MRT and RDA plot. Interestingly, early decay classes (DC1, 2) were distinct from late decay classes for samples from both snag RDs and ETs. This suggests that differences in assemblages suggested by these two similar methods might be explained by changes in snag microclimate when RD samples were cut, transported, and reared *ex situ*. As suggested by Hammond (1997), this process can be highly disruptive, causing high mortality of some species. As rearings of logs produced a larger proportion of unique species and adult specimens than snag RD samples, snag substrates may be particularly sensitive to disturbance. Certainly, snag moisture properties may be more dramatically altered than in log substrates, as snags still have one end intact. The RDs used in this study seemed to perform less efficiently than those used by Hammond (1997); contrary to that study I found individual-based species richness estimates were much lower in RDs compared to WTs. Clearly, results of rearings can vary greatly between studies conducted in close proximity, suggesting either large temporal effects or that saproxylic

faunas are so large that that effective sampling is difficult, as suggested in Fig 2.3c.

In summary, FE is preferable over RD or ET methods to generate the most information from a particular deadwood sample through rearing. However, FE and RD methods are both destructive, requiring deadwood habitats to be cut and removed from the ecosystem. When studying saproxylic beetles in threatened ecosystems, or to preserve sensitive host species, or rare habitats, *in situ* sampling (e.g., ET) may be more appropriate. Researchers can also improve upon ET catch without expending more effort, by enclosing longer lengths of substrates.

2.5.3. Hand-collecting

Hand-collection proved to be very effective for sampling saproxylic beetles. In particular, HC yielded many more beetle species per unit of sampling time than any other method, and was as efficient as TWTs in accumulation of species in individual-based rarefactions. Samples from HC contained the largest portion of obligate saproxylic species (Sx^{++}), and the lowest proportion of non-target (Sx^{-}) species, while also capturing all main functional guilds of saproxylic beetles (except phloeophages, which were also rarely collected by other methods). Although hand-collection is considered poor for capturing species associated with polypores, microfungi, and habitats deep within deadwood (Siitonen 1994), the

particular HC protocol of this study, involved searching all depths of woody substrates (bark, sapwood, heartwood) as well as polypores within the sample area. Thus, I found that HC returned a proportion of general mycophages and myxomycetophages similar to other methods. I also collected numerous *Ampedus* spp. (Elateridae) inhabiting the rotten heartwood of moderately-well decayed logs through HC. It is also notable that no species appeared to be collected disproportionately by HC, a feature that may translate to a more even distribution of species abundances across samples, as opposed to having a few species locally dominant in one particular method.

Despite the low number of species generated per sample or per volume of wood sampled, the low cost of employing HC, high accumulation per sampling time and individual, high proportion of Sx^{++} species, and utility in making natural history observations, makes HC a desirable collection technique. As it is important to use collection techniques that provide the most complete information possible, I recommend that if HC is used, the sorted wood should not be discarded. Clearly, subsequent sampling of wood with Tullgren funnels will yield a diverse portion of the saproxylic community otherwise missed by hand collection alone. Of course, use of HC is limited to researchers that are able to spend considerable time in the field in comparison to the investment of setting a trap and leaving the field site. For studies in which

field time is constrained, it would be prudent to bear the higher initial cost associated with constructing and employing WTs or rearing methods.

2.5.4. Conclusions

All methods considered here have merit as all uniquely contributed species to the overall dataset. Even though FWTs, ETs, and RDs are inferior to other methods in some ways, they respectively accounted for eleven, nine, and six saproxylic species not detected by any other method. Thus, my results underscore the value of sampling with a variety of collection methods. Despite the EMEND landscape being extensively sampled with TWT and pitfall traps during the previous decade, I contributed 47 new species records for Alberta and discovered seven species confirmed as new to science in just 4 months of sampling (Appendix 5-A).

If all the performance categories in star plots are equally weighted in terms of importance, then HC and TWTs should be regarded as the 'best' choices for sampling saproxylic beetles. Because these two methods also sample different portions of the saproxylic beetle community, their combined use could provide valuable depictions of the local saproxylic fauna in the boreal region. Furthermore, as FEs produce many additional species (especially unique species) their use in conjunction with HC techniques would help make inventories more

complete, in addition to providing improved understanding of habitat associations.

Information about trapping biases is useful for design of subsequent studies seeking to target sampling to a particular species (or group). For example, if I wanted to monitor the new monotomid species, *Rhizophagus n.sp.1* reported here, I would employ TWTs to optimize sampling for that particular species. Knowledge of collection biases can also help to determine which methods are most appropriate for testing the particular hypotheses under examination. If I were to study the influence of forest harvesting on saproxylic beetles, and utilized only window traps, for example, my conclusions would clearly miss a large fraction of saproxylic beetles in the community.

A more thorough understanding of the saproxylic community is needed to support better conservation of this fauna through North American forest management. Given the formidable diversity of the Boreal Nearctic fauna and the lack of basic natural history information, this remains a challenging task. This situation can be changed only through further work, and this is much needed. Use of direct-habitat collection techniques in addition to window traps will greatly improve faunistic knowledge. Choosing collection methods to meet specific research goals

will yield a more accurate and diverse understanding of saproxylic biodiversity and better support conservation efforts.

2.6. Literature Cited

Agematsu, Y., I. Ikarashi, Y. Furuyama, N. Kobayashi, K. Barada and K. Tauchi. 1993. A new visual method for evaluating multiple data (diagnostic radar chart) in general toxicological study. The Journal of Toxicological Sciences 18: 33-42.

Alinvi, O., J.P. Ball, K. Danell, J. Hjalten, and R.B. Pettersson. 2007. Sampling saproxylic beetle assemblages in dead wood logs: Comparing window and eclector traps to traditional bark sieving and a refinement. Journal of Insect Conservation 11(2): 99-112.

Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. Austal Ecology 26: 32–46.

Anderson, M.J. 2005. PERMANOVA: a FORTRAN computer program for permutational multivariate analysis of variance, version 1. Department of Statistics, University of Auckland, Aukland.

Anderson, M.J. 2006. Distance-based tests for homogeneity of multivariate dispersions. Biometrics 62: 245-253.

Anderson, M.J., K.E. Ellingsen and B.H. McArdle. 2006. Multivariate dispersion as a measure of beta diversity. Ecology Letters 9: 683-693.

Arnett, R.H., Jr., and M.C. Thomas. (eds.). 2000. American Beetles. Volume 1. Archostemmata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia. CRC Press LLC, Boca Raton, FL. xvi + 443 pp.

Arnett, R.H., Jr., M.C. Thomas, P.E. Skelley and J.H. Frank. (eds.). 2002. American Beetles. Volume 2. Polyphaga: Scarabaeoidea through Curculionoidea. CRC Press LLC, Boca Raton, FL. xiv + 861 pp.

Bashford, R., R. Taylor, M. Driessen, N. Doran and A. Richardson. 2001. Research on invertebrate assemblages at the Warra LTER Site. Tasforests 13 (1): 109-118.

Beckingham, J. and J.H. Archibald. 1996. Field guide to ecosites of Northern Alberta. Special Report 5. Natural Resources Canada, Canadian Forest Service. Northwest Region. Edmonton, AB.

Betz, O., M.K. Thayer and A.F. Newton. 2003. Comparative morphology and evolutionary pathways of the mouthparts in spore-feeding Staphylinoidea (Coleoptera). Acta Zoologica (Stockholm) 84: 179–238.

Bousquet, Y. (ed.). 1991. Checklist of beetles of Canada and Alaska. Agriculture Canada: Research Branch, Publication 1861/E, Ottawa. 430 pp.

Chambers J. M., W. S. Cleveland, B. Kleiner, and P. A. Tukey. 1983. Graphical methods for data analysis. Belmont, CA: Duxbury Press.

Cobb, T.P., J.L. Morissette, J.M. Jacobs, M.J. Koivula, J.R. Spence, and D.W. Langor. 2011. Effects of postfire salvage logging on deadwood-associated beetles. Conservation Biology 25(1): 94-104.

Colwell, R. 2009. EstimateS: Statistical estimation of species richness and shared species from samples. Version 8.2. http://viceroy.eeb.uconn.edu/EstimateS

Colwell, R.K., C.X. Mao, J.Chang. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology 85 (10): 2717-2727.

Crites, S. and M.R.T. Dale. 1998. Diversity and abundance of bryophytes, lichens, and fungi in relation to woody substrate and successional stage in aspen mixedwood boreal forests. Canadian Journal of Botany 76: 641-651.

De'Ath, G. 2002. Multivariate regression trees: a new technique for modeling species-environment relationships. Ecology 83(4): 1105-1117.

De'Ath, G. 2010. MVPART: Multivariate Partitioning, version 1.3-1. R Package.

De Caceres, M., P. Legendre and M. Moretti. 2010. Improving indicator species analysis by combining groups of sites. Oikos 119(10): 1674-1684.

Downie, N.M. and R.H. Arnett, Jr. 1996. The Beetles of Northeastern North America. Volumes I and II. The Sandhill Crane Press, Gainseville. 1721 pp.

Dufrêne, M. and P. Legendre. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecological Monographs 67: 345–366.

Gibb, H., R.B. Pettersson, J. Hjälten, J. Hilszczanski, J.P. Ball, T. Johansson, O. Atlegrim, and K. Danell. 2006c. Conservation-oriented forestry and early successional saproxylic beetles: responses of functional groups to manipulated dead wood substrates. Biological Conservation 129: 437–450.

Gotelli, N. and Colwell, R.K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4: 379–391.

Grove, S.J. 2000. Trunk window trapping: An effective technique for sampling tropical saproxylic beetles. Memoirs of the Queensland Museum 46(1): 149-160.

Grove, S.J. 2002a. Saproxylic insect ecology and the sustainable management of forests. Annual Review of Ecological Systems 33: 1-23.

Grove, S.J. 2002b. The influence of forest management history on the integrity of the saproxylic beetle fauna in an Australian lowland tropical rainforest. Biological Conservation 104: 149–171.

Halpern, H.I. 1996. Development and applications of light-hydrocarbon based star diagrams. American Association of Petroleum Geologists Bulletin 79: 801-15.

Hammond, H.E.J. 1997. Arthropod biodiversity from *Populus* coarse woody material in north-central Alberta: A review of taxa and collection methods. The Canadian Entomologist 129(6): 1009-1033.

Hammond, H.E.J., D.W. Langor and J.R. Spence. 2001. Early colonization of *Populus* wood by saproxylic beetles (Coleoptera). Canadian Journal of Forest Research 31(7): 1175-1183.

Hammond, H.E.J., D.W. Langor and J.R. Spence. 2004. Saproxylic beetles (Coleoptera) using *Populus* in boreal aspen stands of western Canada: spatiotemporal variation

and conservation of assemblages. Canadian Journal of Forest Research 34(1): 1-19.

Hatch, M.H. 1962. The Beetles of the Pacific Northwest. Part III: Pselaphidae and Diversicornia I. University of Washington Press. Seattle, WA. ix + 503 pp.

Heathcote, G.D. 1957. The comparison of yellow cylindrical, flat, and water traps and of Johnson suction traps, for sampling aphids. Annals of Applied Biology 45:133-139.

Hyvarinen, E., J. Kouki and P. Martikainen. 2006. A comparison of three trapping methods used to survey forest-dwelling Coleoptera. European Journal of Entomology 103(2): 397-407.

Jacobs, J.M., J.R. Spence and D.W. Langor. 2007a. Influence of boreal forest succession and dead wood qualities on saproxylic beetles. Agricultural and Forest Entomology 9(1): 3-16.

Jacobs, J.M., J.R. Spence and D.W. Langor. 2007b. Variable retention harvest of white spruce stands and saproxylic beetle assemblages. Canadian Journal of Forest Research 37(9): 1631-1642.

Jonsell, M. and G. Nordlander. 1995. Field attraction of Coleoptera to odours of the wood decaying polypores *Fomitopsis pinicola* and *Fomes fomentarius*. Annales Zoologica Fennici 32: 391-402.

Kaila, L. 1993. A new method for collecting quantitative samples of insects associated with decaying wood or wood fungi. Entomologica Fennica 4: 21-23.

Kishchuk, B.E. 2004. Soils of the Ecosystem Management Emulating Natural Disturbance (EMEND) experimental area, northwestern Alberta. Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre, Edmonton Alberta. Information Report NOR-X-397.

Kosaka, A., M. Osaku, Y. Watabiki, M. Hojo, A. Kasezawa and F. Hamao. 1995. QOL of breast-conserved patients analyzed by radar chart. Biotherapy 9: 1023-30.

Lachat, T., S. Attignon, J. Djego, G. Goergen, P. Nagel, B. Sinsin and R. Peveling. 2006. Arthropod diversity in Lama forest reserve (South Benin), a mosaic of natural, degraded and plantation forests. Biodiversity and Conservation 15(1): 3-23.

Langor, D.W., H.E.J. Hammond, J.R. Spence, J. Jacobs and T.P. Cobb. 2008. Saproxylic insect assemblages in Canadian forests: diversity, ecology, and conservation. The Canadian Entomologist 140(4): 453-474.

Lengendre, P. and L. Legendre. 1998. Numerical Ecology: Developments in environmental monitoring, 20. 2nd English Edition. Elsevier, Amsterdam, 853 pp.

Lindhe, A. and A. Lindelow. 2004. Cut high stumps of spruce, birch, aspen and oak as breeding substrates for saproxylic beetles. Forest Ecology and Management 203(1-3): 1-20.

Lindroth, C.H. 1961. The ground beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Part 2. Opuscula Entomologica Supplementum 20: 1-200.

Lindroth, C.H. 1963. The ground beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Part 3. Opuscula Entomologica Supplementum 24: 201-408.

Lindroth, C.H. 1966. The ground beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Part 4. Opuscula Entomologica Supplementum 29: 409-648.

Lindroth, C.H. 1968. The ground beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Part 5. Opuscula Entomologica Supplementum 33: 649-944.

Lindroth, C.H. 1969a. The ground beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Part 6. Opuscula Entomologica Supplementum 34: 945-1192.

Lindroth, C.H. 1969b. The ground beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Part 1. Opuscula Entomologica Supplementum 35: i-xlviii.

Majka, C.G., D. Langor, and W.H. Rücker. 2009. Latridiidae (Coleoptera) of Atlantic Canada: new records, keys to identification, new synonyms, distribution, and zoogeography. The Canadian Entomologist 141: 317-370.

Martikainen, P. and J. Kouki. 2003. Sampling the rarest: threatened beetles in boreal forest biodiversity inventories. Biodiversity and Conservation 12(9): 1815-1831.

Martikainen, P., J. Siitonen, P. Punttila, L. Kaila and J. Rauh. 2000. Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biological Conservation 94(2): 199-209.

Mao, C.X., R.K. Colwell, J. Chang. 2005. Estimating the species accumulation curve using mixtures. Biometrics 61(2): 433-441.

McArdle, B.H. and M.J. Anderson. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82: 290–297.

McCullough, H.A. 1948. Plant Succession on Fallen Logs in a Virgin Spruce-Fir Forest. Ecology 29 (4): 508-513.

McCune, B. and M.J. Mefford. 2006. PC-ORD: Multivariate Analysis of Ecological Data, Version 5.31. MjM Software Design, Gleneden Beach, Oregon, USA.

Niemelä, J., Y. Haila and E. Ranta. 1986. Spatial heterogeneity of carabid beetles dispersion in uniform forests on the Åland Islands. Annales Zoologici Fennici 23: 289-296.

Nieto, A. and K.N.A. Alexander. 2010. European Red List of Saproxylic Beetles. Luxembourg: Publications Office of the European Union.

Økland, B. 1996. A comparison of three methods of trapping saproxylic beetles. European Journal of Entomology 93(2): 195-209.

Owen, J.A. 1989. An emergence trap for insects breeding in dead wood. British Journal of Entomology and Natural History 2(2): 65-67.

R Development Core Team. 2010. R: A language and environment for statistical computing, version 2.11.1. R Foundation for Statistical Computing, Viena. http: //www.R-project.org.

Ranius, T. and N. Jansson. 2002. A comparison of three methods to survey saproxylic beetles in hollow oaks. Biodiversity and Conservation 11(10): 1759-1771.

Saary, M.J. 2008. Radar plots: a useful way for presenting multivariate health care data. Journal of Clinical Epidemiology 61(4): 311-317.

Saint-Germain, M., P. Drapeau and C. Hebert. 2004. Comparison of Coleoptera assemblages from a recently burned and unburned black spruce forests of northeastern North America. Biological Conservation 118(5): 583-592.

Saint-Germain, M., C.M. Buddle and P. Drapeau. 2006. Sampling saproxylic Coleoptera: Scale issues and the importance of behavior. Environmental Entomology 35(2): 478-487.

Siitonen, J. 1994. Decaying wood and saproxylic Coleoptera in 2 old spruce forests – A comparison based on 2 sampling methods. Annales Zoologici Fennici 31(1): 89-95.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins 49: 11–41.

Simila, M., J. Kouki, P. Martikainen and A. Uotila. 2002. Conservation of beetles in boreal pine forests: the effects of forest age and naturalness on species assemblages. Biological Conservation 106(1): 19-27.

Smetana, A. 1990. Revision of the tribe Quediini of America North of Mexico (Coleoptera: Staphylinidae). Supplementum 6. The Coleopterists Bulletin 44: 95–104.

Speight, M.C.D. 1989. Life in Dead Trees - a Neglected Part of Europe Wildlife Heritage. Environmental Conservation 16(4): 354-356.

Stehr, F.W. 1991. Immature insects. Volume 2. Kendall/Hunt, Dubuque, Iowa. 975 pp.

Tughu, N., A. Ladiwala, C.M. Breneman and S. Cramer. 2003. Identification of chemically selective displacers using parallel batch screening experiments and quantitative structure efficacy relationship models. Analytical Chemistry 75: 5806-16.

Väisänen, R., O. Bistrom and K. Heliovaara. 1993. Subcortical Coleoptera in dead pines and spruces - Is primeval species composition maintained in managed forests. Biodiversity and Conservation 2(2): 95-113.

Weaver, H. E. 2000. Petroleum and source rock characterization based on C7 star plot results: examples from Egypt. American Association of Petroleum Geologists Bulletin 84: 1041-54.

Webb, A., C.M. Buddle, P. Drapeau and M. Saint-Germain. 2008. Use of remnant boreal forest habitats by saproxylic beetle assemblages in even-aged managed landscapes. Biological Conservation 141(3): 815-826.

Weston, P.A. and R.B. Barney. 1998. Comparison of three trap types for monitoring insect populations in stored grains. Journal of Economic Entomology 91: 1449-1457.

Wheeler, Q. and M. Blackwell. (eds.). 1984. Fungus-Insect Relationships: Perspectives in Ecology and Evolution. New York: Columbia University Press. 514 pp.

Wikars, L. O. 2002. Dependence on fire in wood-living insects: an experiment with burned and unburned spruce and birch logs. Journal of Insect Conservation 6: 1-12.

Wikars, L. O., E. Sahlin, and T. Ranius. 2005. A comparison of three methods to estimate species richness of saproxylic beetles (Coleoptera) in logs and high stumps of Norway spruce. The Canadian Entomologist 137(3): 304-324.

Yamaguchi, N., Matsubara, S., Momonoi, F., Morikawa, K., Takeyama, M., and Maeda, Y. 1998. An attempt of radar chart expression of a self-rating scale for sleep disturbance. Psychiatry and Clinical Neurosciences 52(2): 165-167.

Yee, M., Z.-Q. Yuan, and C. Mohammed. 2001. Not just waste wood: decaying logs as key habitats in Tasmania's wet sclerophyll *Eucalyptus obliqua* production forests: the ecology of large and small logs compared. Tasforests 13 (1): 119-128.

3. INFLUENCE OF ASPEN DEADWOOD DIAMETER ON SAPROXYLIC BEETLE ASSEMBLAGES IN BROAD-LEAVED BOREAL STANDS

3.1. Introduction

Deadwood is crucial for supporting biodiversity in forest ecosystems (Siitonen 2001; Esseen et al. 1997), while also contributing to many valuable ecosystem services such as carbon storage and nutrient cycling (Harmon et al. 1986). An immense diversity of saproxylic organisms (e.g., birds, small mammals, arthropods, and cryptogams) depend on deadwood for development, breeding, and/or overwintering habitat (Speight 1989). Many of these species are sensitive to forest management practices (Siitonen 2001) of the sort that have dramatically transformed forest landscapes across northern Europe (Östlund et al. 1997; Kouki et al. 2001) and North America (Cyr et al. 2009; Shorohova et al. 2011). In response to these changes, populations of some saproxylic beetle species, in particular, are apparently threatened with extirpation (Siitonen and Martikainen 1994). In fact, extensive reductions in the amount and quality of deadwood have resulted in ‘red-listing’ of a large number of threatened Palaearctic species, many of which are saproxylic (Martikainen et al. 2000; Siitonen 2001; Simila et al. 2002; Nieto and Alexander 2010).

Large-scale clear-cutting and whole-tree harvesting has been widespread in Canadian boreal forest regions (Hesselink 2010), despite concerns about forest productivity (e.g., Kimmins 1977). Although 16- 30% of harvest residue may be left as slash (Erikson 1993; Hesselink 2010), the amount and composition of deadwood in managed forests differs markedly from pre-harvest conditions (Gibb et al. 2005). In Finland, for example, the volume of large (>30 cm) diameter wood is considerably reduced (25-35- fold), while small (6-10 cm) diameter, less-merchantable wood remains comparable (Siitonen 2001). As a result, saproxylic species inhabiting rare deadwood habitats (e.g., large diameter and well-decayed logs and snags) are among those most likely to be negatively affected by forest management (Siitonen 2001; Stenbacka 2009).

Beetles are among the most diverse saproxylic organisms, both in number of species and trophic guilds (Speight 1989; Esseen et al. 1997). They contribute to many important ecological processes, including decomposition of matter and nutrient cycling (Ausmus 1977; Swift 1977; Shaw et al. 1991, Cobb et al. 2009). Saproxylic beetle species depend on a range of deadwood attributes, such as host species, orientation (standing or fallen), wood density, decay stage, and diameter (e.g., Grove 2002a, b; Hammond et al. 2004; Jonsell 2007; Janssen et al. 2011; Bouget et al. 2011), and thus the diversity of their assemblages is affected by qualitative and quantitative changes to the deadwood pool. In

particular, the importance of deadwood diameter is becoming increasingly well known, and positive relationships between diameter and saproxylic beetle richness and abundance have been demonstrated in Europe (e.g., Väisänen et al. 1993; Jonsell et al. 1998; Martikainen et al. 2000; Ranius and Jansson 2000; Siitonen and Saaristo 2000; Stenbacka 2009; Brin et al. 2011). Large diameter substrates are especially important habitats for rare and threatened species (Warren and Key 1991; Jonsell et al. 1998; Lindhe et al. 2005; Yee et al. 2006). However, in North America relationships between saproxylic beetles and deadwood attributes remain largely unexplored.

Over the past two decades *Populus* stands of the boreal mixedwood forest of the Canadian Prairie Provinces have come under large-scale industrial harvest (Pratt and Urquhart 1994). Thus, questions about the saproxylic beetles using this resource have become important conservation issues (Hammond et al. 2004; Langor et al. 2008). In this study, I investigated differences in saproxylic beetle species richness, assemblage composition and habitat use in four different size classes of downed trembling aspen deadwood in broad-leaved forest stands of boreal northwest Alberta, Canada.

3.2. Methods

3.2.1. Study Area

Four broadleaf-dominated stands in an area of c. 16.3 km^2 were selected for this study based on visual assessment to verify a high density and heterogeneity of deadwood, including a range of decay states and sizes of deadwood. The stands were located in northwestern Alberta, Canada near the Ecosystem Management Emulating Natural Disturbance (EMEND) experimental site (study centre: 56°40’39.30" , 118°06’30.02").

Living overstory tree composition in the stands selected was dominated by trembling aspen (85.4%) with minor additions of balsam poplar (*P. balsamifera* Linnaeus; 12.3%), white birch (*Betula papyrifera* Marshall; 1.8%) and white spruce (*Picea glauca* [Moench] Voss; 0.5%). The understory vegetation cover was mainly (>70%) comprised of prickly rose (*Rosa acicularis* Lindley), low-bush cranberry (*Viburnum edule* [Michaux] Rafinesque), wild sarsaparilla (*Aralia nudicaulis* Linnaeus) and fireweed (*Chamerion angustifolium* [Linnaeus] Holub). Elevation ranged from 741 to 874 meters above sea level. Soils in the area are primarily Luvisolic, well drained, and originated from either fine-textured glacial till or glaciolacustrine parental material (Beckingham & Archibald 1996; Kishchuk 2004).

3.2.2. Deadwood Selection and Measurement

A total of 88 aspen logs (≥ 7 cm in diameter) were selected from the four stands. Logs were cut with a chainsaw to sample a portion of their

length (0.5 to 0.7 m long). Diameter was measured at the center of each sample with a large caliper. Deadwood characteristics, such as presence of fungus (macrofungi fruiting bodies, microfungi, and polypores), moss cover, and bark cover, were recorded. Sampling was stratified according to four size classes (SC), based on diameter: seven to <16 cm, 16 to <25 cm, 25 to <34 cm, and 34 to 43 cm (each covering a range of 9 cm). For calculations of surface area and volume, I assumed that deadwood samples were cylindrical. Throughout this chapter, surface area refers to the outer, surface area of samples, excluding the cut ends.

The local deadwood pool was measured in three randomly located fixed area plots (10 m x 10 m) in each stand. To avoid the inaccuracy of simple log counts, I calculated the proportions of each log that fell within plot boundaries. Diameter was measured at the centre of each log, and logs were categorized into one of four SCs. Availability of logs in each SC was then expressed as number of logs per hectare.

3.2.3. Beetle Samples

Saproxylic beetles were sampled from log sections during the summer of 2008, using direct collection methods (rearing drums and funnel extraction) that avoid catch of non-target beetles (see Chapter 2). Each of 18 rearing drums were constructed from 121-L plastic garbage bins, with a wide-mouth jar containing propylene glycol attached to the bottom for

killing and preserving beetles that emerged from the deadwood samples held in the drums. Each of 18 log samples (cut portions of logs, 0.7 m long) were placed on coarse (15 mm x 15 mm) wire-mesh held 10 cm above the bottom of the drum. Two ventilation holes (10 cm x 10 cm) in each side of the drum were covered with fine (~0.8 mm x 0.8 mm) mesh affixed with adhesive. Rearing drums were set on low plywood tables and kept in a forest stand near the EMEND camp for rearing beetles from the samples. Beetles were collected from jars and propylene glycol was refreshed every 14 days over a period of 88 days.

A total of 70 log sections (each 50 cm long) were also cut and sampled by hand collection and funnel extraction. Sections were dissected into pieces and any live beetles encountered were removed by hand, prior to transporting the samples in plastic bags to an indoor facility that housed the funnels. The cylindrical upper part of each plastic funnel (40.6 cm height x 47 cm diameter) was fit with coarse (2cm x 2cm) stainless steel wire mesh, which suspended wood samples above the funnel base (29 cm height) and allowed extracted beetles to pass through and into the collection jar. A Whirl-Pak™ bag containing ~50 mL of propylene glycol was attached to each funnel spout (2.5 cm height x 4.6 cm diameter). Each funnel was fit with a ‘lid’ constructed of fine wire-mesh (~2mm x 2mm). A 100-watt light bulb was suspended above each funnel, and beetles were collected after ~10 days.

After rearing or extraction, all beetles were transferred to 70% ethanol for storage before being identified to species, or to the lowest taxonomic level possible (Staphylinidae: Aleocharinae were not identified). Once identified, beetles were classified according to the degree of strength of their deadwood-association (obligate or facultative) and trophic guild based on the known species feeding habit and habitat requirements as determined from the literature.

3.3. Analyses

In selecting log samples, I ensured that all decay stages were equally represented in each SC to avoid confounding SC with decay class in the following analyses (see Brin et al. 2011).

3.3.1. Species Richness and Assemblage Composition

I calculated the number of species expected (with 95% confidence intervals), using the sample-based rarefaction approach to account for sample heterogeneity and to avoid overestimates of species richness (Gotelli and Colwell 2001). I chose the incidence-based binomial mixing approach (Mao-Tau Method of Moments, Colwell et al. 2004; Mao et al. 2005) as an alternative to resampling to allow for direct statistical comparison of richness between sample sets. The sample axis was rescaled based on average numbers of individuals per sample, as

suggested by Gotelli and Colwell (2001) for cases in which individual density varies by sample. All rarefactions were performed in EstimateS 8.2 (Colwell 2009). I compared richness per sample, individual, volume, and surface area in relation to deadwood SC. I also examined trophic richness (mean number of feeding guilds ± 1 S.E.) for each SC.

I used Permutational Multivariate Analysis of Variance analyses (PerMANOVA; Anderson 2001, McArdle and Anderson 2001) to test for differences in assemblage composition across each SC. Analyses were performed using the relative Sørenson distance measure (to account for differences in volume between samples) and 9999 permutations. To conform to the balanced design structure required for PerMANOVA (Anderson 2005), I randomly selected a subset of 4 samples from each SC. Because the results of the first PerMANOVA were only suggestive, I performed a second analysis as above, but for this second analysis I pooled data from SC1+ SC2 and SC3+ SC4 logs (i.e., 8 samples in each of two broad groups).

To further examine differences in beetle assemblages associated with SC, I performed a hierarchical agglomerative cluster analysis using the relative Sørensen distance measure and the flexible beta linkage method (β = -0.25), as suggested for ecological analyses (Legendre and Legendre 1998). Indicator species analyses (ISA, Dufrêne and Legendre

1997) were performed according to the resulting cluster groups. Indicator species were considered significant if IndVal >25 and $p< 0.05$ after 2000 permutations. PerMANOVA, Cluster and ISA analyses were performed in PC-ORD version 5.10 (McCune and Mefford 2006).

3.3.2. Size Associations for Saproxylic Beetles

I used Manly's selection index (Manly et al. 2002; Krebs 1999) to test the null hypothesis of beetles using log habitats proportionate to their availability. I assessed deadwood-habitat use in relation to availability of each log SC in the study. Manly's index generates a selection coefficient (w_i) that represents the proportion of a habitat type (i.e., log size class) used in relation to the availability of that habitat type in the local area. Coefficients >1 indicate an association with the particular habitat, whereas coefficients <1 show negative association with that habitat (Manly et al. 2002; Krebs 1999). Manly's selection coefficients were calculated as $w_i = o_i/p_i$, where w_i was the selection coefficient for each deadwood SC_i, o_i was the ratio of the number of deadwood samples occupied in category i to the total number of deadwood samples occupied, and p_i was the ratio of the number of logs in category i located in the study area to the total number of logs in the study area. Only data from funnel extraction samples were used to calculate the habitat use ratio (o_i); I used counts of the number of log samples, in each SC_i, for both obligate and facultative saproxylic

beetles. The habitat availability ratios (p_i) were calculated for the study area from estimates of the local deadwood pool.

Standard errors were calculated as $SE(w_i) = \{[(1 – o_i)/Uo_i] + [(1 – p_i)/Mp_i]\}$, where U was the total number of occupied logs and M was the total number of logs observed. Coefficients were tested for significance using the log-likelihood ratio goodness of fit test (G-test; Zar 1999). Obligate and facultative saproxylic species were analyzed separately for resource selection indices, as I expected the strength of association for deadwood habitats would be stronger for obligate saproxylic beetles. I also examined selection indices for the family Elateridae.

Patterns of resource use depend on many factors in addition to resource availability, including processes such as competition and predation (McLoughlin et al. 2010; Buskirk and Millspaugh 2006). Therefore, I assessed predation risk and potential competition in each log SC in order to infer the possible influence of these two factors on selection of log habitats. Mean predator density and mean density of other saproxylic beetles were calculated as the number of individuals in each group per cubic meter of deadwood in each of the 4 SCs. Confidence intervals ($\alpha = 0.05$) for each mean were calculated based on the Student's t-distribution.

3.4. Results

In total, 1595 individuals representing 142 saproxylic beetle species and 31 families were collected (Appendix 5-A). Forty-seven species were classified as obligate saproxylics based on published information about their habits, while the remaining 95 species were deemed facultatively saproxylic. Beetles represented a range of feeding guilds (e.g., phloeophages, xylophages, detritivores), with mycophages (1038 individuals of 67 species) and zoophages (340 individuals of 45 species) being most common. Mean trophic richness (± 1SE) increased consistently, if non-significantly, with SC as follows: SC1: 1.8 (±0.2), SC2: 2.1 (±0.2), SC3: 2.5 (±0.3), and SC4: 2.6 (±0.4) feeding guilds per sample.

3.4.1. Species Richness and Assemblage Composition

Species richness differed between log SCs (Figure 3.1). Not surprisingly, species richness per sample was greater in larger diameter logs than small diameter log samples (Figure 3.1a); however, large logs (SC4: ≥34 cm diameter) had the lowest species richness, both per individual (Figure 3.1b), and per volume (Figure 3.1c). Rarefied species richness was identical between SCs of logs, when standardized by surface area (Figure 3.1d). There were species exclusively found in each size class, with 7 spp. unique to SC1, 36 spp. to SC2, 18 spp. to SC3, and 26 spp. to SC4.

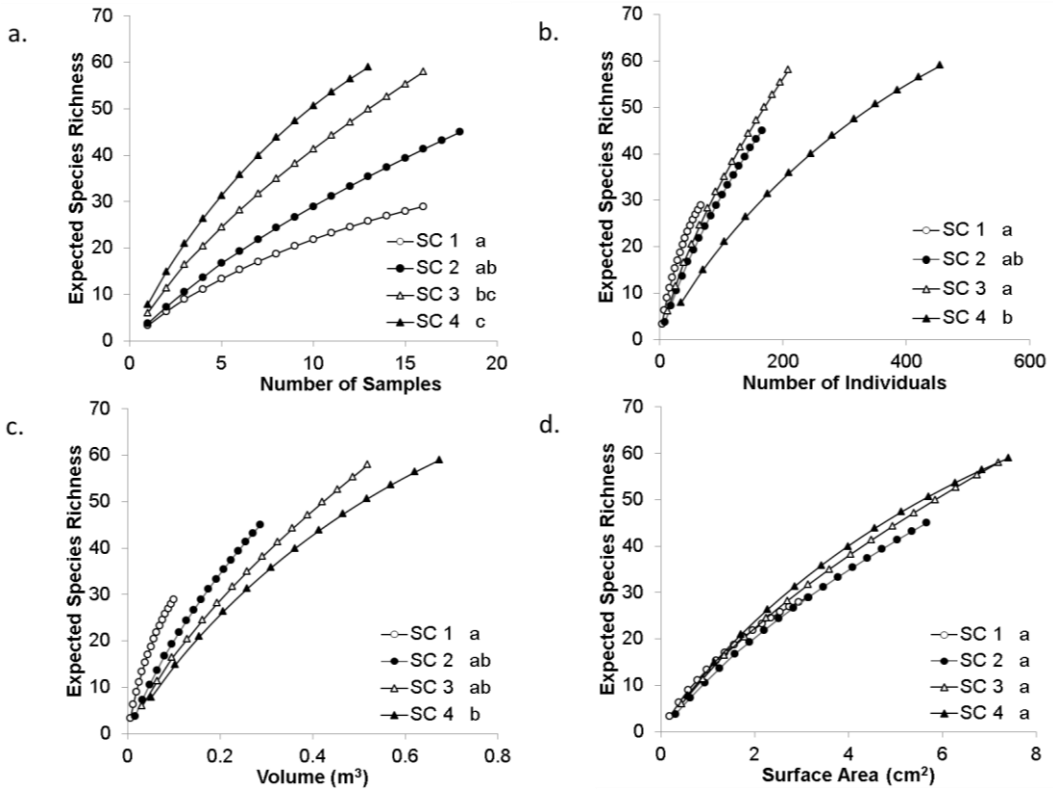

Figure 3.1 Accumulation of saproxylic beetle species with increasing sample size for logs by size class (SC). Species richness at increasing numbers of samples (a) numbers of individuals (b), sample volume (c), and sample surface area (d) were calculated as Mao-Tao interpolations of species density. In the figure legends, SCs followed by the same letter are not statistically different, based on 95% confidence intervals.

Composition of saproxylic beetle assemblages differed significantly among the four SCs (PerMANOVA: $F = 2.19$, df= 3, $p < 0.001$), although *post hoc* multiple comparison tests did not detect significant differences between particular SCs after Bonferroni correction (α= 0.0083, Table 3.1). However, after pooling the two upper and lower SCs, a subsequent PerMANOVA test showed significant differences between these broader classes of deadwood diameter ($F = 1.85$, df= 1, $p = 0.02$).

Table 3.1 Results of pairwise comparison tests of assemblage differences between log size classes, conducted after a significant PerMANOVA. P-values shown are uncorrected for multiple comparisons; none are significant when the Bonferroni-correction (α= 0.0083) is applied.

Size Class Comparisons	*t*	*p*
1 vs. 2	1.397	0.045
1 vs. 3	1.365	0.031
1 vs. 4	1.355	0.036
2 vs. 3	1.402	0.041
2 vs. 4	1.868	0.030
3 vs. 4	1.458	0.056

In cluster analyses, beetle assemblages from SC1 logs were distinct from those in all larger SCs, and SC 4 logs were most similar to SC3 logs (Figure 3.2). Overall there were 19 significant indicators of log groups (Figure 3.2). Only the latridiid, *Corticaria ferrunginea* Marsham 1802, was associated with SC1 logs. The ptiliids, *Pteryx* sp. 1 and *Acrotrichis* sp. 1, and the cantharid, *Podabrus* sp. 2, were indicators of SC2 logs. However, fifteen species were indicators of larger logs, six of which were indicators of SC4 logs (Figure 3.2).

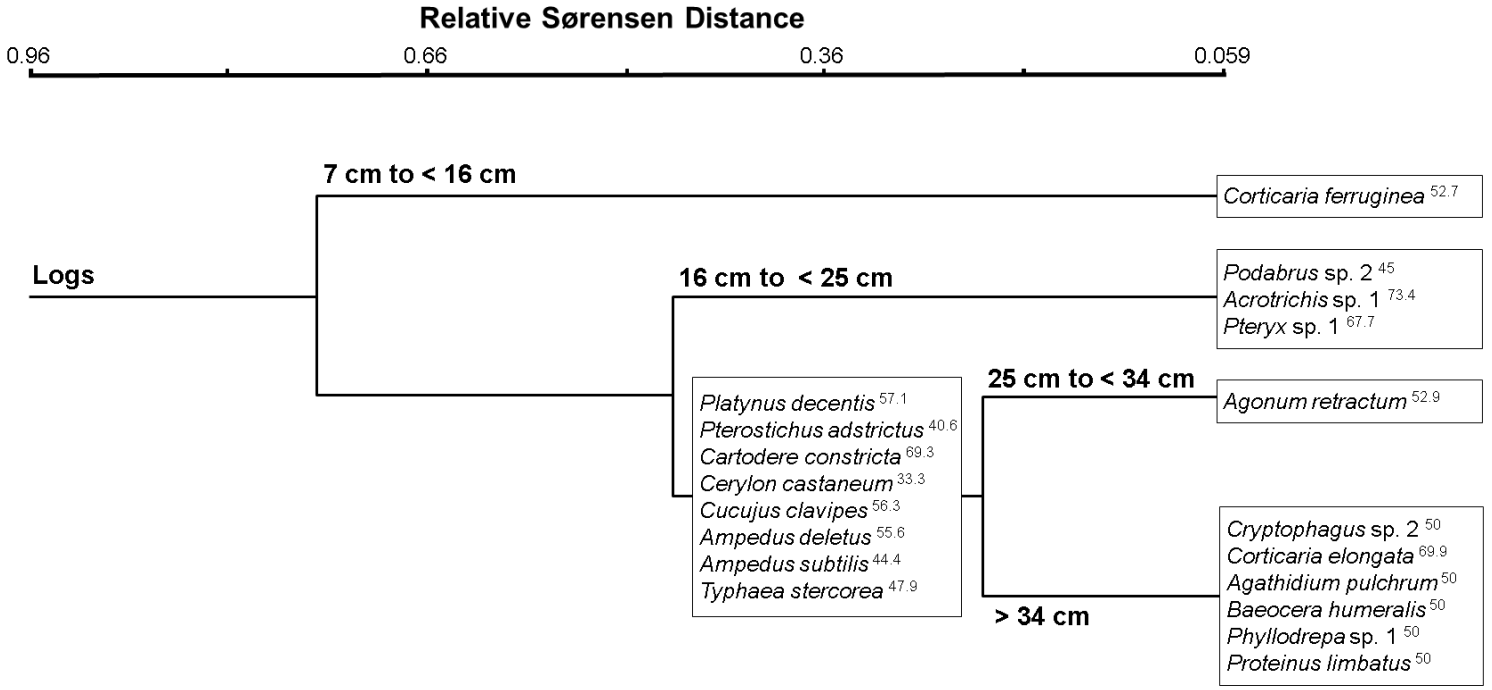

Figure 3.2 Hierarchical cluster dendrogram with indicator species for particular deadwood SCs. Cluster analysis was performed using the Relative Sørensen distance measure and flexible beta linkage method, where β = -0.25. Only significant indicators (P < 0.05) with indicator values (IV, shown as superscripts) greater than 25 are given.

3.4.2. Size Associations for Saproxylic Beetles

Beetles were found disproportionately in larger logs in relation to availability (Table 3.2). Although SC1 (<16 cm) logs were much more available in the study area (p_1= 0.8), they contained fewer beetle occurrences in all categories (Table 3.2, o_1<1). Obligate and facultative saproxylic beetles both were found disproportionately in SC 2, 3, and 4 logs (Table 3.2; w_i > 1), with strength of association increasing with log SC (Table 3.2; w_i < 1). Obligate saproxylic beetles were more strongly associated with SC4 habitats (w_i= 14.6) than were facultative saproxylic beetles (w_i= 11.7), though patterns were similar for both groups. As a family, elaterids also showed significantly disproportional use of larger SCs, especially SC 3 and 4 (G=44.45, df=3, p<0.0001).

After calculating selection indices, I examined predator density and density of all other beetles in each log SC as proxies of predation risk and competition. Small diameter logs had a significantly greater density of predatory beetles than large logs (Figure 3.3). In terms of competition, there was a general trend toward a lower density of non-predatory beetles in large logs, but this difference was only significant between SC3 and SC1 logs (Figure 3.3).

Table 3.2 Deadwood habitat selection by degree of saproxylic association. Selectivity coefficients (*wi*) are a ratio of habitat use (o_i) in relation to habitat availability (p_i) for each size class (*i*) of aspen logs in the study area. Size classes (SC) are defined as follows: (1) 7 to <16 cm, (2) 16 to <25 cm, (3) 25 to <34 cm, and (4) >34 cm. Disproportionate use of a habitat is indicated by w_i >1 (bold), whereas habitat lower use than expected is indicated by w_i <1. Standard errors (S.E.) are given for w_i values and the G-test statistic was calculated for each beetle category (see methods section; ***p<0.001).

Beetle Category	SC_i	# of samples occupied	o_i	p_i	w_i (± 1 S.E.)		G statistic
Obligate	1	4	0.11	0.80	0.14	(0.47)	**100.85**
	2	10	0.28	0.16	**1.77**	(0.27)	
	3	10	0.28	0.02	**13.43**	(0.28)	***
	4	12	0.33	0.02	**14.59**	(0.25)	
Facultative	1	11	0.24	0.80	0.31	(0.26)	**40.39**
	2	12	0.27	0.16	**1.70**	(0.25)	
	3	10	0.22	0.02	**10.74**	(0.29)	***
	4	12	0.27	0.02	**11.67**	(0.26)	

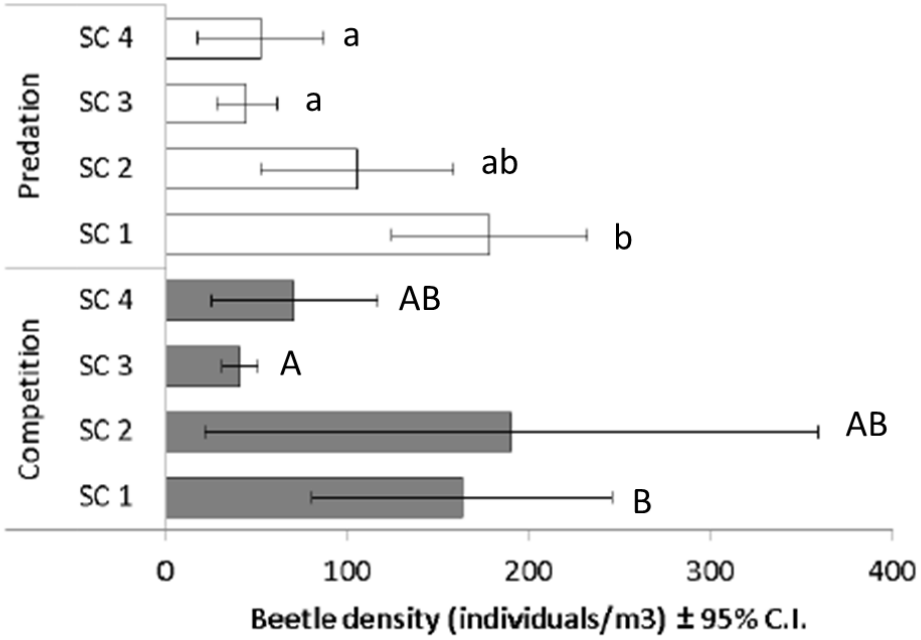

Figure 3.3 Mean densities of predatory beetles (proxy for predation) and other beetles (proxy for competition) in each deadwood size class from extraction funnel samples. Significantly different groups are indicated by letters beside 95% confidence interval bars (α= 0.05).

3.5. Discussion

Each of the four log diameter classes studied harbored a distinctive saproxylic beetle assemblage, with most species indicative of large diameter logs. Differences between assemblages were more pronounced between the largest and smallest diameter classes (Figure 3.2), as also reported by other authors (Jonsell et al. 2007; Hammond et al. 2004; Brin et al. 2011). In fact, assemblages from <16 cm (SC1) logs were only 26% similar to assemblages from larger (≥16 cm) logs, whereas the two largest log SCs (≥25 cm) were 77% similar in their assemblages (Figure 3.2). Though species richness was lowest, both per individual collected and per unit volume, in the largest SC (≥34 cm; Figure1), this habitat was the most used relative to other SCs (Table 3.2). Sixty-one percent of obligate and 49% of facultative saproxylic beetle occurrences were in logs ≥25 cm diameter (SC3 and SC4), despite the rarity of those log habitats- only 4% of logs in the local deadwood pool were ≥25 cm in diameter (Table 3.2, "p_i"). Further, 92% of beetle species that were unique to one size class were found in logs ≥16 cm diameter. These results suggest that a range of SCs support saproxylic diversity, yet large diameter logs are particularly important habitats.

Several hypotheses have been suggested to explain the relationship between deadwood size and saproxylic diversity. Large wood

has a longer persistence on the landscape (i.e., higher stability; Holeksa et al. 2008; Grove and Meggs 2003), has more stable microclimatic conditions (Boddy 1983; Palm 1959), has thicker bark (Hayes et al. 2008; Brin et al. 2011), exhibits greater richness of fungi and unique wood-decay dynamics (Nordén and Paltto 2001; Yee et al. 2006; Kruys and Jonsson 1999), and provides increased substrate heterogeneity (Kolström and Lumatjärvi 2000; Grove 2002b; Brin et al. 2011). In this study, I have additionally shown that differential predation and competition across log SCs could be an important factor determining the distribution of saproxylic beetles in boreal mixedwood habitats. Below, I discuss evidence for these various hypotheses in relation to my results, in turn.

3.5.1. Deadwood Persistence

Smaller-sized wood decays much faster than large deadwood (Holeksa et al. 2008; Harmon et al. 1986; Stevens 1997), mainly because large wood has proportionately more heartwood, which is highly lignified and decays more slowly (Maser and Trappe, 1984). Thus, the heartwood of large logs is a more persistent and stable habitat. Theoretically, species associated with stable habitats are held to be inefficient at dispersal (Southwood 1977; Zera and Denno 1997) and less adapted for quick resource capture (Yee et al. 2006). However, many of the indicator species of ≥25 cm diameter logs in my study, for example *Ampedus*

deletus (LeConte) (Elateridae)*, Cartodere constricta* Gyllenhal (Latridiidae)*,* are readily collected in flight-intercept traps (Hammond 1997; Jacobs et al. 2007), and thus dispersal ability may not play a large role in their disproportionate use of large logs. Some species, particularly beetles with long developmental times and specialists for rare habitats (e.g., *Pytho kolwensis* Sahlberg*;* Siitonen and Saaristo 2000) would likely benefit from longer substrate persistence of large-diameter logs.

3.5.2. Fungi and Wood-Decay Dynamics

Ten of the 17 indicator species for various log SCs in this study were mycophagous or myxomycetophagous, so differences in the fungal communities between SCs are likely important drivers of beetle diversity. For example, *Baeocera humeralis* Fall (Staphylinidae) was found to be a strong indicator of logs ≥34 cm diameter (Figure 3.2). This species requires moist deadwood habitats as it is an obligate consumer of slime molds, and also uses them as a breeding substrate (Betz et al 2003; Wheeler and Blackwell 1984).

Both decomposition pathways and decay organisms can vary considerably between large and small logs, resulting in different beetle assemblages and species occurrences (Yee et al. 2006). For example, large *Eucalyptus obliqua* L'Héritier de Brutelle logs were dominated by brown-rot fungi, whereas white-rot fungi were more prevalent in small logs

(Yee 2005). In aspen, the common white-rot fungus becomes more prevalent with tree age (Basham 1958), and thus is less common in small diameter stems. Additionally, brown-stain fungal isolates are dominated by *Peniophora polygonia* (Persoon) Bourdot and Galzin in young (40-80 year old) trembling aspen, whereas *Radulum casearium* (Morgan) Lloyd is isolated more often from brown-stain in old (>100 year old) aspen (Basham, 1958). These “young” aspen correspond to a diameter of ≤15 cm in the broad-leaved forests of Alberta (Lee et al. 1995).

3.5.3. Deadwood Microclimate

Other characteristics also vary with deadwood diameter and could influence saproxylic assemblages. For example, large diameter wood has greater capacity to hold moisture than smaller wood (Harmon et al. 1986), and thus offers more stable micro-climatic conditions (Boddy 1983; Palm 1959). The greater water-holding capacity of large logs influences the occurrence of drought-sensitive bryophytes and lichens (Söderström 1988) and thus might also drive the habitat selection of hygrophilous beetles. Samuelsson et al. (1994) suggest that invertebrates that are dependent on high moisture, such as most click beetle species (Martin 1989) would be found disproportionately in large diameter substrates. Consistent with this proposition, two click beetle species (*Ampedus deletus* [LeConte] and *A. subtilis* [LeConte]) were indicators of logs ≥25

cm diameter, and elaterids showed significantly disproportional use of larger SC.

3.5.4. Bark Thickness and Persistence

Thicker bark and longer persistence of bark on large logs could explain habitat association patterns observed for other species. For example, the flat bark beetle *Cucujus clavipes clavipes* Fabricius (Cucujidae) is a subcortical predator and was a strong indicator of logs ≥25cm diameter (Figure 3.2). Loss of larger sized logs through intensive forestry could negatively affect such species. Two congeneric European species are included on the European Red List of Saproxylic Beetles (Nieto and Alexander 2010). *Cucujus haematodes* Erichson is listed as endangered in Europe and *C. cinnaberinus* (Scopoli) is listed as near threatened. Six other species of flat bark beetles are indicators of ecological continuity (Alexander 2004), indicating that some flat bark beetles are highly sensitive to disturbance. Given that *C. cinnaberinus* prefers habitat similar to that observed for *C. clavipes* in this study (i.e., large diameter deadwood of broad-leaved trees; Bussler 2002), I suggest that closely-related species that occupy the same ecological niches in the boreal zone of Canada warrant conservation concern.

3.5.5. Deadwood Heterogeneity

Large diameter substrates may provide more heterogeneous habitats (Kolström and Lumatjärvi 2000; Grove 2002b) resulting in greater trophic diversity of saproxylic beetles in large diameter substrates (Brin et al. 2011). I also found evidence for a trend toward greater trophic richness in larger logs, with SC1 logs containing 25% lower richness of feeding guilds compared to SC4. Greater habitat diversity may also support more specialist species (Kolström and Lumatjärvi 2000), perhaps explaining why more unique species were found in large diameter logs in this study.

3.5.6. Predation Risk and Competition

Another possible explanation for differences in habitat associations for saproxylic beetles is differential predation and competition pressure across log SCs. The importance of predation risk on selection functions of prey is well known (e.g., Mao et al. 2005), as predation can be an important limiting factor for many species. In fact, selection indices could reflect either action or avoidance of such limiting factors. I found that higher predator density in small SC logs (Figure 3.3) was correlated with under-utilization of this habitat by saproxylic beetles (Table 3.2). In addition, competition pressure may be greater in small diameter logs. There is also a trend towards higher density of non-predatory beetles (Figure 3.4) and higher density of species per unit volume (Figure 3.1c) in small diameter logs. Thus, competition may also influence habitat

selection due to fitness costs incurred in small logs for some saproxylic beetles.

In summary, mechanisms that govern relative beetle density across deadwood classes may be explained by behavioural (e.g., habitat preferences, dispersal ability), ecological (e.g., action of predation), and/or physical properties of the habitat. Notably, the surface area-to-volume ratio (SAVR) decreases with increasing log diameter. As colonization of logs is undoubtedly affected by log surface area (particularly in early decay classes), the lower SAVR of large logs allows for less crowding in these habitats relative to small diameter logs. Thus, encounter rate of predatory beetles or potential competitors should be lowest in large logs. Saproxylic beetles with low vagility (e.g., *Ampedus* larvae), would be particularly prone to predation in smaller logs. Indeed, two species of *Ampedus* (Elateridae: *A. deletus* [LeConte] and *A. subtilis* [LeConte]) were significant indicators of logs ≥25 cm. Further understanding of the mechanisms that underpin patterns of habitat use by saproxylic beetles is needed to identify the value of particular deadwood qualities in saproxylic beetle conservation.

3.5.7. Small Diameter Deadwood

Smaller-sized logs also supported a distinct fauna, with the highest richness per individual and unit volume. In contrast to the general pattern

of saproxylic beetles being found disproportionately in large diameter habitats, *Corticaria ferruginea* Marsham (Latridiidae) was a strong indicator for SC1 (<16 cm) logs (Figure 3.2) and small diameter logs did harbor high numbers of saproxylic beetle species (Figure 3.1). Seven species were found only in this size class, albeit with fewer than 3 individuals each. Thus, my results concur with those of Brin et al. (2011) in suggesting that a full range of deadwood sizes is important for conservation of saproxylic beetles.

3.5.8. Implications for Deadwood Management

Both large diameter deadwood (e.g., Jonsell et al. 1998; Tikkanen et al. 2006; Lindhe et al. 2005) and European aspen (e.g., Jonsell 2007; Lindhe and Lindelow 2004; Sahlin and Schroeder 2010) have been highlighted as important habitats for saproxylic biodiversity in Europe. However, few studies have examined the entire saproxylic beetle community associated with its ecological equivalent, trembling aspen, in North America (but see Hammond et al. 2001, 2004; Jacobs et al. 2007), and even fewer have considered the effect of deadwood diameter. Hammond et al. (2004) found differences in saproxylic beetle assemblages among diameter classes of standing aspen deadwood (i.e., snags) and both species richness and number of species associations

appear to be greatest in snags ≥41 cm diameter. My study extends this knowledge to aspen logs.

Clearly, aspen logs of different size classes provide distinct habitats for different factions of the saproxylic beetle community. Thus, deadwood management focused only on volume of deadwood retention after harvest is unlikely to achieve the goal of sustaining biodiversity. Larger logs do not simply equate a greater volume of small logs; they are unique and complex habitats that are required by numerous saproxylic species. I have found evidence that <16 cm diameter logs are distinct in species richness and composition, though this SC has only one indicator species and tends to be underutilized by saproxylic beetles. I detected 15 indicator species for logs ≥25 cm diameter. These habitats have much more similar species composition than smaller logs, and are the habitats most often used by saproxylic beetles. Thus, management of aspen deadwood in Canada should aim to retain a range of variation in deadwood diameters (particularly ≥25 cm diameter) in order to maintain critical habitats for saproxylic beetles. However, deadwood left exposed to the sun will provide much different microclimatic conditions than substrates in un-harvested stands (Langor, Pers. obs.), and may be suitable for open-habitat species but unable to support the saproxylic fauna of old forests (Kaila et al. 1997). In forest operations, it has been suggested that leaving deadwood in shaded positions as well as exposed to sun would be

advantageous for biodiversity conservation (Jonsell et al. 2004). Retention schemes could use shrub cover over retained wood (Caners et al. 2010) or retention in patches of uncut forest to help preserve closed-forest microclimatic conditions.

3.6. Literature Cited

Alexander, K. N. A. 2004. Revision of the Index of Ecological Continuity as used for saproxylic beetles. English Nature Research Reports 574: 1-60.

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. Austal Ecology 26: 32–46.

Anderson, M. J. 2005. PERMANOVA: a FORTRAN computer program for permutational multivariate analysis of variance, version 1. Department of Statistics, University of Auckland, Aukland.

Ausmus, B. S. 1977. Regulation of wood decomposition rates by arthropod and annelid populations. Ecological Bulletin 25: 180-192.

Basham, J. T. 1958. Decay of trembling aspen. Journal of Botany 36: 491–505.

Beckingham, J. and J. H. Archibald. 1996. Field guide to ecosites of Northern Alberta. Special Report 5. Natural Resources Canada, Canadian Forest Service. Northwest Region. Edmonton, AB.

Betz, O., M. K. Thayer, and A. F. Newton. 2003. Comparative morphology and evolutionary pathways of the mouthparts in spore-feeding Staphylinoidea (Coleoptera). Acta Zoologica (Stockholm) 84: 179–238.

Boddy, L. 1983. Microclimate and moisture dynamics of wood decomposing in terrestrial ecosystems. Soil Biology and Biochemistry 15: 149–157.

Bouget, C., A. Brin, and H. Brustel. 2011. Exploring the "last biotic frontier": Are temperate forest canopies special for saproxylic beetles? Forest Ecology and Management 261(2): 211-220.

Brin, A., C. Bouget, H. Brustel, and H. Jactel. 2011. Diameter of downed woody debris does matter for saproxylic beetle assemblages in temperate oak and pine forests. Journal of Insect Conservation 15(5): 653-669.

Buskirk, S. W. and J. J. Millspaugh. 2006. Metrics of use and availability in studies of resource selection. Journal of Wildlife Management 70:358-366.

Bussler, H. 2002. Studies of faunistics and ecology of *Cucujus cinnaberinus* (Scop., 1763) in Bavaria, Germany. Nachrichtenblatt der Bayerischen Entomologen 51(3-4):42-60.

Caners, R.T., S.E. Macdonald, and R.J. Belland. Responses of boreal epiphytic bryophytes to different levels of partial canopy harvest. Botany 88: 315-328.

Cobb, T.P., K.D. Hannam, B.E. Kishchuk, D.W. Langor, S.A. Quideau, and J.R. Spence. 2009. Wood-feeding beetles and soil nutrient cycling in burned forests: implications of post-fire salvage logging. Agricultural and Forest Entomology 12(1): 9-18.

Colwell, R. 2009. EstimateS: Statistical estimation of species richness and shared species from samples. Version 8.2. http://viceroy.eeb.uconn.edu/EstimateS

Colwell, R.K., C.X. Mao, and J. Chang. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology 85 (10): 2717-2727.

Cyr, D., S. Gauthier, Y. Bergeron, and C. Carcaillet. 2009. Forest management is driving the eastern North American boreal forest outside its natural range of variability. Frontiers in Ecology and the Environment 7: 519–524.

Dufrêne, M. and P. Legendre. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecological Monographs 67: 345–366.

Eriksson, L.-G. 1993. Mängd trädrester efter trädbränsleskörd. Rapport från Vattenfall Utveckling AB. Projekt Bioenergi 28. 27 p.

Esseen, P. A., B. Ehnström, L. Ericson, and K. Sjöberg. 1997. Boreal forests. Ecological Bulletins 46: 16–47.

Gibb, H., J. P. Ball, T. Johansson, O. Atlegrim, J. Hjalten, and K. Danell. 2005. Effects of management on coarse woody debris volume and composition in boreal forests in northern Sweden. Scandinavian Journal of Forest Research 20(3): 213-222.

Gotelli, N. and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4: 379–391.

Grove, S. J. 2002a. Saproxylic insect ecology and the sustainable management of forests. Annual Review of Ecological Systems 33: 1-23.

Grove, S.J. 2002b. The influence of forest management history on the integrity of the saproxylic beetle fauna in an Australian lowland tropical rainforest. Biological Conservation 104: 149–171.

Grove, S. J. and J. Meggs. 2003. Coarse woody debris biodiversity and management: a review with particular reference to Tasmanian eucalypt forests. Australian Forestry 66: 258–272.

Hammond, H. E. J. 1997. Arthropod biodiversity from *Populus* coarse woody material in north-central Alberta: A review of taxa and collection methods. The Canadian Entomologist 129(6): 1009-1033.

Hammond, H.E.J., D.W. Langor, and J R. Spence. 2001. Early colonization of *Populus* wood by saproxylic beetles (Coleoptera). Canadian Journal of Forest Research 31(7): 1175-1183.

Hammond, H.E.J., D.W. Langor, and J.R. Spence. 2004. Saproxylic beetles (Coleoptera) using *Populus* in boreal aspen stands of western Canada: spatiotemporal variation and conservation of assemblages. Canadian Journal of Forest Research 34(1): 1-19.

Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaenper, K. J. Cromack, and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15: 133–302.

Hayes, C. J., T. E. DeGomez, J. D. McMillin, J. A. Anhold, and R. W. Hofstetter. 2008. Factors influencing pine engraver (*Ips pini* Say) colonization of ponderosa pine (*Pinus ponderosa* Dougl. ex. Laws.) slash in Northern Arizona. Forest Ecology and Management 255(8-9):3541-3548.

Hesselink, T.P. 2010. Increasing pressures to use forest biomass: A conservation viewpoint. The Forestry Chronicle 86(1): 28-35.

Holeksa, J., T. Zielonka, and M. Zywiec. 2008. Modeling the decay of coarse woody debris in a subalpine Norway spruce forest of the West Carpathians, Poland. Canadian Journal of Forest Research 38(3):415-428.

Janssen, P., C. Hébert, and D. Fortin. 2011. Biodiversity conservation in old-growth boreal forest: black spruce and balsam fir snags harbour distinct assemblages of saproxylic beetles. Biodiversity Conservation 20: 2917-2932.

Jacobs, J.M., J.R. Spence, and D.W. Langor. 2007. Influence of boreal forest succession and dead wood qualities on saproxylic beetles. Agricultural and Forest Entomology 9(1):3-16.

Jonsell, M., J. Hansson, and L. Wedmo. 2007. Diversity of saproxylic beetle species in logging residues in Sweden - Comparisons between tree species and diameters. Biological Conservation 138(1-2):89-99.

Jonsell, M., J. Weslien, and B. Ehnstrom. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodiversity and Conservation 7(6):749-764.

Kimmins, J. P. 1977. Evaluation of the consequences for future tree productivity of the loss of nutrients in whole-tree harvesting. Forest Ecology and Management 1: 169–183.

Kishchuk, B. E. 2004. Soils of the Ecosystem Management Emulating Natural Disturbance (EMEND) experimental area, northwestern Alberta. Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre, Edmonton, AB. Information Report NOR-X-397.

Kolstrom, M. and J. Lumatjarvi. 2000. Saproxylic beetles on aspen in commercial forests: a simulation approach to species richness. Forest Ecology and Management 126(2):113-120.

Kouki, J., S. Lofman, P. Martikainen, S. Rouvinen, and A. Uotila. 2001. Forest fragmentation in Fennoscandia: Linking habitat requirements of wood-associated threatened species to landscape and habitat changes. Scandinavian Journal of Forest Research:27-37.

Krebs, C. J. 1999. Ecological Methodology. 2. Addison-Wesley, California, 620 pp.

Kruys, N. and B. G. Jonsson. 1999. Fine woody debris is important for species richness on logs in managed boreal spruce forests of northern Sweden. Canadian Journal of Forest Research 29:1295–1299.

Langor, D.W., H.E.J. Hammond, J.R. Spence, J. Jacobs and T.P. Cobb. 2008. Saproxylic insect assemblages in Canadian forests: diversity, ecology, and conservation. The Canadian Entomologist 140: 453–474.

Lee, P.C., S. Crites and J.B. Stelfox. 1995. Changes in forest structure and floral composition in a chronosequence of aspen mixedwood stands in Alberta. In: Stelfox, J.B. (ed.). 1995. Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forests in Alberta. Alberta Environmental Centre, Vegreville, AB, and Natural Resources Canada, Canadian Forest Service, Edmonton, AB. pp. 308.

Lengendre, P. and L. Legendre. 1998. Numerical Ecology: Developments in environmental monitoring, 20. 2nd English Edition. Elsevier, Amsterdam, 853 pp.

Lindhe, A. and A. Lindelow. 2004. Cut high stumps of spruce, birch, aspen and oak as breeding substrates for saproxylic beetles. Forest Ecology and Management 203(1-3):1-20.

Lindhe, A., A. Lindelow and N. Asenblad. 2005. Saproxylic beetles in standing dead wood density in relation to substrate sun-exposure and diameter. Biodiversity and Conservation 14(12): 3033-3053.

Manly, B.F.J., L.L. McDonald, D.L. Thomas, T.L. McDonald and W.P. Erickson. 2002. Resource Selection by Animals: Statistical Analysis and Design for Field Studies, 2nd ed. Kluwer Academic Publishers, Boston, MA.

Mao, C.X., R.K. Colwell, and J. Chang 2005. Estimating the species accumulation curve using mixtures. Biometrics 61(2):433-441.

Martikainen, P., J. Siitonen, P. Punttila, L. Kaila, and J. Rauh. 2000. Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biological Conservation 94(2):199-209.

Martin, O. 1989. Click beetles Coleoptera Elateridae from old deciduous forests in Denmark. Entomologiske Meddelelser 57(1-2):1-110.

Maser, C. and J.M. Trappe. (eds.). 1984. The seen and unseen world of the fallen tree. USDA Forest Service General Technical Report. PNW-164. Pacific Northwest Forest Range Experimental Station, Portland, OR, pp. 56.

McArdle, B. H. and M. J. Anderson. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82: 290–297.

McCune, B. and M. J. Mefford. 2006. PC-ORD: Multivariate Analysis of Ecological Data, Version 5.31. MjM Software Design, Gleneden Beach, Oregon, USA.

McLoughlin, P.D., Morris, D.W., Fortin, D., Vander Wal, E., and Contasti, A.L. 2010. Considering ecological dynamics in resource selection functions. Journal of Animal Ecology 79: 4-12.

Nieto, A. and K.N.A. Alexander. 2010. European red list of saproxylic beetles. Luxembourg: Publications Office of the European Union.

Nordén, B. and H. Pallto. 2001. Wood-decay fungi in hazel wood: species richness correlated to stand age and dead wood features. Biological Conservation 101:1–8.

Östlund, L., Zackrisson, O., and Axelsson, A.-L. 1997. The history and transformation of a Scandinavian boreal forest landscape since the 19th century. Canadian Journal of Forest Research 27: 1198–1206.

Palm, T. 1959. Die holz- und Rindenkafer der sud-und mittelschwedischen Laubbaume [The wood- and bark-beetles of south and mid-Swedish broadleaves]. Opuscula Entomologica Supplementum 16: 1–374.

Pratt, L. and I. Urquhart. 1994. The last great forest: Japanese multinationals and Alberta's Northern Forests. Edmonton, AB, NeWest Press. 232 pp.

Ranius, T. and N. Jansson. 2000. The influence of forest regrowth, original canopy cover and tree size on saproxylic beetles associated with old oaks. Biological Conservation 95(1):85-94.

Sahlin, E. and L.M. Schroeder. 2010. Importance of habitat patch size for occupancy and density of aspen-associated saproxylic beetles. Biodiversity and Conservation 19(5):1325-1339.

Samuelsson, J., L. Gustafsson, and T. Ingelog. 1994. Dying and dead trees: a review of their importance for biodiversity. Swedish Threatened Species Unit, Uppsala, Sweden. 110 pp.

Shaw, C.H., H. Lundkvist, A. Moldenke and J.R. Boyle. 1991. The relationships of soil fauna to long-term forest productivity in temperate and boreal ecosystems: processes and research strategies, pp. 39-77. In: W.J. Dyck and C.A. Mees. (eds.). 1990. Long-Term Field Trials to Assess Environmental Impact of Harvesting. Proceedings, IEA/BE T6/A6 Workshop, Florida, USA. IEA/BE T6/A6 Report No. 5.

Shorohova, E., D. Kneeshaw, T. Kuuluvainen and S. Gauthier. 2011. Variability and Dynamics of Old-Growth Forests in the Circumboreal Zone: Implications for Conservation, Restoration and Management. Silva Fennica 45(5): 785-806.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins 49:11–41.

Siitonen, J. and P. Martikainen. 1994. Occurrence of rare and threatened insects living on decaying *Populus tremula* – A comparison between Finnish and Russian Karelia. Scandinavian Journal of Forest Research 9(2):185-191.

Siitonen, J. and L. Saaristo. 2000. Habitat requirements and conservation of *Pytho kolwensis*, a beetle species of old-growth boreal forest. Biological Conservation 94(2):211-220.

Simila, M., J. Kouki, P. Martikainen, and A. Uotila. 2002. Conservation of beetles in boreal pine forests: the effects of forest age and naturalness on species assemblages. Biological Conservation 106(1):19-27.

Söderström, L. 1988. Sequence of bryophytes and lichens in relation to substrate variables of decaying wood in northern Sweden. Nordic Journal of Botany 8:89-97.

Söderström, L. 1988. The occurrence of epixylic bryophyte and lichen species in an old natural and a managed forest stand in northeast Sweden. Biological Conservation 45:169-178.

Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? Journal of Animal Ecology 46: 337-365.

Speight, M. C. D. 1989. Saproxylic invertebrates and their conservation. Nature and Environment Series 42 Council of Europe. Strasbourg, France.

Stenbacka, F. 2009. Response of saproxylic insect communities to forestry: Implications for Conservation. Ph.D. Thesis. Swedish University of Agricultural Sciences, Sweden

Stevens, V. 1997. The ecological role of coarse woody debris: an overview of the ecological importance of CWD in B.C. forests. Research Branch, B.C. Ministry of Forests, Victoria, B.C. Working Paper 30: iii-26.

Swift, M. J. 1977. The ecology of wood decomposition. Scientific Progress 64:175–199.

Tikkanen, O.P., P. Martikainen, E. Hyvarinen, K. Junninen, and J. Kouki. 2006. Red-listed boreal forest species of Finland: associations with forest structure, tree species, and decaying wood. Annales Zoologici Fennici 43(4): 373-383.

Väisänen, R., O. Bistrom, and K. Heliovaara. 1993. Subcortical Coleoptera in dead pines and spruces - is primeval species composition maintained in managed forests. Biodiversity and Conservation 2(2): 95-113.

Warren, M.S. and R.S. Key. 1991. Woodlands: Past, present and potential for insects. In: The Conservation of Insects and Their Habitats. (ed.). N. M. Collins and J. A. Thomas, London, Academic, pp. 155–203.

Wheeler, Q.D. and M. Blackwell. 1984. Fungus-Insect Relationships: Perspectives in Ecology and Evolution. Columbia University Press, New York.

Yee, M. 2005. The ecology and habitat requirements of saproxylic beetles native to Tasmanian wet eucalypt forests: potential impacts of commercial forestry practices. Ph.D. Thesis. University of Tasmania, Australia.

Yee, M., S.J. Grove, A.M.M. Richardson, and C.L. Mohammed. 2006. Brown rot in inner heartwood: why large logs support characteristic saproxylic beetle assemblages of

conservation concern. General Technical Report - Southern Research Station, USDA Forest Service: 42-56.

Zera, A.J. and R.F. Denno. 1997. Physiology and ecology of dispersal polymorphism in insects. Annual Review of Entomology 42: 207-230.

4. HABITAT ASSOCIATIONS OF SAPROXYLIC BEETLES IN TREMBLING ASPEN DEADWOOD

4.1. Introduction

Deadwood substrates are among the most important structural features in forest ecosystems (Harmon et al. 1986). Structural attributes of standing dead trees (i.e., 'snags') and fallen dead trees (i.e., 'logs'), for example, differ from those of surrounding live trees, providing a multitude of habitats for associated forest organisms. Indeed, there is a rich community of bryophytes, lichens, and invertebrates associated with dying, dead, and decaying trees. Furthermore, deadwood habitats present much habitat variability for the 'saproxylic' organisms that depend on this resource (e.g., see Chapter 3).

Since deadwood-dependent organisms are negatively affected by forestry in northern Europe (Simila et al. 2002; Siitonen and Martikainen 2004) these organisms and their habitats have become a conservation priority (Ehnström and Waldén 1986; Jonsell et al. 1998; Tikkanen 2006). In particular, the beetles (Coleoptera), which comprise the most diverse multi-cellular animal order world-wide, dominate most saproxylic communities. Recently, 436 saproxylic beetle species were included in the European Red-List, with their elevated risks of extinction mainly due to logging and wood harvesting (Nieto and Alexander 2010). Designation of critical forest areas for preservation as a part of overall conservation plans would be more effective if structural indicators of saproxylic biodiversity,

such as deadwood attributes, could be used as a guide. Habitats known to support rare or threatened taxa would also be of much conservation value. The use of structural indicators, or 'surrogates' of biodiversity is gaining popularity in conservation planning, particularly for taxa in which field surveys are expensive, taxonomic expertise is scarce, and species diversity is high (Juutinen et al 2006; Lassauce et al. 2011).

Development of useful surrogates depends on having strong habitat associations at the community and/or species level. Despite recent studies of saproxylic beetles in North America, knowledge of habitat associations remains limited, and more often qualitative than statistically rigorous. However, it is known that forestry practices will negatively impact saproxylic taxa in the Canadian boreal (Cobb et al. 2011), as they have elsewhere in the world (Martikainen et al. 2000; Siitonen 2001; Simila et al. 2002; Nieto and Alexander 2010). Given well-established threats to saproxylic diversity on harvested landscapes, there is serious need to prioritize saproxylic beetle conservation in North America. An important first step is increasing knowledge of saproxylic beetle-deadwood habitat associations.

In this chapter, I focus on associations between saproxylic beetles and substrate qualities of aspen deadwood in broad-leaved stands of the boreal mixedwood forest. Specifically, my objectives were to: 1) characterise fine-scale species richness, diversity, and dominance patterns of saproxylic beetles, and 2) assess relationships between

saproxylic assemblages and substrate variables in order to delineate important habitats and possible structural indicators for the saproxylic beetle fauna of aspen in western Canada.

4.2. Methods

4.2.1. Study Area

Four mature, deciduous-dominated stands were selected in a 16.3 km^2 area of the boreal mixedwood forest in Northwest Alberta, Canada (Study area: 56°40’39.30", 118°06’30.02" W) after confirming that deadwood substrates were sufficiently available to support replicated sampling for saproxylic beetles across the complete range of factors of interest in this work. The study area centre was located approximately 17 km from the Ecosystem Management Emulating Natural Disturbance (EMEND) research forest. None of the selected stands had been previously harvested, though the surrounding landscape was in various stages of regeneration following clear-cut and variable retention harvesting. Forest overstory was dominated by trembling aspen (*Populus tremuloides* Michaux; 85.43%) with minor composition of balsam poplar (*Populus balsamifera* Linnaeus; 12.26%), white birch (*Betula papyrifera* Marshall; 1.83%) and white spruce (*Picea glauca* [Moench] Voss; 0.48%). Understory vegetation was mainly (>70%) comprised of prickly rose (*Rosa acicularis* Lindley), low-bush cranberry (*Viburnum edule* [Michaux] Rafinesque), wild sarsaparilla (*Aralia nudicaulis* Linnaeus) and fireweed

(Chamerion angustifolium [Linnaeus] Holub). Elevation varied between 741 and 874 meters above sea level. Soils were primarily Luvisolic, well drained, and derived from fine-textured glacial till and glaciolacustrine parent materials (Beckingham & Archibald 1996; Kishchuk 2004).

4.2.2. Deadwood Substrate Sampling

A total of 60 standing ('snag') and 73 fallen ('log') deadwood substrates were selected across the four stands, stratified according to decay class (DC) and sampled for various structural characteristics (as in Chapter 2, Table 2.1). Additionally, one live tree from three of the stands was sampled, giving a total of 136 substrate samples. All live trees had tightly attached, green bark, green leaves, and fine twigs present when felled. Two live trees appeared to have some heart-rot, but no conks were present on the sampled piece of wood. Only substrates with a diameter ≥7 cm and occurring >30 m from the nearest logging road were selected. In this chapter, I examine eleven main 'Habitat Classes', which comprise substrate type and decay class, as follows: Live trees= 'Tr0', Snag DC1= 'Sn1', Snag DC2= 'Sn2', Snag DC3= 'Sn3', Snag DC4= 'Sn4', Log DC1= 'Lg1', Log DC2= 'Lg2', Log DC3= 'Lg3', Log DC4= 'Lg4', Log DC5= 'Lg5', and Log DC6= 'Lg6'. Note that log and snag decay classes are not equivalent, as they are assessed by different criteria (i.e., Snag DC3 ≠ Log DC3) (Chapter 2, Table 2.1).

4.2.3. Beetle Sampling

Beetles were collected using a variety of methods to improve the likelihood of sampling the entire saproxylic community associated with aspen. For snags, I employed both window traps and emergence traps on twelve replicate snags in each of the four snag decay classes, for a total of 48 emergence traps and 48 window traps (See Chapter 2 for complete description of collection methods). Emergence traps were made of grey nylon 'no-see-um' netting (mesh size= 0.6 mm x 0.6mm), which enclosed a 1m length of the trunk, from 1.3 m above ground to 2.3 m above ground. The base of the emergence trap tapered to a single (100 mL) plastic collection jar. Window traps (Kaila 1993; Hammond 1997) were made of a clear plastic pane (1.5 mm x 20 cm x 30 cm) with a cloth funnel underneath attached to a (100 mL) plastic collection jar. Window traps were attached at 1.3 m above ground (base of emergence traps), such that each of the 48 snags (12 reps of each DC) was equipped with a single window trap and single emergence trap.

Beetles were also sampled from 3 replicate samples (0.7m long) of each of: the four snag decay classes (Sn1-4), the six log decay classes (Lg1-6), and live trees (Tr0) by use of rearing drums. The 33 rearing drums were made from plastic (121 L) garbage bins that were modified by drilling a single hole in the bottom to allow for collection of beetles into an attached glass canning jar (9 cm x 12 cm). Rearing occurred at ambient outdoor temperature, in a forest near the EMEND camp.

Logs were dissected to make hand-collections of beetles, searching exterior log microhabitats first (e.g., moss), before proceeding systematically to the innermost log microhabitats (e.g., heartwood). Microhabitat locations for beetles were categorised as: i) ‘fungus’- within or on fruiting bodies of macrofungi (basidiomycetes and ascomycetes) growing on logs; ii) ‘moss’- within a bryophyte layer growing on logs; iii) ‘lichen’- within or on a lichen thallus growing on logs; iv) ‘bark layers’- within the layers of bark (includes all tissues to the outside of the vascular cambium); v) ‘under bark’- within the ‘subcortical’ space (between the xylem and bark); or vi) ‘wood’- within the xylem. The ‘wood’ category was further subdivided by radial depth within the xylem as: ‘shallow’- the outer third of the xylem radius, ‘middle’- the middle third of the xylem radius; and ‘heart’- the inner third portion of the xylem radius (not physiologically analogous to the heartwood).

Modified Tullgren funnels were used to extract beetles from the residues remaining after hand collection from 55 (0.5m long) log sections. The funnel extractors, made from plastic, were held in a warehouse near to the field site. Each funnel held wood fragments in a (40.6 cm height x 47 cm diameter) cylindrical chamber, which was separated from the (29 cm high) funnel portion by coarse (2 cm x 2 cm) metal hardware cloth. The funnel lids were tight fitting and largely made of (2 mm x 2 mm) metal mesh, allowing heat and light from a 100-watt light bulb to transfer to the contained substrate. Light bulbs were was suspended 1 – 2 cm above the

lid, and shone continuously for the extraction period. The base of each funnel was fitted with a plastic bag for collection of beetles as they were extracted.

Beetles were collected from window traps, emergence traps, and rearing drums from May through August 2008, while hand collections and funnel extractions began in June and carried through August of the same year. All collection containers were filled with 30 – 50 mL of propylene glycol as a killing agent. Window trap, emergence trap, and rearing drum samples were collected and refreshed every 14 days, whereas funnel samples were collected once, after an average extraction period of 9.9 days and hand collections occurred once on each log, for 2.7 hours on average. Subsequent to collection, beetles were sorted and preserved in 70% ethanol.

Beetles were identified to species (or to the lowest taxonomic level possible) in the laboratory, excluding aleocharines (Staphylinidae). Once identified, specimens were classified as obligatorily or facultatively saproxylic based on the known species feeding habit (e.g., phloeophagous, mycophagous, detritivore) and habitat requirements (e.g., sapwood, polypore fruiting bodies, under bark) as determined from the literature.

4.3. Analyses

Non-saproxylic beetles (24 species and 288 individuals) and immature beetles (2227 individuals) in the samples were excluded from all the analyses presented here. In addition, 77 species that were not collected by other methods were excluded from the window trap data set, in an attempt to restrict analyses to species with true affiliations for saproxylic habitats.

4.3.1. Environmental Variables

Variation in saproxylic beetle catch was studied in relation to three classes of environmental variables: 'local variables', 'habitat variables', and 'habitat attributes' (Table 4.1). Local variables described aspects of each stand sampled. Habitats were described in relation to deadwood position, type, decay class, and habitat class as described above. Additionally, I assessed various substrate attributes (e.g., bark cover, presence of moss, presence of fungal fruiting bodies) for relationships with saproxylic beetle assemblages and species, as outlined in Table 4.1.

4.3.2. Community Structure

I used a constrained Canonical Correspondence Analysis (CCA) ordination (ter Braak 1986) to explore relationships between environmental variables and saproxylic beetle assemblages. CCA is an appropriate approach for investigating community-environment relationships, even if the effects are hidden by other large sources of

variation (ter Braak and Verdonschot 1995). Analysis was computed in R (R Development Core Team 2010) with the VEGAN package (Oksanen et al. 2009) using the aforementioned environmental variables and dummy variables coding for decay classes. For substrate attributes, the average value for each of the pooled replicates was used in the analysis. All variables and factors were tested for significance using Monte Carlo permutation tests (999 permutations). Replicate samples of each decay class and substrate type were pooled within sites for community analyses, and relative abundance of species (abundance of sp_i / sum of abundance of all spp in sample) was used to account for variation in sampling method performance or sample volume, for example. Additionally, variation in species composition was examined across the eleven habitat classes (Tr0, Sn1-4, Lg1-6) studied through cluster analysis based on Bray-Curtis dissimilarity using the average-linkage method.

Table 4.1 Environmental variables selected for analyses.

Variables	Name	Description	Units
Local Variables:	DIST	Landscape position	km distance between sites
	ELEV	Elevation	m above sea level
	SITE	Stand identity	Factor A to D
Habitat Variables:	POS	Vertical position	Factor Standing, Fallen
	TYPE	Substrate type	Factor Tr, Sn, Lg[a]
	HabC11	11 Habitat Classes	Class 0 to 10[b]
	DEATH	Health Status	Dead=1, Alive=0
	FRESH	Live or recently dead (Sn1 or Lg1)	Presence/absence
Substrate Attributes:	xDIAM	Mean sample diameter	cm
	LTH	Total length (or height)*	m
	Length	Length class	Factor high, low[c]
	VOL	Mean sample volume	m^3[c]
	Volume	Volume class	Factor high, low[c]
	CrackW	Cracks in wood	Presence/absence
	FragW	Wood fragmented	Presence/absence
	%Bark	Bark cover	%
	BarkCC	Bark cover class	Class 0 to 7[d]
	SAbark	Surface area of bark	m^2
	BarkSAc	Bark surface area class	Factor high, low[c]
	CrackB	Cracks in bark	Presence/absence
	PeelB	Peeling of outer bark	Presence/absence
	TIGHT	Bark tight to wood	Presence/absence
	BRANCH	Branches	Presence/absence
	TWIG	Twigs	Presence/absence
	LEAF	Brown/green leaves	Presence/absence
	AntN	Ant nest	Presence/absence
	totFUNG	Any visible fungus*	Presence/absence
	POLY	Polypore fungi*	Presence/absence
	Ptrem	*Phelinus tremulae**	Presence/absence
	FUNG	Any visible fungus	Presence/absence
	MACRO	Macrofungi fruiting bodies	Presence/absence
	MICRO	Microfungi or slime mold	Presence/absence
	MOSS	Bryophytes	Presence/absence
	LICHEN	Lichens	Presence/absence
	VASC	Vascular plants	Presence/absence

[a]Tr= live tree, Sn= snag, Lg= log; [b]0= Tr0, 1= Sn1, 2= Sn2, 3= Sn3, 4= Sn4, 5= Lg1, 6= Lg2, 7= Lg3, 8= Lg4, 9= Lg5, 10= Lg6; [c]high= >average, low= <average; [d]0= 0%, 1= >0%, 2= >10%, 3= >25%, 4= >50%, 5= >75%, 6= >90%, 7= 100%; ***** measured along entire substrate.

4.3.3. Richness and Diversity

Saproxylic beetles were pooled within each of the eleven habitat classes in order to compare i) observed mean species richness (per sample), ii) rarefied species richness, iii) Shannon's (H'), and iv) Simpson's (1-D) diversity measures among habitats. The number of expected species was calculated for each using the Mao-Tau Method of Moments approach (Colwell et al. 2004; Mao et al. 2005) to allow for direct statistical comparison of richness between sample sets. All rarefactions were performed in EstimateS v. 8.2 (Colwell 2009).

4.3.4. Indicator Species

An Indicator Species Analysis (ISA) (Dufrêne and Legendre 1997) was conducted to describe species relationships to substrate position, type, and decay class. Further, environmental variables (Table 4.1) were coded as factors (or dummy variables) and subjected to ISAs, to describe species relationships to substrate qualities (such as bark cover or sample volume). A species was considered an indicator for a given substrate when its maximum indicator value (IV) was >25% and differed significantly from random ($\alpha = 0.05$) after a Monte Carlo test based on 2000 permutations. An IV of 25% translates to a species having half of its total abundance in half of the samples. To focus on the most characteristic species for each variable, I distinguished 'strong indicators' as having an

IV threshold of ≥60%, which coincides with a species that has three-quarters of its abundance in three-quarters of the samples (as in Pinzón & Spence 2010). A perfect indicator would theoretically have an IV of 100% (Dufrêne and Legendre 1997), and is thus found only in the indicated habitats.

4.3.5. Species Dominance

To further analyse the structure of saproxylic beetle assemblages in each habitat class and substrate type, dominance values (Pinzón & Spence 2010) were calculated for species in each habitat class. Relative dominance values (DV') for each species were calculated as a product of proportional presence (w) and proportional abundance (AP), relative to all other species in the assemblage. As suggested by Pinzón & Spence (2010), species dominance classes were assigned based on w_i and AP_i scores for each species, i, in relation to the mid-value [(max-min)/2] (or quarter-value: mid-value/2) for w and AP. Dominance classes are as follows: D= "dominant" (w_i and AP_i > mid-value), S= "subdominant" (w_i > mid-value; AP_i<mid-value), C= "common" (quarter-value<w_i<mid-value; AP_i<mid-value), and U="uncommon" (w_i<quarter-value; AP_i<mid-value).

4.3.6. Log microhabitats

Beetle data from hand-collecting in log habitats allowed for investigation of microhabitats within logs and how these may structure

beetle assemblages. A cluster analysis (Sorensen similarity, presence/absence of species, Ward flexible β= -0.25) was performed on a dataset with 192 individuals from 20 species (after removing 42 species represented by only one or two individuals) collected from 7 of the 8 log microhabitats (no beetles were collected in lichen). An Analysis of Similarities (ANOSIM; Clarke 1993) was used to test whether beetle assemblages differed among log microhabitats.

4.4. Results

In total, 4087 saproxylic beetles representing 44 families and 242 species were collected during this study (Appendix 4-A). The sampling effort contributed substantially to our understanding of saproxylic beetles in northern Alberta. For example, seven species were confirmed as new to science (six undescribed *Corticaria* spp. and one undescribed *Rhizophagus* sp.) and will be formally described elsewhere. One other species (unconfirmed) is likely undescribed; a 'round fungus beetle', here referred to *Agathidium* n. sp. 1, could not be determined from the recent revisions of the genus (Wheeler and Miller 2005; Miller and Wheeler 2005) and upon inspection of genitalia, appears to be new. An additional 45 species were new records for Alberta including nine latridiid species and seven cryptophagids (Appendix 5-A).

After removing species that were only collected in window traps, 179 species and 3874 individuals remained for analyses. Of all saproxylic

beetles collected, 36 species were found uniquely in snag habitats, while 64 species were collected only from logs. Interestingly, all species reared from live trees were also collected from deadwood habitats. Staphylinidae (rove beetles) was the most species rich family, having 52 species, followed by Latridiidae (minute brown scavenger beetles) with 26 species, and Cryptophagidae (silken fungus beetles), with 21 species. Individuals of the Staphylinidae and Latridiidae were also most abundant, accounting for 1123 individuals and 1058 individuals, respectively.

4.4.1. Community Structure

Canonical Correspondence Analysis (CCA) produced a significant ordination (p= 0.005 after 999 permutations) in relation to environmental variables (Figure 4.1). The first two canonical axes explained only 11.85% of the total variance in saproxylic beetle assemblages, with Axis 1 (CCA1) and Axis 2 (CCA2) explaining 6.0% and 5.2%, respectively. The large amount of unexplained variance could result from stochastic variation in species occurrences, or variation within “replicate” deadwood samples; either or both effects are quite plausible for these assemblages. However, noise in species data does not seriously affect the ability of CCA to illuminate what patterns there are (Palmer 1993).The strongest saproxylic beetle-environment correlations were among the variables: DEATH, TYPE, HabC11, %Bark, and MOSS (Table 4.2), suggesting that these substrate characteristics are related to the underlying structure of beetle

assemblages. Assemblages differed significantly across substrate TYPE (ANOSIM: R= 0.5158, p= 0.001, 999 permutations), and appeared to group clearly with respect to this characteristic in the ordination (Figure 4.1a).

Axis 1 appears to be driven mainly by position ('POS'), and is interpreted as a gradient from standing to fallen wood. Not surprisingly, some biotic characteristics, such as moss and lichen cover, are also strongly correlated with position along Axis 1, as their values are high on fallen substrates (Figure 4.1c). The beetle species sort out well and in logical pattern along the position gradient also (Figure4.1b), e.g., *Canifa pallipes* (Melsheimer) (Scraptiidae; species score CCA1= -1.01) is encountered in standing substrates, whereas *Agonum retractum* LeConte (Carabidae; CCA1= +1.06) occurs in fallen substrates. The species with low Axis 1 scores are typical of live trees and snags (e.g., *Epuraea flavomaculata* Mäklin, *Cossonus pacificus* Van Dyke), and those with high Axis 1 scores are associated with fallen deadwood (e.g., *Cartodere constricta* (Gyllenhal), *Pteryx* sp. 1*, Corticaria elongata* Gyllenhal).

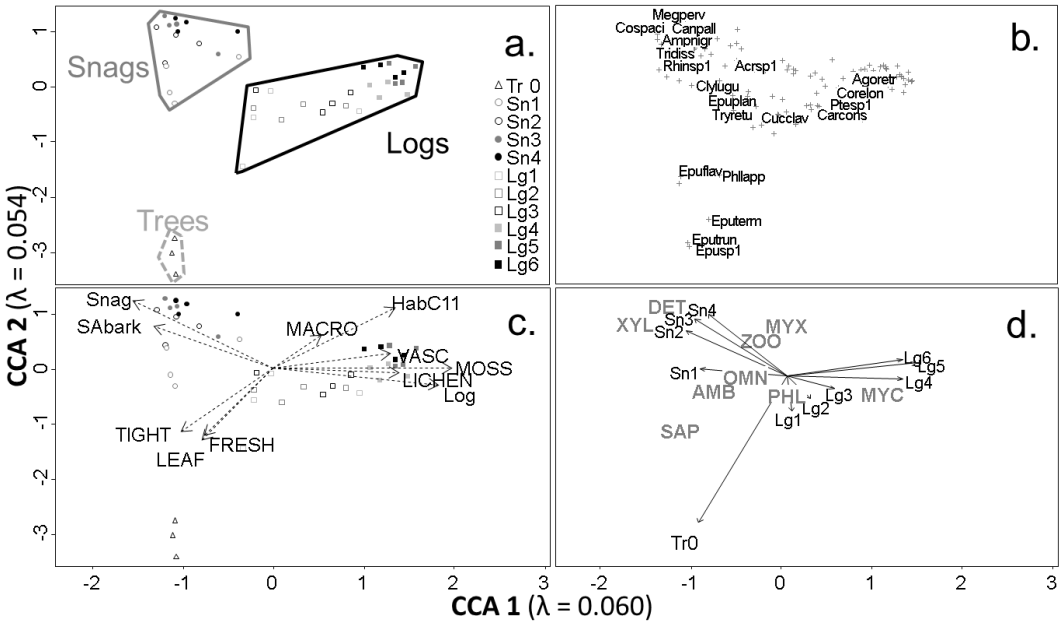

Figure 4.1 Canonical Correspondence Analysis (CCA ordination) of saproxylic beetle assemblages (pooled relative abundance data) from aspen substrates; a) sample points (symbolised according to the legend; top, right) distinguish various substrates by habitat class; b) species centroids (+; with selective labeling of strong indicator species); c) significant environmental vectors (dashed arrows) ; and d) feeding guild (grey) relationship with habitat class (black vectors); variables are explained in Table 4.2; Acrsp1= *Acrotrichis* sp. 1, Agoretr= *Agonum retractum*, Ampnigr= *Ampedus nigricans*, Canpall= *Canifa pallipes*, Carcons= *Cartodere constricta*, Clylugu= *Clypastraea lugubris*, Corelon= *Corticaria elongata*, Cospaci= *Cossonus pacificus*, Cucclav= *Cucujus clavipes*, Epuflav= *Epuraea flavomaculata*, Epuplan= *Epuraea planulata*, Eputerm= *Epuraea terminalis*, Eputrun= *Epuraea truncatella*, Epusp1= *Epuraea* sp. 1, Megperv= *Megatoma perversa*, Phllapp= *Phloeostiba lapponica*, Ptesp1= *Pteryx* sp. 1, Rhinsp1= *Rhizophagus* n.sp. 1, Tridiss= *Triplax dissimulator*, Tryretu= *Trypodendron retusum*; AMB= ambrosia feeder, DET= detritivore, MYC= mycetophage, MYX= myxomycetophage, OMN= omnivore, PHL= phloem feeder, SAP= sap feeder, XYL= xylem feeder, ZOO= zoophagous.

Axis 2 mainly reflects tree death, separating live trees widely from snags and logs. Interestingly, decay class is arrayed to a lesser extent along axis 2, with loadings increasing from the lowest values in live wood

(Tr0), freshly-dead substrates lying below the origin, early-decayed substrates occurring near the origin, and well-decayed substrates with the highest scores along Axis 2 (Figure 4.1a). Species, such as the sap beetles *Epuraea truncatella* Mannerheim (CCA2= -2.78) and *Epuraea terminalis* Mannerheim (CCA2= -2.36), with low scores along Axis 2 are strongly associated with live trees (Tr0) (Figure 4.1b). The flat bark beetle, *Cucujus clavipes* Fabricius (CCA2= -0.42) is associated with dead substrates, occurring most frequently in DC2 logs and DC2 snags, and thus lying close to the origin. Species with the highest scores along Axis 2, such as *Megatoma perversa* Fall (Dermestidae; CCA2= +1.06), are associated with substrates in more advanced stages of decay (Sn4).

Saproxylic beetle assemblages were strongly correlated with the 11 habitat classes (r^2= 0.93, p=0.001), confirming that assemblages are well predicted when both substrate TYPE and DC are considered. Feeding guilds, particularly those of sap-feeders (SAP), ambrosia-feeders (AMB), phloem-feeders (PHL), xylem-feeders (XYL), and detritus-feeders (DET), were also clearly sorted along CCA axis 2, across habitats from live to dead (Figure4.1d). Not surprisingly, fungus-feeders (MYC) were more strongly associated with log habitats, thus sorting along CCA axis 1 (Figure4.1d).

The dissimilarity dendrogram (Figure4.2) shows a clear pattern in composition of saproxylic beetle assemblages across HCs. As expected, species composition was most similar between neighboring habitat

classes within each substrate type, and assemblages were most dissimilar between live trees (Tr0) and deadwood (Sn1-4, Lg1-6). Additionally, communities of snag habitats (Sn1-4) were quite dissimilar to those of log habitats (Lg1-6), suggesting that position of deadwood is an important consideration for maintenance of biodiversity.

4.4.2. Richness and Diversity

Rarefaction estimates of species richness varied significantly among living tree, logs and snags (Figure4.3). Although few live trees were sampled (n=3), volume-scaled rarefaction estimates (Figure4.3b) allow for comparison of live trees with snags and logs. Live trees had the lowest richness estimates for saproxylic beetles; however, it was surprising to find nine species of deadwood-associated beetles living on live aspen trees. Furthermore, although based on fewer samples, collections from live trees yielded beetle abundances and estimates of overall saproxylic beetle diversity comparable to that in snags and logs (Figure4.4a, b). Species richness estimates were greatest for log substrates, when rarefied by number of individuals (Figure4.3a) and volume (Figure4.3b) per subsample. However, no single decay class of logs or snags was responsible for producing the resulting diversity for these substrates; all decay classes were similar in richness and diversity (Figure 4.4a, b).

Table 4.2 Results from the CCA analysis of saproxylic beetle habitats in aspen. Relationship of each significant (after 999 permutations) environmental variable with the ordination axes and correlation coefficient (r) are shown.

Variable	CCA 1	CCA 2	r2	P (>r)
DEATH	0.35	0.94	0.75	***
FRESH	-0.54	-0.84	0.47	***
POS			0.39	***
Fallen	0.79	-0.13		
Standing	-0.99	0.17		
TYPE			0.80	***
Live tree	-1.09	-3.05		
Log	0.79	-0.13		
Snag	-0.98	0.77		
HabC11: *as factors*			0.93	***
Tr0	-1.09	-3.05		
Sn1	-0.95	0.13		
Sn2	-1.10	0.81		
Sn3	-1.00	1.03		
Sn4	-0.86	1.10		
Lg1	0.05	-0.62		
Lg2	0.25	-0.40		
Lg3	0.51	-0.23		
Lg4	1.25	-0.06		
Lg5	1.41	0.23		
Lg6	1.25	0.29		
HabC11: *as dummy variables*				
Tr0	-0.35	-0.94	0.75	***
Sn2	-0.81	0.58	0.18	*
Sn3	-0.71	0.71	0.20	*
Sn4	-0.62	0.78	0.19	*
Lg4	1.00	-0.04	0.16	*
Lg5	0.99	0.16	0.20	*
Lg6	0.97	0.23	0.16	*

Table 4.2 -Continued-

Variable	CCA 1	CCA 2	r2	P (>r)
Attributes:				
LTH	-0.26	-0.97	0.27	**
VOL	-0.69	0.72	0.38	***
CrackW	0.86	0.50	0.43	***
FragW	0.81	0.59	0.31	***
%Bark	-0.97	-0.23	0.66	***
SAbark	-0.87	0.49	0.53	***
PeelB	0.60	0.80	0.14	*
TIGHT	-0.67	-0.74	0.54	***
BRANCH	-0.94	-0.35	0.50	***
TWIG	-0.99	-0.12	0.39	***
LEAF	-0.53	-0.85	0.53	***
AntN	1.00	0.05	0.26	**
Ptrem	-0.75	0.66	0.16	*
MACRO	0.67	0.75	0.15	*
MOSS	1.00	0.01	0.89	***
LICHEN	1.00	-0.05	0.44	***
VASC	0.98	0.20	0.40	***
Feeding Guilds:				
SAP	-0.791	-0.612	0.33	***
DET	-0.701	0.714	0.49	***
MYC	0.958	-0.286	0.10	
AMB	-0.974	-0.226	0.06	
MYX	-0.036	0.999	0.08	
OMN	-0.997	0.077	0.00	
PHL	-0.366	-0.931	0.01	
XYL	-0.834	0.552	0.46	***
ZOO	-0.484	0.875	0.08	

Significance codes: *<0.05, **<0.01, ***<0.001; variables explained in Table 4.2.

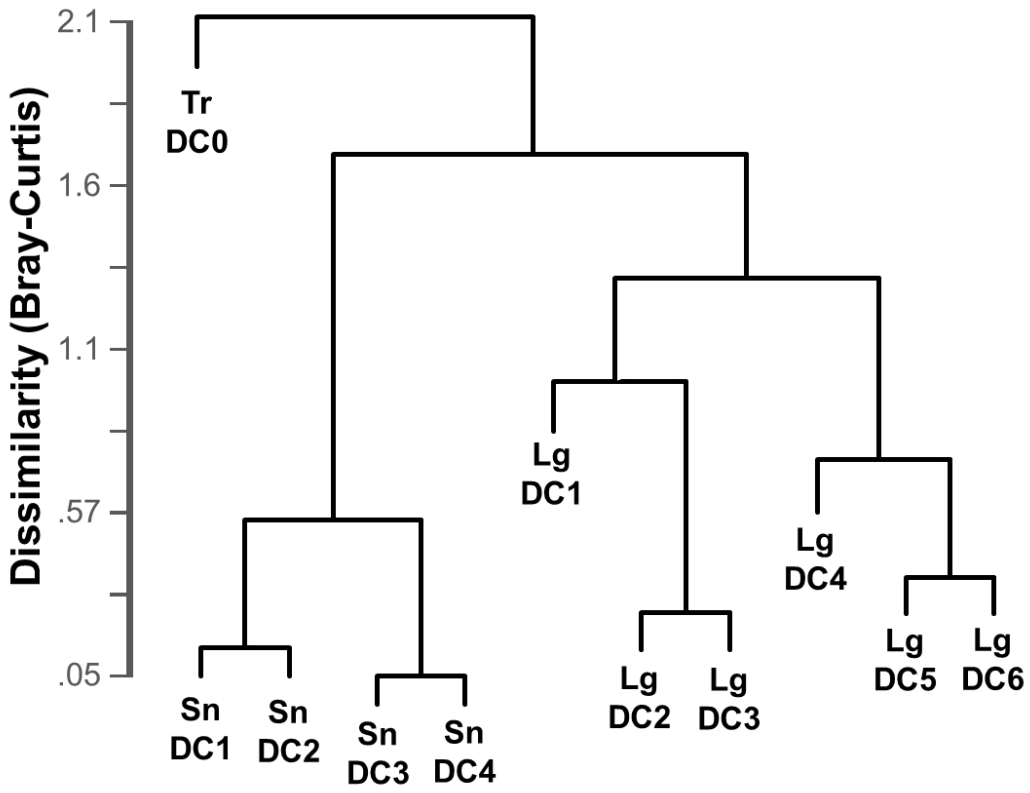

Figure 4.2 Dissimilarity dendrogram (average-linkage cluster, Bray-Curtis distance, relative abundance) showing relationships among saproxylic beetle assemblages in various substrates of aspen. Description of substrate types and decay class (DC) designation is explained in the Methods section (Tr= living tree, Sn= snag, Lg= log).

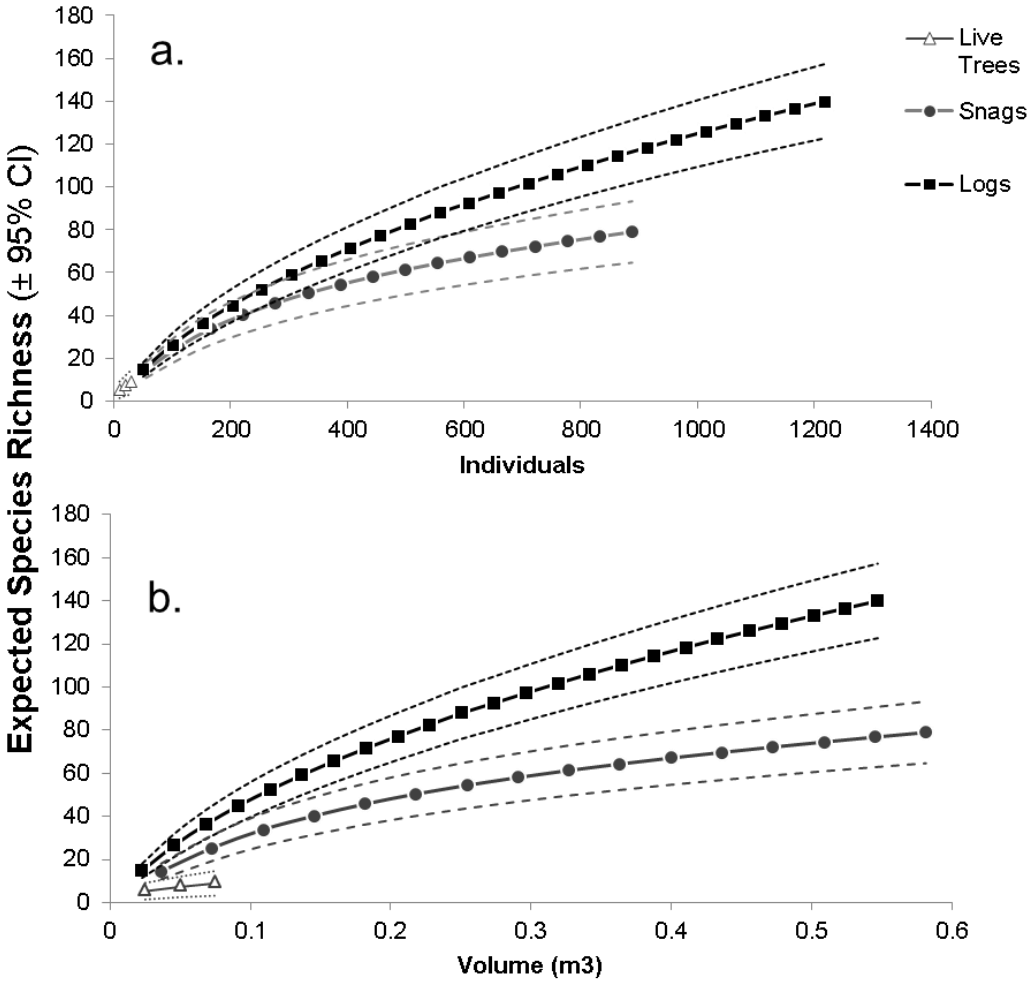

Figure 4.3 Accumulation of saproxylic beetle species by type of substrate. Species richness at increasing (a) numbers of individuals and (b) deadwood volume were calculated for live trees (open triangles), snags (open circles) and logs (filled circles) as Mao-Tao interpolations of species density. Significantly different groups are indicated by 95% confidence intervals (dashed lines) bounding each rarefaction curve.

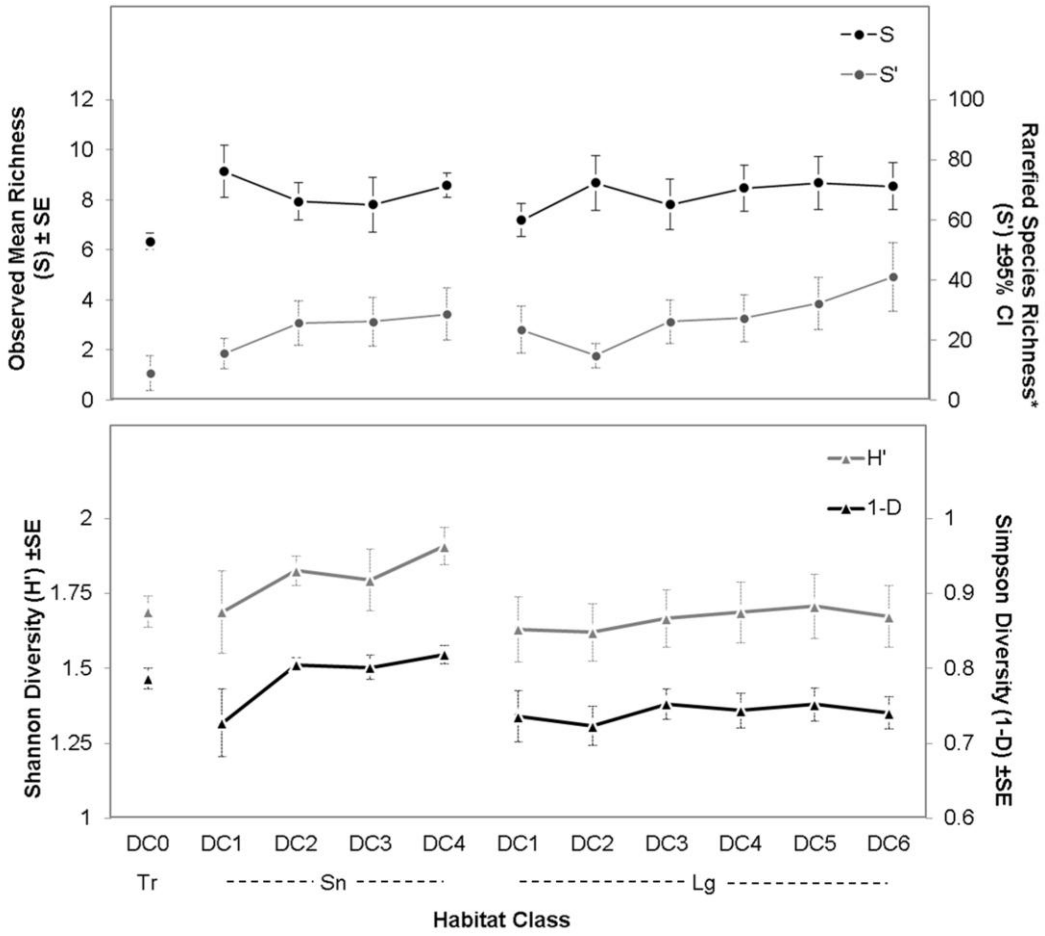

Figure 4.4 Richness and diversity of saproxylic beetles across each habitat type. Observed (S) and estimated (individual-based rarefaction, S' ± 95% CI) saproxylic beetle richness across each habitat class (substrate type x decay class) in (a); and saproxylic beetle diversity (Simpson's 1-D, Shannon's H' ± 1SE) across each habitat class in (b). *Richness estimates were rarefied at 94 individuals (except live Tr0, for which maximum richness is given, corresponding to 31 individuals). Description of decay class (DC) is explained in the Methods section (Tr= living tree, Sn= snag, Lg= log).

4.4.3. Indicator Species

Indicator species analyses resulted in association of 87 indicator species with particular habitat variables (Table 4.3). Most (87%) of these species were indicative of only one substrate decay class. Nearly half of all indicator species were specific to position, with 33 indicators of

standing substrates and 9 indicators of fallen substrates. Substrate type also appeared to be an important variable characterizing habitat use of 31 saproxylic beetle species as indicator species. A total of 51 species significantly indicated one of the 11 habitat classes. An additional 25 species had a greater range of habitat use than could be accommodated by a single habitat class. For example, *Cerylon castaneum* Say (Cerylonidae) had a greater IV for snag habitats of DC1 and DC2, than for either decay class alone (Table 4.4; 'Cercast', 'SN1+2', IV=69.7).

The sap beetles, *Epuraea terminalis* Mannerheim and *E. flavomaculata* Mäklin, were the strongest indicators (IV: 95.7 and 87.5, respectively) for live tree habitats, and both indicated habitats with tight, unpeeling bark and leaves present.

For snag habitats, the false flower beetle, *Canifa pallipes* (Melsheimer), snout beetle, *Cossonus pacificus* Van Dyke, and pleasing fungus beetle, *Triplax dissimilator* (Crotch) were the strongest indicator species (IV: 75, 68.7, and 67.8, respectively). Unlike the latter species which is an indicator of early decay class snags (Sn1+2), *C.pacificus* was an indicator for more well decayed snags (Sn2-4) and high bark surface area, consistent with reports that this species lives under loose bark of dead *Populus* (O'Brien 1997).

Moss cover appeared to be related to saproxylic beetle habitat associations. The plaster beetle, *Cartodere constricta* (Gyllenhal), was a strong indicator of log habitats (IV: 66.7) and in particular, logs with moss

cover (IV: 64.9), perhaps suggesting association with moist habitats. Interestingly, the two species of featherwing beetles collected in this study indicated very different habitats; *Acrotrichis* sp. 1 was a strong indicator of DC2 snags, while *Pteryx* sp. 1 indicated DC4 log habitats with moss cover.

Of the substrate attributes examined, bark characteristics generated the most indicator species. Thirty-nine species were indicators of high or low bark surface area (Table 4.3, 'BarkSA'), while 36 species were associated to a more precise measure of bark cover (Table 4.3, '%Bark').

Table 4.3 Significant indicator species for saproxylic beetle assemblages in aspen substrates (after a Monte-Carlo test with 2000 permutations, α= 0.05). Indicator values (IV) are given for each variable; IV>60 are shown in bold (significance:

Spp	Variable (IV)
Acrotrichis sp. 1	
	Type
	TYPE:Sn (59.3 *)
	Decay
	SN2 (73 *)
Agathidium depressum	
	Attribute
	CrackB:A (29.9 **)
Agathidium pulchrum	
	Attribute
	BarkCC:>10-25% (33.3 *)
Agonum retractum	
	Position
	POS:Fallen (40.4 *)
	Decay
	LG5 (79.6 **)
	Attribute
	AntN:P (38.3 *)
	FragW:P (34.2 *)
	CrackW:P (32.1 *)
	LICHEN:P (38.1 **)
	MOSS:P (36.2 *)
	BarkCC:>10-25% (36.9 *)
	BarkSAc:low (34.2 *)
	VASC:P (61.2 *)**
Agrilus liragus	
	Decay
	LG1 (48 *)
Ampedus deletus	
	Attribute
	BarkCC:>10-25% (50 *)
Ampedus nigricans	
	Position
	POS:Standing (52.6 ***)
	Type
	TYPE:Sn (62.5 **)
	Decay
	SN1 (59.7 *)
	Attribute
	CrackB:A (29.9 *)
	Branch:P (41.8 **)
	LICHEN:A (40.8 **)
	MOSS:A (50 ***)
	BarkCC:>50-90% (37.2 *)
	Ptrem:P (43.4 **)
	BarkSAc:high (66.7 *)**
	TWIG:P (45.3 **)
	Volume:high (55.6 ***)
Ampedus subtilis	
	Attribute
	BarkCC:>10-25% (33 *)
Atrecus macrocephalus	
	Position
	POS:Fallen (37.3 **)
	Decay
	LG4 (63.4 *)
	Attribute
	AntN:P (32.4 *)
	CrackW:P (33 *)
	MOSS:P (39 **)
	BarkCC:0-10% (37.1 *)
	BarkSAc:low (31.9 *)
	VASC:P (40.3 *)
Baeocera humeralis	
	Attribute
	BarkCC:>20-30% (33.3 *)
Caenoscelis ferruginea	
	Decay
	SN1 (48.3 **)
	Attribute
	LEAF:P (25.9 *)
	BarkSAc:high (26.7 *)
	TWIG:P (26.7 *)
Canifa pallipes	
	Position
	POS:Standing (63.2 *)**
	Type
	TYPE:Sn (75 **)
	Decay
	SN2-4 (74 *)**
	Attribute
	Branch:P (40.2 *)
	LICHEN:A (52 **)
	MOSS:A (60 *)**
	BarkCC:>50-90% (46.2 **)
	Ptrem:P (53.7 **)
	BarkSAc:high (80 *)**
	TWIG:P (44.1 **)
	Volume:high (66.7 *)**
Cartodere constricta	
	Position
	POS:Fallen (66.7 *)**
	Type
	TYPE:Lg (66.7 *)
	Decay
	LG2 (90.9 **)
	Attribute
	AntN:P (46.8 *)
	Branch:A (46.2 *)
	LICHEN:P (47.8 **)
	MOSS:P (64.9 *)**
	POLY:P (44.5 *)
	TWIG:A (47.6 *)
Carphacis nepigonensis	
	Position
	POS:Standing (52.6 **)
	Type
	TYPE:Sn (62.5 **)
	Decay
	SN1+2 (73.2 *)**
	Attribute
	Branch:P (45.8 ***)
	TIGHT:P (35.4 *)
	LEAF:P (35.5 *)
	LICHEN:A (36.6 *)
	MOSS:A (50 ***)
	Ptrem:P (33.2 *)
	BarkSAc:high (66.7 *)**
	TWIG:P (49.2 ***)
	Volume:high (55.6 **)
Cerylon castaneum	
	Position
	POS:Standing (39.7 *)
	Type
	TYPE:Sn (47.6 *)
	Decay
	SN1+2 (69.7 *)**
	Attribute
	Branch:P (41.1 *)
	FragW:A (34 *)
	MOSS:A (37.5 *)
	TWIG:P (44.1 **)
Cis americanus	
	Attribute
	Ptrem:P (29.4 *)
	BarkSAc:high (26 *)
Clypastraea lugubris	
	Position
	POS:Standing (30.5 *)
	Decay
	SN1 (73.3 **)
	Attribute
	TIGHT:P (33.2 *)
	BarkSAc:high (42.4 **)
	TWIG:P (30.1 *)
	Volume:high (33 *)
Corticaria elongata	
	Position
	POS:Fallen (45.6 **)
	Decay
	LG2-4 (56.1 **)
	Attribute
	AntN:P (56.1 ***)
	LICHEN:P (44.7 **)
	MOSS:P (42.7 **)
	POLY:P (39.9 *)
	TWIG:A (39 *)
Cortinicara gibbosa	
	Position
	POS:Standing (55.7 ***)
	Type
	TYPE:Sn (67.4 *)
	Decay
	SN1+2 (65.3 **)
	Attribute
	CrackB:A (35.3 *)
	Branch:P (54.6 ***)
	LICHEN:A (44.5 **)
	MOSS:A (52.3 ***)
	Ptrem:P (57.1 **)
	BarkSAc:high (73.3 *)**
	TWIG:P (59 ***)
	Volume:high (59.4 ***)
Corticaria n. sp. 1	
	Position
	POS:Standing (47.4 **)
	Type
	TYPE:Sn (56.2 *)
	Decay
	SN1+2 (72.4 *)**
	Attribute
	Branch:P (49.1 ***)
	LICHEN:A (37.4 **)
	MOSS:A (45 **)
	BarkSAc:high (60 *)**
	TWIG:P (52.4 ***)
	Volume:high (50 **)
Corticaria n. sp. 3	
	Position
	POS:Standing (42.1 **)
	Type
	TYPE:Sn (50 *)
	Decay
	SN2-4 (48.7 **)
	Attribute
	Branch:P (30.1 *)
	LICHEN:A (32.1 *)
	MOSS:A (40 **)
Corticaria n. sp. 3 *-continued-*	
	BarkSAc:high (53.3 ***)
	TWIG:P (32.8 *)
	Volume:high (44.4 ***)
Corticaria rubripes	
	Decay
	SN4 (72.2 *)
	Attribute
	BarkCC:>50-75% (35.5 *)
Cossonus pacificus	
	Position
	POS:Standing (57.9 ***)
	Type
	TYPE:Sn (68.7 **)
	Decay
	SN2-4 (73.2 *)**
	Attribute
	AntN:A (35.5 *)
	Branch:P (35.3 *)
	LICHEN:A (46 **)
	MOSS:A (55 ***)
	BarkCC:>50-90% (45.6 **)
	Ptrem:P (44.8 *)
	BarkSAc:high (73.3 *)**
	TWIG:P (38.8 **)
	Volume:high (61.1 *)**
Cryptophagus acutangulus	
	Position
	POS:Fallen (32.5 *)
	Decay
	LG2-4 (42.9 **)
	Attribute
	AntN:P (49 **)
	MACRO:P (32.1 *)
	POLY:P (39.1 **)
	TWIG:A (32.1 *)
Ctenicera nitidula	
	Decay
	SN2-4 (26.3 *)
	Attribute
	BarkSAc:high (28 *)
	Volume:high (33.3 **)
Ctenicera striata	
	Decay
	SN1+2 (44.9 **)
Cucujus clavipes	
	Decay
	LG2 (70 *)
	Attribute
	FragW:A (47 *)
	CrackW:A (54.6 **)
	POLY:P (51.7 *)
Cyphon variabilis	
	Decay
	SN1 (61.9 *)
	Attribute
Denticollis denticornis	
	Decay
	SN2 (43.3 *)
Didion longullum	
	Decay
	SN1 (49 *)
	Attribute
	LEAF:P (27 *)

*<0.05,**<0.01,***<0.001).

-***Table 4.3*** *continued-*

Spp	Variable (IV)
Dolichocis manitoba	
	Position
	POS:Standing (35.2 **)
	Decay
	SN3 (61.4 *)
	Attribute
	BarkCC:>75-90% (32.6 *)
	Branch:P (35.7 **)
	LICHEN:A (42.9 **)
	MOSS:A (45 ***)
	POLY:P (31 *)
	Ptrem:P (41.8 **)
	BarkSAc:high (47.1 ***)
	Volume:high (37.8 **)
Enicmus tenuicornis	
	Position
	POS:Standing (47.4 ***)
	Type
	TYPE:Sn (56.2 **)
	Decay
	SN3+4 (70.2 *)**
	Attribute
	CrackW:P (27.1 *)
	LICHEN:A (36.9 **)
	MOSS:A (45 **)
	BarkCC:>50-90% (49.5 **)
	POLY:P (29.3 *)
	Ptrem:P (46.4 **)
	BarkSAc:high (60 *)**
	Volume:high (50 ***)
Epuraea flavomaculata	
	Position
	POS:Standing (61.8 *)**
	Type
	TYPE:Tr (87.5 **)
	Decay
	HEALTH:Alive (94.5 **)
	Attribute
	BarkCC:100% (45.3 *)
	CrackB:A (47.9 **)
	PeelB:A (45.5 **)
	Branch:P (67.4 *)**
	TIGHT:P (65.1 *)**
	FragW:A (41.1 *)
	CrackW:A (43.6 *)
	MACRO:A (43.8 **)
	LEAF:P (83.6 *)**
	Length:high (38.6 *)
	LICHEN:A (46.2 **)
	MOSS:A (58.6 ***)
	BarkCC:>90% (53.2 **)
	BarkSAc:high (39.4 *)
	TWIG:P (72 *)**
Epuraea planulata	
	Decay
	SN1 (72.5 *)**
	Attribute
	TIGHT:P (32.4 **)
	CrackW:A (30 **)
	LEAF:P (32.5 *)
Epuraea sp. 1	
	Type
	TYPE:Tr (66.1 **)
	Decay
	HEALTH:Alive (66.3 **)

Spp	Variable (IV)
Epuraea sp. 1 -continued-	
	Attribute
	LEAF:P (28.2 *)
Epuraea terminalis	
	Type
	TYPE:Tr (95.7 *)**
	Decay
	HEALTH:Alive (97.5 *)**
	Attribute
	PeelB:A (33.9 *)
	TIGHT:P (47.2 **)
	LEAF:P (53.6 **)
Epuraea truncatella	
	Type
	TYPE:Tr (32.8 *)
Euplectus duryi	
	Position
	POS:Standing (47.4 **)
	Type
	TYPE:Sn (56.2 **)
	Decay
	SN3 (57.4 *)
	Attribute
	Branch:P (35 **)
	LICHEN:A (42.9 ***)
	MOSS:A (45 **)
	BarkCC:>50-90% (37.5 *)
	Ptrem:P (41.5 **)
	BarkSAc:high (60 *)**
	TWIG:P (38.1 **)
	Volume:high (50 ***)
Gabrius brevipennis	
	Decay
	LG5 (66 **)
	Attribute
	BarkCC:>20-30% (33.5 *)
	VASC:P (42.2 **)
Glischrochilus sanguinolentus	
	Position
	POS:Standing (36.8 **)
	Type
	TYPE:Sn (43.7 *)
	Decay
	SN1 (62.2 **)
	Attribute
	TIGHT:P (26.1 *)
	LICHEN:A (25.2 *)
	MOSS:A (35 **)
	BarkSAc:high (46.7 ***)
	Volume:high (38.9 **)
Glischrochilus siepmanni	
	Position
	POS:Standing (26.3 *)
	Type
	TYPE:Sn (31.2 *)
	Decay
	SN3 (44.5 *)
	Attribute
	Ptrem:P (39.3 **)
	BarkSAc:high (33.3 **)
	Volume:high (27.8 **)
Glischrochilus vittatus	
	Position
	POS:Standing (36.8 **)

Spp	Variable (IV)
Glischrochilus vittatus -continued-	
	Decay
	SN1+2 (61.2 *)**
	Attribute
	CrackB:A (39.9 **)
	PeelB:A (30.4 *)
	Branch:P (43.7 ***)
	TIGHT:P (49.4 **)
	LEAF:P (54.7 **)
	MOSS:A (35 **)
	TWIG:P (46.7 ***)
Grammoptera subargentata	
	Position
	POS:Standing (46 **)
	Type
	TYPE:Sn (54.9 **)
	Decay
	SN1+2 (71.3 *)**
	Attribute
	CrackB:A (32.7 *)
	Branch:P (55.1 ***)
	TIGHT:P (34.9 *)
	LICHEN:A (35.8 *)
	MOSS:A (43.6 **)
	BarkSAc:high (66.7 *)**
	TWIG:P (58.9 ***)
	Volume:high (55.6 ***)
Hemicoelus carinatus	
	Position
	POS:Standing (41.8 **)
	Type
	TYPE:Sn (51.3 *)
	Decay
	SN4 (95.1 *)**
	Attribute
	CrackW:P (34 *)
	Length:low (38 *)
	LICHEN:A (36.3 *)
	MOSS:A (38.9 *)
	BarkCC:>50-90% (43 *)
Ischnosoma splendidum	
	Decay
	SN3+4 & LG4-6 (26.3 *)
	Attribute
	BarkCC:>10-25% (46.7 **)
	Volume:high (27.8 **)
Lathrobium fauveli	
	Position
	POS:Fallen (33.3 *)
	Decay
	LG5 (92.1 **)
	Attribute
	AntN:P (29.4 *)
	Branch:A (29.6 *)
	FragW:P (40 **)
	CrackW:P (34.8 **)
	Length:low (37.7 **)
	LICHEN:P (36.4 **)
	MOSS:P (34.8 **)
	BarkCC:0-10% (40.2 **)
	POLY:A (26.4 *)
	BarkSAc:low (28.6 *)
	TWIG:A (28.6 *)
	VASC:P (88.9 *)**

Spp	Variable (IV)
Latridius hirtus	
	Position
	POS:Standing (36.8 **)
	Type
	TYPE:Sn (43.7 *)
	Decay
	SN2 (63.5 **)
	Attribute
	CrackB:A (34 **)
	Branch:P (43.7 ***)
	LICHEN:A (33.3 **)
	MOSS:A (35 **)
	BarkSAc:high (46.7 **)
	TWIG:P (46.7 ***)
	Volume:high (38.9 **)
Latridius minutus	
	Decay
	SN3 (48.9 *)
	Attribute
	POLY:P (49.3 ***)
Lathrobium washingtoni	
	Position
	POS:Fallen (32.8 *)
	Decay
	LG5+6 (69.2 **)
	Attribute
	AntN:P (38.5 **)
	Branch:A (33.3 *)
	FragW:P (35.3 *)
	CrackW:P (39.1 **)
	Length:low (43.1 ***)
	MOSS:P (34.3 *)
	TWIG:A (32.1 *)
	VASC:P (62.2 *)**
Lordithon bimaculata	
	Position
	POS:Standing (36.8 **)
	Type
	TYPE:Sn (43.7 *)
	Decay
	SN1+2 (41.2 *)
	Attribute
	CrackB:A (32.6 **)
	Branch:P (34.4 **)
	LICHEN:A (33.3 **)
	MOSS:A (35 **)
	BarkSAc:high (46.7 **)
	TWIG:P (37 **)
	Volume:high (38.9 **)
Megatoma perversa	
	Position
	POS:Standing (52.6 ***)
	Type
	TYPE:Sn (62.5 **)
	Decay
	SN2-4 (74.8 *)**
	Attribute
	BarkCC:>75-90% (36.5 *)
	LICHEN:A (47.6 ***)
	MOSS:A (50 ***)
	BarkCC:>50-90% (51.9 **)
	POLY:P (30.6 *)
	Ptrem:P (57.5 **)
	BarkSAc:high (66.7 *)**
	Volume:high (55.6 ***)

-**Table 4.3** *continued*-

Spp	Variable (IV)
Melanophthalma americana	
	Position
	POS:Standing (26.3 *)
	Decay
	SN1 (42.4 *)
	Attribute
	Ptrem:P (28.4 *)
	BarkSAc:high (33.3 **)
	Volume:high (27.8 **)
Melanophthalma pumila	
	Position
	POS:Standing (52.6 **)
	Type
	TYPE:Sn (64.2 *)
	Decay
	SN4 (79 **)
	Attribute
	Branch:P (42.2 *)
	LICHEN:A (41.2 *)
	MOSS:A (49.2 **)
	BarkCC:>50-90% (37.1 *)
	Ptrem:P (57.6 **)
	BarkSAc:high (62.1 **)
	TWIG:P (46.5 **)
	Volume:high (42.2 *)
Melandrya striata	
	Position
	POS:Standing (42.8 **)
	Type
	TYPE:Sn (51.7 *)
	Decay
	SN2 (65 *)
	Attribute
	Branch:P (44.6 **)
	LICHEN:A (47.6 ***)
	MOSS:A (50 ***)
	Ptrem:P (39.5 *)
	BarkSAc:high (56 ***)
	TWIG:P (38.4 **)
	Volume:high (45.6 **)
Myrmedophila americana	
	Position
	POS:Standing (42.1 ***)
	Type
	TYPE:Sn (50 *)
	Decay
	SN2 (59.7 *)
	Attribute
	BarkCC:>75-90% (37.1 *)
	Branch:P (34.2 **)
	LICHEN:A (38.1 **)
	MOSS:A (40 **)
	BarkSAc:high (53.3 ***)
	TWIG:P (37.2 **)
	Volume:high (44.4 **)
Orchesia castanea	
	Decay
	SN4 (41.5 *)
Pediacus fuscus	
	Decay
	LG2 (41.5 *)
Phloeostiba lapponica	
	Type
	TYPE:Tr (84.1 **)

Spp	Variable (IV)
Phloeostiba lapponica -continued-	
	Decay
	HEALTH:Alive (90.6 **)
	Attribute
	BarkCC:100% (45.1 *)
	Branch:P (36.9 *)
	TIGHT:P (79 *)**
	FragW:A (45.8 **)
	CrackW:A (49.2 **)
	LEAF:P (71.6 **)
	BarkCC:>90% (45 *)
	TWIG:P (40.7 *)
Phyllodrepa sp. 1	
	Attribute
	BarkCC:>10-25% (33.1 *)
Platynus decentis	
	Decay
	fresh:0 (56.7 *)
	Attribute
	MICRO:P (50.8 *)
	Volume:high (55.5 *)
Podabrus sp. 2	
	Decay
	SN2+3:1 (50.9 *)
	Attribute
	FragW:P (46.9 *)
	CrackW:P (48.9 *)
	VASC:P (47.6 *)
Proteinus limbatus	
	Attribute
	BarkCC:>10-25% (33.3 *)
Pseudopsis propola	
	Decay
	SN1 (67.2 **)
	Attribute
	BarkSAc:high (36.2 **)
	Volume:high (46.5 **)
Pseudopsis sagitta	
	Decay
	LG5 (95.1 **)
	Attribute
	FragW:P (28.6 *)
	Length:low (26.9 *)
	VASC:P (54.9 **)
Pterostichus adstrictus	
	Attribute
	BarkCC:>10-25% (32.3 *)
Pterostichus pensylvanicus	
	Decay
	LG4 (45.3 *)
Pteryx sp. 1	
	Position
	POS:Fallen (46 *)
	Decay
	LG4 (70.9 **)
	Attribute
	MOSS:P (43.6 *)
Ptilinus lobatus	
	Position
	POS:Standing (37.9 **)
	Decay
	SN3 (69.6 **)
	Attribute
	BarkCC:>50-75% (39.8 *)
	LICHEN:A (33.6 *)

Spp	Variable (IV)
Ptilinus lobatus -continued-	
	MOSS:A (35.7 *)
	BarkCC:>50-90% (62.5 **)
	POLY:P (34.2 *)
	Ptrem:P (45.3 **)
	BarkSAc:high (57.2 ***)
	Volume:high (55.6 **)
Quedius frigidus	
	Decay
	LG5 (50 **)
Quedius plagiatus	
	Position
	POS:Standing (32.6 *)
	Decay
	SN4 (62.8 *)
	Attribute
	BarkCC:>50-75% (38.1 *)
	LICHEN:A (33.9 *)
	MOSS:A (36.6 *)
	BarkCC:>10-20% (52.9 **)
	POLY:P (37.1 *)
	Ptrem:P (47.2 **)
	BarkSAc:high (59.2 **)
	Volume:high (58.2 ***)
Quedius velox	
	Position
	POS:Standing (53.9 ***)
	Type
	TYPE:Sn (64.8 *)
	Decay
	SN2-4 (60.6 *)**
	Attribute
	LICHEN:A (42.4 **)
	MOSS:A (50.9 **)
	Ptrem:P (39.2 *)
	BarkSAc:high (69.9 *)**
	TWIG:P (36.2 *)
	Volume:high (66.7 *)**
Rhizophagus dimidiatus	
	Decay
	SN1 (50 **)
	Attribute
	LEAF:P (28.6 *)
Rhizophagus n. sp. 1	
	Position
	POS:Standing (56.9 ***)
	Type
	TYPE:Sn (67.8 *)
	Decay
	SN1+2 (73.5 *)**
	Attribute
	Branch:P (53.7 ***)
	TIGHT:P (38.1 *)
	LICHEN:A (35.1 *)
	MICRO:P (35.8 *)
	MOSS:A (54 **)
	BarkSAc:high (72.5 *)**
	TWIG:P (57.6 ***)
	Volume:high (66.7 *)**
Rhizophagus remotus	
	Decay
	SN1 (67.4 **)
	Attribute
	TIGHT:P (36.5 *)
	FragW:A (37.8 *)

Spp	Variable (IV)
Rhizophagus remotus -continued-	
	CrackW:A (43.8 **)
Schizotus cervicalis	
	Decay
	LG4 (45.9 *)
	Attribute
	AntN:P (36.7 *)
	MACRO:P (32.1 *)
	LICHEN:P (30.8 *)
	MOSS:P (29.4 *)
	VASC:P (40.8 *)
Stephostethus liragus	
	Decay
	SN1 (62.2 *)
	Attribute
	CrackB:A (33.7 *)
Stenichmus ovipennis	
	Position
	POS:Standing (37.6 **)
	Type
	TYPE:Sn (45.4 *)
	Decay
	SN2 (60.7 *)
	Attribute
	CrackB:A (30.4 *)
	Branch:P (38.7 **)
	MOSS:A (35.3 **)
	BarkSAc:high (49.3 **)
	TWIG:P (41.7 **)
	Volume:high (40 **)
Sulcacis curtula	
	Position
	POS:Standing (27.8 *)
	Decay
	SN3 (62.2 *)
	Attribute
	MOSS:A (26.1 *)
	Ptrem:P (32.8 *)
	BarkSAc:high (46.7 ***)
	TWIG:P (25.5 *)
	Volume:high (38.9 ***)
Tachyporus borealis	
	Position
	POS:Fallen (37.2 **)
	Decay
	LG5+6 (67.9 *)**
	Attribute
	BarkCC:>10-25% (49.5 **)
	Branch:A (33 *)
	FragW:P (41.6 **)
	CrackW:P (43.5 **)
	Length:low (33 *)
	LICHEN:P (40.6 **)
	MOSS:P (38.8 **)
	BarkCC:>10-25% (58.2 **)
	POLY:A (34.4 *)
	BarkSAc:low (31.8 *)
	TWIG:A (31.8 *)
	VASC:P (62.4 *)**
Tachinus elongatus	
	Position
	POS:Standing (37.5 **)
	Decay
	SN3 (67 **)
	Attribute

-***Table 4.3*** *continued-*

Spp	Variable (IV)
Tachinus elongatus -continued-	
	CrackW:P (28.2 *)
	LICHEN:A (33.1 *)
	MOSS:A (35.2 **)
	POLY:P (30.4 *)
	Ptrem:P (45.1 **)
	BarkSAc:high (49.2 **)
	Volume:high (50 ***)
Tachinus fumipennis	
	Decay
	LG6 (44 *)
	Attribute
	VASC:P (32.9 **)
Teretrius montanus	
	Decay
	SN4 (72.5 **)
	Attribute
	BarkCC:>50-90% (36.4 *)
Thymallus marginicollis	
	Decay
	SN2+3:1 (48.4 **)
	Attribute
	BarkSAc:high (33.3 **)
	Volume:high (27.8 *)
Triplax dissimulator	
	Position
	POS:Standing (57.9 ***)
	Type
	TYPE:Sn (68.7 **)
	Decay
	SN1+2 (71.6 *)**
	Attribute
	Branch:P (50.8 **)
	LICHEN:A (43.7 **)
	MOSS:A (55 **)
	BarkSAc:high (73.3 *)**
	TWIG:P (54.7 **)
	Volume:high (61.1 *)**
Triplax thoracica	
	Decay
	SN3 (40.8 *)
Trypodendron retusum	
	Decay
	SN1 (72.1 **)
	Attribute
	CrackB:A (35.4 **)
	TIGHT:P (49.7 ***)
	FragW:A (30.8 *)
	CrackW:A (34.7 *)
	LEAF:P (33 *)
	Length:high (32 *)
	BarkCC:>90% (38.3 *)
Typhaea stercorea	
	Attribute
	AntN:P (32.9 **)

4.4.4. Species Dominance

Despite the large number of indicator species generated, only 20 species met the criteria for being 'Dominant' in particular aspen substrates (Table 4.4). The overall saproxylic community was dominated by four species, including the two 'Minute Brown Scavenger beetles', *Cartodere constricta* and *Corticaria elongata,* and two 'Feather-winged beetles', *Acrotrichis* sp. 1 and *Pteryx* sp. 1.

Patterns of the overall dominant species: *Cartodere constricta* and *C. elongata* were both dominant in logs, but while *C. constricta* was dominant in early decay class logs (Lg1-3) and declined in later decay classes (subdominant in Lg4, common in Lg5, and absent in Lg6), *C. elongata* had a less consistent pattern with decay classes. *C. elongata* was common in Lg1, increased in relative dominance in Lg2 and Lg3 where it became locally dominant, was most dominant in Lg4, declined in Lg5 where it was common, yet again became dominant in Lg6 assemblages. Clearly *C. elongata* uses a much larger range of habitats and is quite an important component of saproxylic communities across much of the decay succession. Likewise, while *Acrotrichis* sp. 1 was most dominant in snag communities (Sn 1-3), it was still subdominant in logs. *Pteryx* sp. 1 was dominant in the assemblages of logs (Lg4 & Lg5), but uncommon in snags.

Dominance patterns according to habitats: Live trees contained only two dominant species, the 'Sap beetles' *Epuraea flavomaculata* and

E. terminalis , which shifted in status to subdominant and common, respectively, in snags. Another sap beetle, *Epuraea* sp. 1 was subdominant in live trees, and absent from snag assemblages. The ‘Rove beetle’, *Phloeostiba lapponica* was subdominant in live trees, freshly dead snags (Sn1), and fresh logs (Lg1).

Freshly dead trees were most dominated by *Acrotrichis* sp. 1, but *Rhizophagus* n. sp. 1 (Monotomidae) was also dominant in Sn1 and Sn2 habitats. Related species of *Rhizophagus* are thought to be predaceous on scolytine larvae in freshly dead trees. Indeed, the ambrosia beetle, *Trypodendron retusum* (Curculionidae: Scolytinae), was subdominant in Sn1 and common in Sn2 habitats, and was also locally dominant in fresh logs (Lg1), becoming absent in later decay classes (Lg4-6).

Well decayed snags were dominated by deathwatch beetles (Coleoptera: Anobiidae). The deathwatch beetle, *Hemicoelus carinatus*, increased in relative dominance from Sn3 to Sn4, while another anobiid species, *Ptilinus lobatus*, decreased in dominance from Sn3 to Sn4, possibly reflecting ecological differences between these two similar species. *Cortinicara gibbosa* (Latridiidae) also appears to occur widely across the different snag habitats, being dominant across Sn2-Sn4. Assemblages of decay class 3 snags were also dominated by the ‘Marsh beetle’ *Cyphon variabilis,* which was subdominant across all other snags, and declined in relative dominance to common in logs. Decay class 4 snags were dominated by *Melanophthalma pumila*, which again was

subdominant across other snag decay classes, but declined to uncommon in log assemblages.

Logs also had distinctive species dominance structure across decay classes. The flat bark beetle, *Cucujus clavipes*, was most dominant in Lg2 habitats, where it is a common underbark predator, though was also subdominant across all snag decay classes. The soldier beetle, *Podabrus* sp. 2, was dominant in well-decayed logs (Lg6) and 'locally dominant' in Lg5 habitats. The 'Ground beetles', *Agonum retractum* and *Platynus decentis,* were dominant predators in late decay class logs (Lg5 and Lg6, respectively), while the 'Rove beetles' *Atrecus macrocephalus* and *Tachyporus borealis* were locally dominant and dominant (respectively) in both Lg5 and Lg6 assemblages.

Table 4.4 Dominance structure classes (D: dominant, L: Locally Dominant, S: subdominant, C: common, U: uncommon) and relative dominance values (DV') for saproxylic beetle species from each substrate type (Live tree, Sn: Snag, Lg: Log) and decay class (DC) of aspen habitat.

Family Species	**Live Trees**	Sn1	Sn2	Sn3	Sn4	**Snags**	Lg1	Lg2	Lg3	Lg4	Lg5	Lg6	**Logs**	**TOTAL**
Anobiidae														
Hemicoelus carinatus		C 0.04	C 0.26	**S** 1.8	**D** 20.04	**S** 4.47			C 2.37				U 0.1	C 1.86
Ptilinus lobatus		C 0.02	C 0.21	**S** 7.92	C 1.83	**S** 2.03			C 1.61				U 0.07	C 0.89
Anthicidae														
Omonadus floralis								C 0.04					U <.01	U <.01
Anthribidae														
Trigonorhinus limbatus							C 0.15						U 0.01	U <.01
Buprestidae														
Agrilus liragus		C 0.02				U <.01	**S** 3.87		C 0.14				U 0.25	U 0.12
Cantharidae														
Podabrus sp. 1		**S** 0.15	C 0.03		C 0.13	C 0.07		C 0.13		C 0.14			U 0.03	C 0.06
Podabrus sp. 2		**S** 0.21	**S** 1.26	**S** 0.94	C 0.2	**S** 0.67		C 0.13		**S** 3.75	L 5.88	**D** 6.26	**S** 2.73	**S** 2.44
Carabidae														
Agonum retractum			C 0.04		C 0.09	U 0.02	C 0.54	C 0.27	C 0.28	C 0.42	**D** 10.55	C 3.83	**S** 2.85	C 1.24
Bembidion fortestriatum										C 0.14			U 0.01	U <.01
Bembidion nigripes			C 0.04			U <.01				C 1.61			U 0.08	U 0.06
Bembidion timidum									C 0.14				U 0.01	U <.01
Perigona nigriceps									C 1.22				U 0.05	U 0.02
Platynus decentis		**S** 2.15	**S** 1.49	**S** 2.01	**S** 6.79	**S** 3.69		**S** 9.25	C 1.61	**S** 3.07	C 1.6	**D** 11.67	**S** 5.59	**S** 6.07
Pterostichus adstrictus					C 0.05	U <.01					C 0.69	C 0.27	U 0.09	U 0.05
Pterostichus pensylvanicus										**S** 1		C 0.27	U 0.11	U 0.04
Trechus apicalis											C 0.11		U 0.01	U <.01
Trechus chalybeus			C 0.03			U <.01					C 0.11		U 0.01	U 0.01
Cerambycidae														
Grammoptera subargentata		**S** 0.77	**S** 1.2	**S** 0.29	C 0.1	**S** 0.59		C 0.04					U <.01	C 0.21
Xylotrechus annosus			C 0.03			U <.01								U <.01
Cerylonidae														
Cerylon castaneum		**S** 0.73	**D** 7.53	**S** 0.34		**S** 1.69		C 0.12	C 0.19				U 0.03	C 0.69
Ciidae														
Cis americanus		C 0.03	C 0.07	C 0.05		C 0.03		C 0.13	C 2.92				U 0.25	U 0.23
Cis levettei		C 0.02				U <.01			C 0.14				U 0.01	U <.01
Cis maritimus										C 0.14			U 0.01	U <.01
Dolichocis manitoba		**S** 0.14	C 0.36	**S** 1.51	C 0.2	**S** 0.53		C 0.27					U 0.01	C 0.22

Family Species	Live Trees	Sn1	Sn2	Sn3	Sn4	Snags	Lg1	Lg2	Lg3	Lg4	Lg5	Lg6	Logs	TOTAL
Sulcacis curtulus		C 0.03	C 0.28	**S** 0.79		C 0.18		C 0.08					U <.01	C 0.07
Coccinellidae														
Didion longulum		**S** 0.21	C 0.04			C 0.03								U 0.01
Corylophidae														
Clypastraea lugubris		**S** 3.97	C 0.6	**S** 0.34	C 0.07	**S** 1.12			C 1.18				U 0.05	C 0.53
Orthoperus scutellaris		C 0.11	C 0.04		C 0.05	C 0.04	C 2.02	C 0.62	C 2.37				U 0.62	C 0.46
Cryptophagidae														
Atomaria apicalis											C 0.38		U 0.02	U 0.01
Atomaria diluta?								C 0.27					U 0.01	U <.01
Atomaria ephippiata							C 2.02	C 0.13					U 0.18	U 0.06
Atomaria fuscata							C 0.54						U 0.02	U 0.01
Atomaria lewisii								C 0.31					U 0.01	U <.01
Atomaria ochracea			C 0.03			U <.01				C 0.14			U 0.01	U 0.01
Atomaria sp. 1								C 0.4					U 0.02	U 0.01
Atomaria sp. 2											C 0.11	C 0.83	U 0.09	U 0.03
Atomaria subangulata		C 0.02				U <.01		L 8.31					U 0.38	U 0.27
Caenoscelis antennalis		C 0.05		C 0.05	C 0.07	C 0.04				C 0.22	C 0.97		U 0.12	U 0.12
Caenoscelis ferruginea		**S** 0.26	C 0.03	C 0.05		C 0.06								U 0.02
Cryptophagus actangulus				C 0.12		U 0.01	C 0.15	C 0.35	C 0.67	**S** 6.72		C 0.89	**S** 1.91	C 0.78
Cryptophagus sp. 2		C 0.04	C 0.51	**S** 1.14	**S** 1.58	**S** 0.79		C 0.04	C 0.28		C 0.11		U 0.06	C 0.4
Myrmedophila americana		C 0.04	**S** 0.5	**S** 0.49	C 0.5	**S** 0.41								C 0.12
Cucujidae														
Cucujus clavipes	C 1.24	**S** 0.21	**S** 0.95	**S** 0.44	**S** 0.98	**S** 0.75	C 0.54	**D** 17.17	C 3.28		C 0.38		C 2.59	**S** 3.22
Pediacus fuscus				C 0.09		U 0.01		C 3.51	C 4.26				U 0.76	U 0.36
Curculionidae														
Carphoborus carri							C 0.15						U 0.01	U <.01
Cossonus pacificus		**S** 0.13	**S** 0.9	**S** 1.8	**S** 1.59	**S** 1.18								C 0.36
Magdalis sp. 1					C 0.05	U <.01								U <.01
Phloeophagus canadensis									C 0.14				U 0.01	U <.01
Trypodendron retusum		**S** 11.43	C 0.28			C 1.52	L 8.44	C 0.04	C 0.14				U 1.05	C 1.72
Dermestidae														
Megatoma cylindrica			C 2.3	C 0.1	C 0.05	C 0.53								U 0.16
Megatoma perversa		C 0.03	**S** 1.43	**S** 7.75	**D** 7.88	**S** 4.12								C 1.25
Elateridae														
Aeolus mellilus comis		C 0.03				U <.01		C 0.13					U 0.01	U 0.01
Ampedus apicatus		C 0.03				U <.01		C 0.04					U <.01	U <.01
Ampedus deletus										C 0.14	C 0.34	C 1.08	U 0.22	U 0.08

Family Species	Live Trees	Sn1	Sn2	Sn3	Sn4	Snags	Lg1	Lg2	Lg3	Lg4	Lg5	Lg6	Logs	TOTAL
Ampedus luctuosus											C 0.23		U 0.01	U <.01
Ampedus nigricans		**S** 0.4	C 0.28	**S** 0.88	**S** 1.05	**S** 0.77								C 0.23
Ampedus sp. 1												C 0.66	U 0.03	U 0.01
Ampedus sp. 2											C 0.11		U 0.01	U <.01
Ampedus sp. 3											C 0.11		U 0.01	U <.01
Ampedus subtilis		C 0.02				U <.01					C 0.34	C 0.54	U 0.08	U 0.05
"Ctenicera" nitidula		C 0.04	C 0.04	**S** 0.29	C 0.07	C 0.1					C 0.11		U 0.01	C 0.05
"Ctenicera" stricklandi		**S** 0.17	C 0.21		C 0.1	C 0.11				C 0.22			U 0.01	C 0.06
Denticollis denticornis			C 0.2	C 0.1		C 0.04				C 0.22			U 0.01	U 0.03
Eanus decoratus										C 0.22			U 0.01	U <.01
Pseudanostirus propolus		**S** 0.54	C 0.04		**S** 0.83	**S** 0.27	C 0.15			C 0.14		C 0.54	U 0.11	C 0.25
Erotylidae														
Triplax californica			C 0.07			U <.01								U <.01
Triplax dissimilator		**S** 0.69	**S** 2.15	**S** 0.79	C 0.28	**S** 1.08								C 0.33
Triplax thoracica			C 0.41	**S** 0.64		C 0.15								U 0.05
Eucnemidae														
Isorhipis obliqua										C 0.22			U 0.01	U <.01
Histeridae														
Teretrius montanus				C 0.09	**S** 5.41	C 0.59								U 0.18
Hydrophilidae														
Cercyon herceus frigidus										C 0.14			U 0.01	U <.01
Laemophloeidae														
Cryptolestes ferrugineus									C 0.19				U 0.01	U <.01
Latridiidae														
Cartodere constricta							**D** 37.13	**D** 20.95	**D** 26.2	**S** 10.98	C 3.2		**D** 20.4	**D** 7.19
Corticaria elongata		C 0.03	C 0.07			U 0.01	C 0.75	L 11.39	L 12.63	**D** 18.38	C 1.03	**D** 8.41	**D** 12.5	**D** 5.16
Corticaria ferruginea	C 1.36	**S** 0.09				U 0.01	C 2.02	C 2.27	C 4.26			C 2.2	C 2.04	C 1.32
Corticaria n. sp. 1		**S** 2.78	**S** 4.93	**S** 1.09	C 0.09	**S** 2.1								C 0.64
Corticaria n. sp. 2				C 0.47	C 0.1	U 0.08								U 0.02
Corticaria n. sp. 3		**S** 0.13	C 0.48	**S** 2.11	C 0.28	**S** 0.82								C 0.25
Corticaria n. sp. 4									C 0.78				U 0.03	U 0.01
Corticaria n. sp. 6					C 0.13	U 0.01								U <.01
Corticaria orbicollis			C 0.07	C 0.24	C 0.1	C 0.08								U 0.03
Corticaria rubripes		**S** 0.09	C 0.43	**S** 2.59	**S** 8.18	**S** 2.6	C 2.02	C 2.57	**S** 11.74		C 0.97	C 0.83	**S** 3.11	**S** 3.88
Corticaria serrata								C 0.04		C 1.61			U 0.17	U 0.06
Corticarina cavicollis								C 0.08					U <.01	U <.01
Cortinicara gibbosa		**S** 3.58	**D** 9.7	**D** 9.8	**D** 7.56	**D** 8.86	C 2.18						U 0.09	**S** 3.32

Family Species	Live Trees		Sn1	Sn2	Sn3	Sn4	Snags	Lg1	Lg2	Lg3	Lg4	Lg5	Lg6	Logs	TOTAL
Enicmus fictus					C 0.05		U <.01				C 0.22			U 0.01	U 0.01
Enicmus tenuicornis			C 0.02	C 0.21	**S** 1.59	**S** 0.63	**S** 0.54								C 0.17
Latridius hirtus			**S** 0.3	**S** 1.61	C 0.7	C 0.1	**S** 0.73								C 0.22
Latridius minutus				C 0.07	**S** 1.22	C 0.28	C 0.26	**S** 1.69	C 0.04	C 0.14	C 3.9			C 1.2	C 1.07
Melanophthalma americana			**S** 0.18		C 0.28	C 0.69	C 0.26								U 0.08
Melanophthalma inermis									C 0.04	C 0.19				U 0.02	U 0.01
Melanophthalma pumila			**S** 1.88	**S** 5.73	**S** 2.77	**D** 16.03	**S** 7.11	**S** 5.26						U 0.21	**S** 3.05
Stephostethus liratus			**S** 0.34	C 0.43	C 0.09	C 0.1	**S** 0.27		C 0.62				C 0.89	U 0.14	C 0.33
Leiodidae															
Agathidium angulare					C 0.05		U <.01					C 0.69		U 0.03	U 0.03
Agathidium athabascanum								C 0.15						U 0.01	U <.01
Agathidium cavisternum				C 0.14	C 0.05	C 0.09	C 0.06					C 0.97		U 0.05	U 0.11
Agathidium depressum			**S** 0.09	C 0.04	C 0.05		C 0.04					C 0.69	C 1.66	U 0.22	C 0.25
Agathidium dubitans													C 0.27	U 0.01	U <.01
Agathidium maculosum												C 0.11		U 0.01	U <.01
Agathidium pulchrum											C 0.14	C 0.57		U 0.07	U 0.02
Agathidium sp. 1			C 0.02	C 0.09			U 0.02								U 0.01
Agathidium sp. 3												C 0.11		U 0.01	U <.01
Catops basilaris													C 0.27	U 0.01	U <.01
Colon elongatum					C 0.05		U <.01						C 0.89	U 0.04	U 0.03
Melandryidae															
Melandrya striata			**S** 0.24	**S** 0.92	**S** 0.58	C 0.32	**S** 0.57		C 0.13					U 0.01	C 0.21
Orchesia castanea						C 0.32	U 0.03			C 0.56				U 0.02	U 0.04
Orchesia sp. 1												C 0.11		U 0.01	U <.01
Monotomidae															
Monotoma longicollis									C 1.13					U 0.05	U 0.02
Monotoma picipes										C 0.14				U 0.01	U <.01
Rhizophagus dimidiatus			**S** 0.1				U 0.01								U <.01
Rhizophagus n. sp. 1			**D** 13.08	**D** 11.5	**S** 3.41	C 1.13	**D** 8.05								C 2.45
Rhizophagus remotus			**S** 3.58	C 2.62		C 0.1	C 1.17	**S** 1.39	L 11.3	C 0.19				C 1.48	C 1.8
Mycetophagidae															
Mycetophagus distinctus										C 0.14				U 0.01	U <.01
Typhaea stercorea								C 0.15	C 0.04	C 0.56	C 0.28	C 0.11		C 0.25	U 0.09
Nitidulidae															
Epuraea flavomaculata	**D**	31.6	**S** 12.5	**S** 2.68	**S** 0.54	C 0.15	**S** 3.74		C 0.46					U 0.02	**S** 3.77
Epuraea linearis			C 0.03	C 0.06	C 0.12		C 0.04								U 0.01
Epuraea planulata			**S** 1.24	C 0.12			C 0.16	C 0.15	C 0.62					U 0.07	C 0.15

Family Species	Live Trees	Sn1	Sn2	Sn3	Sn4	Snags	Lg1	Lg2	Lg3	Lg4	Lg5	Lg6	Logs	TOTAL
Epuraea sp. 1	**S** 7.68							C 0.13	C 0.14				U 0.02	U 0.24
Epuraea terminalis	**D** 35.69	C 0.02	C 0.04	**S** 0.34		C 0.06	C 2.02		C 1.18	C 0.22	C 0.38		C 0.64	C 2.61
Epuraea truncatella	C 4.09						C 0.54						U 0.02	U 0.14
Glischrochilus moratus		C 0.04	C 0.03			U 0.01								U <.01
Glischrochilus sanguinolentus		**S** 0.67	C 0.64	C 0.24	C 0.74	**S** 0.8								C 0.24
Glischrochilus siepmanni		C 0.03	C 0.03	**S** 0.64	C 0.27	C 0.23								U 0.07
Glischrochilus vittatus	C 1.36	**S** 0.87	C 0.5		C 0.05	C 0.27								C 0.24
Ptiliidae														
Acrotrichis sp. 1		**D** 26.02	**D** 20.03	**D** 16.03	C 0.28	**D** 16.69	C 1.09	C 2.57	C 5.29	C 0.14	C 3.04	**D** 10.9	**S** 5.04	**D** 13.4
Pteryx sp. 1	C 1.36	C 0.05				U <.01	**S** 8.15	C 0.61	C 0.14	**D** 27.96	L 7.54	C 1.97	**D** 10.6	**D** 4.64
Pyrochroidae														
Schizotus cervicalis			C 0.11	C 0.05		U 0.02			C 1.22	**S** 6.18	C 2.71	C 0.27	C 1.82	C 0.86
Salpingidae														
Rhinosimus viridiaeneus		C 0.03		C 0.05		U 0.01								U <.01
Scirtidae														
Cyphon variabilis		**S** 1.13	**S** 1.43	**D** 10.31	**S** 2.62	**S** 5.15	**S** 5.13	C 0.08		C 0.14		C 0.81	C 0.76	**S** 3.13
Scraptiidae														
Anaspis rufa									C 0.14				U 0.01	U <.01
Canifa pallipes		**S** 0.27	**S** 2.04	**S** 5.11	**S** 2.96	**S** 2.94								C 0.89
Silvanidae														
Ahasverus advena								C 0.08					U <.01	U <.01
Dendrophagus cygnaei					C 0.05	U <.01	C 2.02	C 1.32					U 0.34	U 0.16
Staphylinidae														
Anotylus sobrinus		C 0.02	C 0.07			U 0.01				C 0.22			U 0.01	U 0.02
Atrecus macrocephalus				C 0.05		U <.01	C 0.54		C 5.01	**S** 7.92	L 9.94	L 3.28	**S** 5.87	C 2.31
Baeocera humeralis										C 0.14	C 1.26		U 0.14	U 0.05
Baeocera sp. 1					C 0.05	U <.01								U <.01
Bolitobius horni			C 0.04			U <.01						C 0.54	U 0.02	U 0.02
Carphacis nepigonensis		**S** 4.43	**S** 3.19	**S** 1.36	C 0.33	**S** 2.47								C 0.75
Coproporus ventriculus												C 0.83	U 0.04	U 0.01
Dinothenarus pleuralis												C 0.27	U 0.01	U <.01
Euplectus duryi		**S** 0.14	C 0.2	**S** 0.79	C 0.48	**S** 0.44								C 0.13
Gabrius brevipennis										C 0.28	**S** 4.38	C 0.66	C 0.58	U 0.21
Ischnosoma splendidum				C 0.05	C 0.07	U 0.02				C 0.14	C 0.11	C 0.81	U 0.15	U 0.1
Lathrobium fauveli										C 0.22	**S** 9.5	**D** 8.47	**S** 2.06	C 0.73
Lathrobium washingtoni					C 0.07	U 0.01			C 1.18	C 0.14	**S** 6	**D** 9.38	**S** 2.38	C 0.96
Leptacinus intermedius									C 0.14				U 0.01	U <.01

Family Species	Live Trees	Sn1	Sn2	Sn3	Sn4	Snags	Lg1	Lg2	Lg3	Lg4	Lg5	Lg6	Logs	TOTAL
Lordithon bimaculata		**S** 0.14	C 0.81	C 0.5	C 0.37	**S** 0.57							C	0.17
Lordithon fungicola			C 0.64			U 0.05							U	0.01
Megarthrus angulicollis											C 0.11		U 0.01	U <.01
Mycetoporus americanus		C 0.02	C 0.03		C 0.09	C 0.03				C 0.14			U 0.01	U 0.02
Nudobius cephalus		C 0.02				U <.01		C 0.08					U <.01	U <.01
Orobanus sp. 1										C 0.14			U 0.01	U <.01
Oropus sp. 1		C 0.02				U <.01								U <.01
Philonthus lindrothi										C 0.14			U 0.01	U <.01
Phloeostiba lapponica	**S** 15.61	**S** 1.93	C 0.5	C 0.12	C 0.05	**S** 0.56	**S** 8.99	C 1.25					U 0.72	**S** 2.41
Phyllodrepa sp. 1		C 0.03				U <.01				C 0.14	C 1.71		U 0.18	U 0.1
Proteinus atomarius												C 0.66	U 0.03	U 0.01
Proteinus limbatus											C 0.11	C 0.27	U 0.04	U 0.01
Pseudopsis sagitta								C 0.13			**S** 8.59	C 0.83	C 0.9	C 0.32
Quedius frigidus											C 4.64		U 0.23	U 0.08
Quedius fulvicollis										C 0.14		C 0.66	U 0.07	U 0.03
Quedius plagiatus		**S** 0.14	C 0.57	**S** 0.44	**S** 1.75	**S** 0.77		C 0.13	C 1.33				U 0.1	C 0.45
Quedius rusticus												C 0.83	U 0.04	U 0.01
Quedius velox		**S** 0.73	**S** 1.51	**S** 2.36	**S** 2	**S** 2.03						C 0.27	U 0.01	C 0.73
Scaphium castanipes									C 0.39				U 0.02	U 0.01
Sepedophilus testaceaus									C 1.42				U 0.06	U 0.02
Stenichnus ovipennis		**S** 0.17	**S** 1.28	C 0.5	C 0.83	**S** 0.82				C 0.22			U 0.01	C 0.32
Stenus austini												C 0.89	U 0.04	U 0.01
Stenus maritimus			C 0.04			U <.01						C 0.27	U 0.01	U 0.01
Syntomium confragosum			C 0.07			U 0.01			C 0.14				U 0.01	U 0.01
Tachinus elongatus		C 0.03	C 0.14	**S** 1.78	C 0.37	**S** 0.48				C 0.14			U 0.01	C 0.19
Tachinus fumipennis		C 0.03				U <.01		C 0.08			C 0.69	C 2.74	C 0.4	U 0.18
Tachyporus borealis					C 0.05	U <.01			C 1.42	**S** 1.09	**D** 8.57	**D** 12.12	**S** 3.7	C 1.46
Tenebrionidae														
Platydema americanum			C 0.07			U <.01								U <.01
Upis ceramboides					C 0.09	U 0.01		C 0.04					U <.01	U 0.01
Trogossitidae														
Ostoma ferruginea									C 0.19				U 0.01	U <.01
Thymalus marginicollis			C 0.28	**S** 0.67		C 0.13		C 0.04					U <.01	U 0.05

4.4.5. Log microhabitats

Saproxylic assemblages differed significantly among log microhabitats (ANOSIM: R=0.0279, p=0.012). The cluster dendrogram clearly distinguished assemblages from fungus fruiting bodies ('fungus') from assemblages occurring in all other log microhabitats (Figure 4.5). This assemblage comprised the obligate polypore feeders *Cis americanus* and *Dolichocis manitoba*, which were hand collected from *Trichaptum abietinum* (Basidiomycetes: Polyporaceae). Beetle assemblages found under bark and between bark layers were most similar (65%) in terms of species composition. Assemblages from various depths of xylem (s, m, h) also grouped together, although composition varied from 38% to 53% similarity.

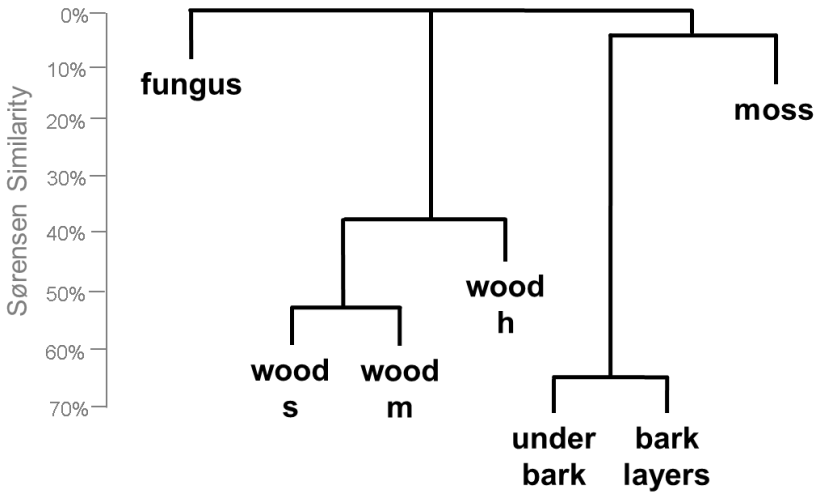

Figure 4.5 Cluster dendrogram of saproxylic beetle assemblages hand-collected from various microhabitats within logs (Sorensen similarity measure, Ward's method). The 'wood' microhabitat was sub-categorized by radial thickness of the xylem, as follows: s= 'shallow' (the outermost third), m= 'middle' (the middle third), and h= 'heart' (the inner third).

4.5. Discussion

Saproxylic beetle assemblages and species vary markedly among different aspen habitats. Beetle species composition was highly dissimilar between habitat classes, and assemblages apparently responded strongly to substrate position (standing or fallen) and extent of decay (from live to well-decayed). In addition, habitat class, defined as the combination of position and decay class, was the single most effective predictor of saproxylic beetle assemblages, with habitat class associated with useful indicator status for 51 species.

The large dissimilarity among beetle assemblages across habitats is probably associated with differences in species-specific natural history. Trophic diversity, for example, is quite large in saproxylic beetle communities, and associated with specific adaptations for particular substrates within the range of substrate types and decay states available (Speight 1989). For instance, through CCA ordination I showed that saproxylic beetle feeding guilds were related to different habitats. Fungivores (e.g., *C. elongata, C. constricta, Pteryx* sp. 1) were more related to log habitats, whereas xylem-feeders (e.g., *Hemicoelus carinatus, Ptilinus lobatus,* and *Atomaria epiphiatta*) were associated with well-decayed snags. This likely reflects use of the different resources provided by these substrates, although such details remain to be worked out for the North American fauna. For deadwood management schemes aiming to conserve saproxylic beetles, the substrate variables and

attributes examined in this study lend useful information, but also caution managers that deadwood is a complex and variable resource with respect to supporting biodiversity. Certainly, these results confirm that the practice of retaining particular substrate types (live trees, snags, and logs) is valuable as a basic conservation tactic. However, retained wood should also encompass the range of attributes and habitats known to support saproxylic biodiversity in mature aspen stands. Bark surface area and moss cover were important for explaining variation in saproxylic beetle assemblages and were related to many indicator species. If only substrates lacking bark, for example, were provided for retention, the distinct subcortical (and between bark) assemblages would not be conserved.

As suggested by the results of this study, the trajectories of saproxylic beetle colonization are distinct for snags and logs. Rather than freshly dead substrates decaying in parallel regardless of substrate position, assemblages of logs and snags diverge along a decay gradient possibly associated with different decay pathways in the two substrates. Deadwood position clearly affects decay rate, with decomposition of fallen logs proceeding more than in standing logs (Yatskov et al. 2003).

It was interesting to find that live aspen supported a distinct assemblage of beetles, and that living trees supported comparable diversity to that found in logs and snags. Although none of the species considered here were unique to live aspen (e.g., *P. lapponica* was also

subdominant in Sn1 and Lg1 habitats), the fact that these species use living trees further underscores that the notion of being ‘saproxylic’ is less clear than concluded from studies of dead wood alone, i.e., some species, often considered as saproxylic, may also use trees that appear to be healthy, at least by our classification. This emerging conception of live trees as usable habitat for saproxylic beetles also signifies the importance of classifying habitats according to the organisms inhabiting them, rather than by our anthropocentric perspective. There are likely cues that indicate suitable habitat for colonizing organisms that are not outwardly obvious to us.

4.5.1. Aspen death and decay

The onset of death and decay begins a succession of physical and chemical changes in the tissues of trees. This deadwood decay cycle (Lofroth, 1998) results from numerous processes (colonization, decomposition, fragmentation) and the communities of fungi, invertebrates, and bacteria present in deadwood appear to interact to generate considerable habitat complexity (Harmon et al 1986, Speight, 1989, Maser and Trappe, 1984). Though the specific deadwood cycle has not been fully documented for trembling aspen, I suggest the following general outline of aspen death and decay based on my observations and work presented above. Conserving the actors in this drama is inextricably associated with also conserving the process.

Declining trees: Tissues that are physiologically active are the first to be attacked and consumed due to their higher relative nutrient status than exists in trees with inactive tissues (Maser and Trappe 1984). Live trees provide suitable habitat for beetle larvae that develop in bark tissue, feeding on sap runs of injured/moribund aspen (*Epuraea spp.*, *Phloeostiba lapponica*). However, because the heartwood of aspen is lower in tannin-rich, decay-inhibiting parenchyma cells than most tree species (Schmidt 2006; Hoadley 1990), heart-rot fungi (e.g., *Phellinus tremulae*) are able to heavily exploit this habitat. Eventually, large decay columns leave living aspen trees hollow, which make them more attractive to cavity nesters, carpenter ants, etc. These trunk-rotten aspen trees are more susceptible to stem breakage and windthrow (Hiratsuka et al., 1995) thus aspen contributes largely to deadwood recruitment.

Early decay: In recently dead wood, primary decomposers, such as some wood-boring beetles target potential hosts by visual and chemical cues (Huber et al. 2000; Campbell and Borden 2005; Borden et al. 1998) and penetrate the periderm to feed on the nutritious inner bark and sapwood tissues, thus exposing the inner wood to invasion by other decomposers and to predators of these primary colonisers (Esseen et al. 1997). The ambrosia beetle *Trypodendron retusum* (Curculionidae: Scolytinae) was most dominant in freshly dead aspen. The monotomid beetles, *Rhizophagus remotus* and *Rhizophagous* n. sp. 1, were also dominant in freshly dead aspen, likely preying on scolytine larvae, as is

the known feeding strategy of beetles in the subfamily Rhizophaginae (Bousquet 1991). As the phloem tissues are consumed and decay continues necrosis of the bark tissue (rhytidome and phloem) becomes evident. The thin outermost white epidermal layer of aspen bark rapidly sloughs off in the first stages of decay, as this photosynthetically active tissue dies.

Moderate decay: Active decomposition of phloem and vascular cambium causes the bark to loosen from the underlying sapwood creating a niche known as the “subcortical zone” (Speight 1989). Most of the species adapted to the subcortical habitat are strikingly flattened dorso-ventrally; e.g., the subcortical habitat of aspen was dominated by the predaceous flat bark beetle *Cucujus clavipes* (Cucujidae). The subcortical habitat is unique in that it is sheltered from extreme temperature and moisture fluctuations and that it is rich in fungi and potential prey items that feed on these fungi. The open space between the rhytidome and sapwood provides excellent and well-provisioned corridors for predators. The subcortical zone also receives sap running from the damaged bole, and this can support sap-feeding *Epuraea* species (Nitidulidae; Speight 1989). As the bark continues to decay and sloughs from the substrate, this subcortical community disappears.

Advanced decay: Sapwood is highly colonized, decomposed, and fragmented by insects and microbes, although not quite so nutritious as the overlying cambial tissues, is subject to high levels of consumption by

saproxylic beetles. Fungivores and their associated predators and detritivores dominate well-decayed habitats. For instance, the detritivore *Megatoma perversa* (Dermestidae) was dominant in late-decay class snags (Sn4). By the time the sapwood is consumed, the last remaining substrate is usually dead xylem tissue of low nutritional quality (Maser and Trappe 1984). Many fungal colonizers of this nutrient-poor habitat adapt to nutrient stress by developing predaceous feeding habits (Boddy 2001; Barron 2003). Likewise, beetle colonizers have also adapted to this low-nutrient environment. For example, many xylem consuming beetles have developed symbiotic relationships with fungi that aid in digestion of wood tissues. Larvae of *Hemicoelus carinatus* (Anobiidae), which was dominant in Sn4 habitats, for example, carry in their guts endosymbiotic yeast that contributes to their nutrition (Csóka & Kovács 1999). Other xylophagous beetles, such as *Melandrya striata* (Melandryidae), consume fungus-ridden wood, and thus it is surmised that fungi likely contribute greatly to their diet. Predatory beetles become dominant in late stages of decay (Esseen et al. 1997; Hammond et al. 2004), as the dominance analysis above revealed predator dominance increasing with log decay (e.g., the rove beetles *Tachyporus borealis, Lathrobium washingtoni,* and *L. fauveli*). Additionally, species with low tolerance for desiccation may be found in late-decay log habitats that are high in moss cover- suggesting locally high moisture, and that moisture can vary over microscales in dead wood. Well-decayed logs continue to be colonised by soil fauna, lichens,

bryophytes, understory plants, seedlings, and bryophytes (Esseen et al. 1997; Maser and Trappe 1984), until they ultimately are incorporated into the forest floor as humus.

4.5.2. Conclusions

Only a few studies have examined the saproxylic beetle fauna associated with trembling aspen substrates (Hammond et al. 2001, 2004; Jacobs et al. 2007). As a result, little is known about the particular microhabitats required by this saproxylic fauna. The forgoing study fills knowledge gaps and provides new information about saproxylic beetle habitat associations, biology, and natural history of species from aspen substrates in broad-leaved stands of boreal mixedwood forests. During the course of this study, for example, I found seven species new to science, including six new species of *Corticaria* (Latridiidae). Currently, there are only 32 species of *Corticaria* reported for North America, while another 130 species of *Corticaria* are known from elsewhere in the world (Rücker 2010). Given the diversity of *Corticaria* in the European boreal forests, my work highlights that a large number of North American species likely remain undiscovered. Development of additional taxonomic expertise in this group (and others like Ptiliidae and Cryptophagidae) would greatly improve our understanding of the North American fauna. Additionally, I provide new provincial records for 45 other species, including two important distribution extensions for the ground beetles *Diacheila arctica*

amoena (Faldermann) (Bourassa and Wood 2011) and *Perigona nigriceps* (Dejean).

As much of North America's forests are still undergoing their first rotation of harvest and our knowledge of saproxylic beetle ecology is quite poor, it is difficult to predict the full impacts of these disturbances on species and overall forest productivity. Given demonstrated risks of extinction in northern Europe (Martikainen et al. 2000; Simila et al. 2002; Siitonen 2001; Nieto and Alexander 2010) and indication of negative impact of forestry on saproxylics in Canada (Cobb et al. 2011), these organisms merit special conservation consideration in management. This may be important to maintain the ecological roles of saproxylics, which contribute to nutrient cycling (Cobb et al. 2009), and to a large pool of prey for higher organisms. Substrate variables and attributes studied here were strongly related to saproxylic beetle diversity, and may be relevant as surrogates for biodiversity for monitoring (York 1999) or in conservation planning (Juutinen et al. 2006).

4.6. Literature Cited

Barron, G. L. 2003. Predatory fungi, wood decay, and the carbon cycle. Biodiversity, Volume 4: 3-9.

Beckingham, J. and J. H. Archibald. 1996. Field guide to ecosites of Northern Alberta. Special Report 5. Natural Resources Canada, Canadian Forest Service. Northwest Region. Edmonton, AB.

Boddy, L. 2001. Fungal community ecology and wood decomposition processes in angiosperms: from standing tree to complete decay of coarse woody debris. Ecological Bulletins 49: 43-56.

Borden , J.H., I.M. Wilson, R. Gries, L.J. Chong , H.D. Pierce , Jr and G. Gries. 1998. Volatiles from the bark of trembling aspen, *Populus tremuloides* Michx. (Salicaceae) disrupt secondary attraction by the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). Chemoecology 8: 69 – 75.

Bourassa, S. and C.M. Wood. 2011. First record of *Diacheila arctica amoena* (Faldermann) (Coleoptera: Carabidae) in Alberta, Canada. The Coleopterists Bulletin 65(2): 144-145.

Campbell , S. A. and J.H. Borden . 2005. Bark reflectance spectra of conifers and angiosperms: implications for host selection by coniferophagous bark and timber beetles . The Canadian Entomologist 137: 719 – 722 .

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18: 117-143.

Cobb, T. P., K. D. Hannam, B. E. Kishchuk, D. W. Langor, S. A. Quideau, and J. R. Spence. 2009. Wood-feeding beetles and soil nutrient cycling in burned forests: implications of post-fire salvage logging. Agricultural and Forest Entomology 12(1):9-18.

Cobb, T. P., J. L. Morissette, J. M. Jacobs, M. J. Koivula, J. R. Spence, and D. W. Langor. 2011. Effects of postfire salvage logging on deadwood-associated beetles. Conservation Biology 25(1):94-104.

Colwell, R. K., C. X. Mao, and J. Chang. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology 85 (10):2717-2727.

Colwell, R. 2009. EstimateS: Statistical estimation of species richness and shared species from samples. Version 8.2. http://viceroy.eeb.uconn.edu/EstimateS

Csóka, GY., and T. Kovács. 1999. Xylophagous insects. Forest Research Institute. Erdészeti Turományos Intézet. Agroinform Kiadó, Budapest. 189 pp.

Dufrêne, M. and P. Legendre. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecological Monographs 67:345–366.

Ehnström, B. and Waldén, H.W. 1986. Faunavård i skogsbruket 2: Den lägre faunan. Jönköping. 351 pp.

Esseen, P. A., Ehnström, B., Ericson, L. and Sjöberg, K. 1997. Boreal forests. Ecological Bulletins 46:16–47.

Hammond, H. E. J. 1997. Arthropod biodiversity from *Populus* coarse woody material in north-central Alberta: A review of taxa and collection methods. The Canadian Entomologist 129(6):1009-1033.

Hammond, H. E., D. W. Langor, and J. R. Spence. 2001. Early colonization of *Populus* wood by saproxylic beetles (Coleoptera). Canadian Journal of Forest Research 31(7):1175-1183.

Hammond, H. E. J., D. W. Langor, and J. R. Spence. 2004. Saproxylic beetles (Coleoptera) using *Populus* in boreal aspen stands of western Canada: spatiotemporal variation and conservation of assemblages. Canadian Journal of Forest Research 34(1):1-19.

Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaenper, K. J. Cromack, and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15: 133-302.

Hoadley, R.B. 1990. Identifying Wood: Accurate results with simple tools. Taunton Press, Conneticut, USA. 223 pp.

Huber, D.P.W., R. Gries, J.H. Borden and H.D. Pierce. 2000. A survey of antennal responses by five species of coniferophagous bark beetles (Coleoptera: Scolytidae) to bark volatiles of six species of angiosperm trees. Chemoecology 10: 103-113.

Jacobs, J. M., J. R. Spence, and D. W. Langor. 2007. Influence of boreal forest succession and dead wood qualities on saproxylic beetles. Agricultural and Forest Entomology 9(1):3-16.

Jonsell, M., J. Weslien, and B. Ehnstrom. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodiversity and Conservation 7(6):749-764.

Juutinen, A., M. Monkkonen, and A. L. Sippola. 2006. Cost-efficiency of decaying wood as a surrogate for overall species richness in boreal forests. Conservation Biology 20(1):74-84.

Kaila, L. 1993. A new method for collecting quantitative samples of insects associated with decaying wood or wood fungi. Entomologica Fennica 29: 21-23.

Kishchuk, B.E. 2004. Soils of the Ecosystem Management Emulating Natural Disturbance (EMEND) experimental area, northwestern Alberta. Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre, Edmonton Alberta. Information Report NOR-X-397.

Lassauce, A., Y. Paillet, H. Jactel, and C. Bouget. 2011. Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. Ecological Indicators 11(5):1027-1039.

Lofroth, E. 1998. The Dead Wood Cycle, In: J. Voller and S. Harrison. (ed.). Conservation Biology Principles for Forested Landscapes. Vancouver, Canada, UBC Press, pp. 185-214.

Mao, C. X., R. K. Colwell, J. Chang 2005. Estimating the species accumulation curve using mixtures. Biometrics 61(2):433-441.

Martikainen, P., J. Siitonen, P. Punttila, L. Kaila, and J. Rauh. 2000. Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biological Conservation 94(2):199-209.

Maser, C. and J.M. Trappe. (eds.). 1984. The seen and unseen world of the fallen tree. USDA Forest Service General Technical Report. PNW-164. Pacific Northwest Forest Range Experimental Station, Portland, OR, pp. 56.

Miller, K.B. and Q.D. Wheeler. 2005. Slime-mold beetles of the genus *Agathidium* Panzer in North and Central America, Part II. Coleoptera: Leiodidae. Bulletin of the American Museum of Natural History 291: 1-167.

O'Brien, C.W. 1997. A catalog of the Coleoptera of America north of Mexico. Family: Curculionidae. Subfamilies: Acicnemidinae, Cossoninae, Rhytirrhininae, Molytinae, Petalochilinae, Trypetidinae, Dryopthorinae, Tachygoninae, Thecesterninae. United States Department of Agriculture. Agriculture Handbook No. 529. 143g: x + 48 pp.

Oksanen, J. R., Blanchet, F. G., Kindt, R. Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., and Wagner, H. 2012. VEGAN: Community ecology package, version 2.0-3. R Package.

Palmer, M. W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. Ecology 74: 2215-2230.

Pinzón, J., and J. R. Spence. Bark-dwelling spider assemblages (Araneae) in the boreal forest: dominance, diversity, composition and life-histories. Journal of Insect Conservation 14(5):439-458.

R Development Core Team. 2010. R: A language and environment for statistical computing, version 2.11.1. R Foundation for Statistical Computing, Viena. http://www.R-project.org.

Rücker, W.H. 2010. Checklist Latridiidae & Merophysiinae of the World. E-Journal: ISSN 1868-2168. Retrieved on 1 May 2012.

Schmidt, O. 2006. Wood and Tree Fungi: Biology, Damage, Protection, and Use. Springer, Heidelberg, Germany. 334 pp.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins 49:11-41.

Simila, M., J. Kouki, P. Martikainen, and A. Uotila. 2002. Conservation of beetles in boreal pine forests: the effects of forest age and naturalness on species assemblages. Biological Conservation 106(1):19-27.

Speight, M. C. D. 1989. Life in Dead Trees - a Neglected Part of Europe Wildlife Heritage. Environmental Conservation 16(4): 354-356.

ter Braak, C. J. F. 1987. Ordination. In Data analysis and landscape ecology. Edited by R. H. G. Jongman, C. J. F. ter Braak, and O. F.R. van Tongeren. Center for Agricultural Publishing and Documentation (PUDOC), Wageningen, the Netherlands. pp. 91-173.

Tikkanen, O. P., P. Martikainen, E. Hyvarinen, K. Junninen, and J. Kouki. 2006. Red-listed boreal forest species of Finland: associations with forest structure, tree species, and decaying wood. Annales Zoologici Fennici 43(4):373-383.

Nieto, A. and K.N.A. Alexander. 2010. European Red List of Saproxylic Beetles. Luxembourg: Publications Office of the European Union.

Wheeler, Q.D. and K.B. Miller. 2005. Slime-mold beetles of the genus *Agathidium* Panzer in North and Central America, Part I. Coleoptera: Leiodidae. Bulletin of the American Museum of Natural History 290: 1-95.

Yatskov, M., M.E. Harmon and O.N. Krankina. 2003. A chronosequence of wood decomposition in the boreal forests of Russia. Canadian Journal of Forest Research 33: 1211-1226.

York, A. 1999. Ecologically sustainable management: the utility of habitat surrogates for assessing terrestrial invertebrate diversity in temperate forests. In: W. Ponder and D. Lunney. (eds.). The Other 99%: The Conservation and Biodiversity of Invertebrates. Mosman, New South Wales, Australia, Royal Zoological Society of New South Wales, Transactions of the Royal Society of New South Wales, p. 34-39.

5. DISCUSSION

This thesis was inspired by the mounting conservation concerns about saproxylic biodiversity in relation to industrial forestry from the boreal region of Europe. Increased interest in conserving forest biodiversity through sustainable forest management practices across Canada requires improved knowledge of the saproxylic fauna and their associated habitats in order to develop effective deadwood management strategies. A large proportion of such biodiversity is found among the arthropods, and members of the order Coleoptera because of their taxonomic and ecological diversity constitute an ideal focal group for such investigation.

I had three main objectives: i) to assess the performance of various collection methods and suitability for sampling saproxylic beetles; ii) to examine saproxylic beetle associations among different diameter classes of logs; and iii) to determine saproxylic beetle associations with substrate type, decay class, and particular deadwood attributes (such as bark and moss cover). From the results of my pursuits emerge two clear messages. Firstly, particular collection method(s) are highly influential on beetle catches and thus resulting datasets. Quantitative comparisons of commonly employed methods can thus help guide appropriate study design and optimize performance for particular study objectives. Secondly,

habitat heterogeneity and a wide range of deadwood habitats are used readily by saproxylic beetles. All substrate types, size classes, and decay classes examined, including live trees, supported saproxylic beetles. Appropriately, it appears that this complex and diverse group of beetles requires a likewise very diverse array of habitats. Forest management protocols will be improved by incorporating a diverse array of habitat qualities, in addition to managing deadwood amounts.

5.1. Main Findings

In the first chapter, I introduced the importance of deadwood habitats to saproxylic biodiversity and forest ecosystems and underscored reasons for choosing saproxylic beetles as the focal taxa of this thesis. I also presented the rationale for focusing on saproxylic habitats of trembling aspen; this tree species is widely distributed in North America, and its saproxylic fauna has been studied less intensively than for coniferous tree species. Additionally, I outlined the rationale for studying the topics of subsequent chapters.

In the second chapter, I compared six different collection methods used to sample saproxylic beetles from various aspen habitats. Knowledge of collection method performance and species-specific collection biases will be useful to design future studies and monitoring programs. Collection method had a greater effect on perceptions of the

structure of beetle assemblages than did differences in substrate type, decay class, surface area, volume, and sampling time. Although hand collection has rarely been employed in saproxylic beetle studies, I found it to be the most productive method, providing efficient species accumulation, high catch of target species, and low sorting time and cost to setup in the field. I found strong support for using modified Tullgren funnels to sample beetles from the wood fragments remaining after hand collection, as funnels extracted a large number of species that would have been otherwise be missed. In short, and funnels were very practical for deriving diverse samples in a short time. While window traps were also efficient at collecting a large number of saproxylic beetle species and have been widely employed in studies of saproxylic insects, they also collected many non-target organisms which inevitably translate to increased laboratory time for sample sorting. Additionally, window traps may be unsuitable for studies wishing to assess ecological associations, such as effects of habitat quality, as this was the only collection method that was insensitive to habitat and collection variables (substrate attachment, decay class of substrate, sampling time, etc.). In chapter two I also demonstrated that catches of many species are biased by particular collection methods, and that such biases were strongly associated with window trap samples. Overall, my work suggests that collection method(s) should be carefully

chosen in relation to the goals of particular investigations, as different methods may profoundly influence the results of individual studies.

In the third chapter I examined responses of saproxylic beetles to diameter of fallen aspen deadwood, in four size classes: 7 to <16 cm (SC 1), 16 to <25 cm (SC 2), 25 to <34 cm (SC 3), and 34 to 43 cm (SC 4). Although small diameter logs were more abundant in deciduous stands, fewer saproxylic beetles were found to use <16 cm diameter logs and assemblages differed significantly between logs greater or less than 25 cm in diameter. Furthermore, more species were associated with ≥25 cm diameter logs than smaller logs. It is possible that these patterns of habitat use could be driven by differential predation and/or competition across log size classes. Additionally, I developed and discussed other hypotheses to explain the relationship between deadwood size and saproxylic diversity. Overall, all size classes of logs supported unique species of saproxylic beetles and thus the log size appears to be an important element of habitat for the saproxylic community. Hammond et al. (2004) found that saproxylic beetle assemblages also differed with respect to diameter of snags, with more species (particularly unique species) and more indicator species being similarly associated with large diameter substrates.

Examining evidence for associations between saproxylic beetles and substrate size throughout other chapters of the thesis, suggests that

dimension of deadwood (diameter, size class, surface area, and/or volume) may, however, influence saproxylic beetles less than substrate type and decay class. For example, substrate dimension (surface area, volume) did not significantly influence the overall saproxylic beetle community, but did have an important role in structuring the beetle assemblages defined by hand collection and funnel extraction samples from logs (Chapter 2). In chapter four, greater substrate length (or height for standing deadwood) and higher mean sample volume were significantly correlated with ordination axes, primarily represented by snag substrates. There were 34 indicator species for greater than average sample volume, while no species were significant indicators of low sample volume. In contrast, five species indicated shorter than average substrate length, while only two were indicators for longer than average substrate length. Given that substrate dimension resurfaced in the analyses of all chapters, I suggest that future studies could usefully provide further examination of these relationships.

In chapter four I assessed saproxylic beetle associations with various habitat qualities. Substrate type (live tree, snag, log) was an important determinant of saproxylic beetle assemblage composition. Although live trees did not host any unique species, they supported an amount of beetle diversity that was surprisingly similar to that found in other decay classes, with assemblages of living trees dominated largely

by sap-feeding beetles. Although richness estimates per individual and volume sampled were lower for snags than logs, these substrate types clearly house quite distinct beetle assemblages. Decay class, percent bark cover, and moss presence were also strongly correlated with patterns in ordinations of the saproxylic beetle community. Species composition was most similar between adjacent decay classes within each deadwood habitat type. A large number of species (87 species) were significant indicators for particular deadwood qualities, most notably decay class.

Few species were found to be dominant in the overall saproxylic beetle community associated with aspen habitats, but instead, the dominance of many species sharply declined in adjacent decay classes of a particular substrate type. Additionally, in chapter four I show that microhabitats within logs support distinct assemblages, with fungal fruiting bodies hosting the most unique assemblages (comprised of the 'minute tree-fungus beetles' of the family Ciidae). Thus, conserving a variety of deadwood habitats with a range of qualities seems to be required to effectively conserve the saproxylic fauna associated with aspen. With respect to management of deadwood resources the question of 'how much?' must be linked to information about deadwood quality.

5.2. New Distributional Records and Undescribed Species

Additionally, this thesis work documents 47 new species records for the province of Alberta, as well as seven new species to science (to be described in a later publication) (Appendix 5-A; Bourassa and Wood 2011). An additional four species were likely new records for Alberta, and one species of *Agathidium* may be novel (this still requires confirmation). I was unable to identify many other species using currently available literature. These were considered 'morphospecies' in the thesis, but many could also be new records. Altogether, 20% of the taxa (59 of 285 species) collected in this study expanded the basic knowledge of Alberta's saproxylic fauna, by documenting new records for species, many of which are groups that are poorly known across North America (e.g., Latridiidae, Cryptophagidae). For example, the latridiid species *Corticaria elongata* (Gyllenhal) was a conspicuously dominant element of the saproxylic community of aspen deadwood, particularly logs (Chapter 4) occurring in especially high abundance in logs >34 cm (Chapter 3). However this is the first record for the species in Canada, outside of the Atlantic region (Majka et al. 2009). As *C. elongata* was reported in North America as early as 1899 from across the USA (Fall 1899), I suggest that the new record here does not represent a recent distributional change for the species. Rather, this example highlights the paucity of accurate distributional records for some beetle groups. Another three latridiid species *Melanophthalma helvola* Motschulsky, *M. inermis* Motschulsky, *and M. americana*

(Mannerheim) were all newly recorded for Alberta; the first two of these are only known from the Atlantic region of Canada, and sparsely from the states of Pennsylvania and Louisiana, respectively (Majka et al. 2009). The subfamily Corticariinae (Latridiidae) is but one example of beetle groups in dire need of further taxonomic work in Canada (also Cryptophagidae: Atomariinae, Ptiliidae, Nitidulidae: Epuraeinae, Staphylinidae: Aleocharinae and Steninae). It is clear that many knowledge gaps still exist, however faunistic studies such as this- aided by improved taxonomic resources- will produce many new records and better understanding of species' habitat-requirements.

5.3. Qualifications and Representativeness of the Study

The work presented in this thesis should be qualified with respect to the particular region and stands studied. These results were derived from four mature deciduous stands in the boreal mixedwood region, which were not chosen at random. The density and diversity of aspen deadwood in these stands, although seemingly representative in this area, may vary from that of typical mature deciduous stands in the region. However, as the focus of this thesis was not to examine stand-level effects, but rather to examine substrate-level associations, my goal was not to select representative stands, but to allow for adequate replication within various habitat types (snags, logs, decay classes, sizes). Compared to nearby

unharvested deciduous stands from the Ecosystem Management Emulating Natural Disturbance (EMEND) experiment, the diameters of substrates examined in this study are within the natural range documented for this stand type (Figure 5.1). Because I sampled only a small amount of the natural variation in snag diameters, the influence of snag size on saproxylic beetle communities was not examined in Chapter three (only logs were examined). As well, log decay class distributions observed in my study sites were similar to those reported by Lee et al. (1997) in other aspen-dominated boreal mixed wood forests in Alberta. Therefore, it is likely that the results of the foregoing chapters translate well to other stands of comparable age and overstory composition in the boreal mixedwood ecoregion of Canada.

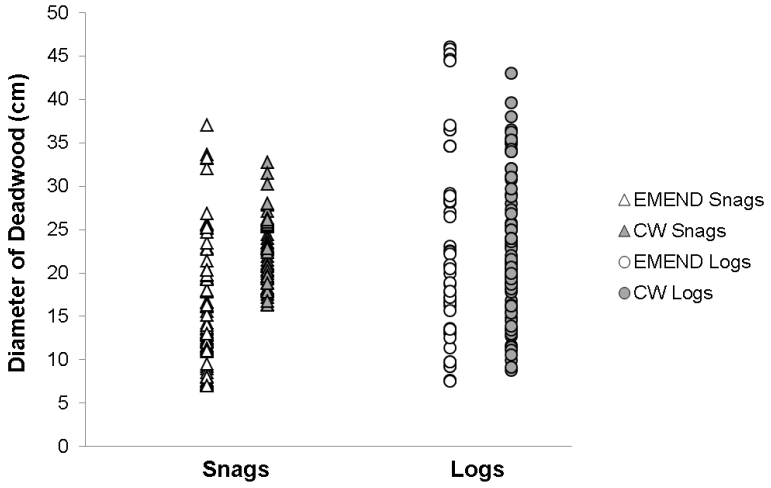

Figure 5.1 Distribution of substrate diameters sampled in the current study (CW) and in the unharvested deciduous-dominated stands of the adjacent EMEND (Ecosystem Management Emulating Natural Disturbance) study area (EMEND data was courtesy of David Langor and EMEND; 'Downed Coarse Woody Debris Summary' and 'Snag Summary' was downloaded from the EMEND Database on 2012-02-17).

In Chapter 4 I included live aspen trees as potentially important habitats of saproxylic communities. This may seem contradictory, and some people might assume that the species associated with live aspen here were merely sampled by chance, perhaps if adults were present on the outside of the boles sampled. Others may conclude that the species of live trees are less deserving of consideration as 'saproxylic'. Firstly, I am confident that a great majority of the beetles sampled from living aspen were truly reared from immature developmental stages collected in these tree sections. Not only did all three replicates each house a similar composition of beetle species (not expected if derived by chance), but also majority of beetles collected from live trees appear to have developed within the tree bole. Rather than collecting beetles in the initial collections after enclosing tree sections (would suggest beetle found on, rather than in, the substrate), beetle abundance was greatest in collections made mid-July through late August (94% of total abundance). One cucujid larva and 56 other larval coleopterans were collected from live trees. Of the nine taxa collected, *Epuraea* spp. (Nitidulidae) were present in all live tree replicates. These species are known to feed on sap runs and spores of microfungi, which are common features of live aspen. Secondly, all of the species collected in live trees were also present in comparable or greater abundances in dead aspen substrates (Appendix 5-A), suggesting that these species do merit consideration as 'saproxylic' insects. Thus, it

appears that there is not an absolute line between insects that feed on living trees and those found in dead or dying trees.

Indeed, other studies have also documented that live trees (both healthy and moribund) do provide habitat for species reasonably classified as ‘saproxylic’ (Speight 1989), because even healthy trees include microsites of dead tissue (e.g., cavities, branch stubs, cankers). Aspen trees align quite well with this thinking, as individual stems of aspen clones exhibit a large amount of decay long before tree death has begun. Mature aspen trees have, for example, characteristic cankers caused by the microfungi *Entoleuca mammata, Leucostoma nivea,* and *Valsa sordida* (Hutchison 1999). The mycelial fans and perithecial fruiting bodies produced in the region of cankers (Hiratsuka et al. 1995) could provide suitable microhabitats for saproxylic species that might feed on microfungi. As well, sap flows are frequented by beetles of the genus *Epuraea*. The aspen trunk rot fungus *Phellinus tremulae* is prominent in mature live aspen trees; often fruiting bodies are produced from holes left from dead branches on the lower portion of aspen stems. This dead area and fungal tissue could host a number of ‘saproxylic’ species. For example, I have reared *Cis americanus* from one conk of this species (C. Wood, unpublished data), and this beetle is known to be an obligate associate of wood-decaying polypores. Also, live trees heart-rotted by this fungus may have greater numbers of cavities than those without conks (Aitken and

Martin 2004). These excavated and rotten hollows can support a diversity of beetles, particularly detritus feeders (Ranius 2002). Overall, it is clear that live aspen trees may very well contain suitable habitat for saproxylic beetle species, and thus habitat associations are not always restricted to deadwood.

5.4. Future Work

Much work remains to fully understand deadwood patterns and processes and how these are related to the biodiversity of saproxylic organisms. Improved knowledge of these relationships will be vital to developing conservation strategies to preserve these components of forest ecosystems thought to play crucial functional roles. In this section, I discuss avenues of research amplified by this thesis and that would aid in these developing more effective approaches to conservation.

5.4.1. Responses to Resource Harvesting

One of the most urgent knowledge gaps to fill, I believe, is to more fully understand the impacts of resource harvesting (for timber and fuel) on forest biodiversity. While the consequences of intensive forest management have been suggested through retrospective studies across much of boreal Europe (Siitonen 2001; Simila et al. 2002), little is known about the potential impacts of resource extraction on saproxylic

communities of Canadian boreal forests. The few studies examining these relationships in boreal Canada, show evident short-term reductions in richness and compositional changes to the fauna in response to current forest management practices (Cobb et al. 2011; Jacobs et al 2007b; Légaré et al. 2011). When taken in concert with large-scale species reductions across boreal Europe and the fact that 436 species are now included on the European Red-List (Martikainen et al. 2000; Siitonen 2001; Nieto and Alexander 2010), it is clear that conservation of these diverse forest organisms would benefit from improved management systems. Still, the Canadian biofuel industry is developing quickly alongside an already mature forestry industry, causing conservation concerns (Hesselink 2010). It would be timely to study the influence of systematic deadwood reductions (and, possibly, additions) on stand-level biodiversity of saproxylic organisms. Such a study should be designed to find threshold volumes of deadwood (of various substrate types, decay classes, etc.) that maintain similar communities to intact forests.

Another research area in need of further development is the study of saproxylic beetle responses to particular harvesting schemes. Aggregated green-tree retention is effective for maintaining late successional species of spiders (Pinzon 2011) and beetles (Pyper 2009) after harvest, and its conservation utility should also be examined for saproxylic beetles. There is a need for optimizing retention patch size,

pattern, and distance from unharvested forest edge for improved biodiversity conservation in managed landscapes. Currently, Seung-Il Lee (U of A) is studying this relationship for spruce-associated saproxylic beetles, but these features have yet to be determined in detail for saproxylic species using aspen. Results from Jacobs et al. (2007b) on variable retention of white spruce is promising, suggesting that saproxylic beetles respond more strongly to deadwood quality and quantity after harvest than to particular levels of stem removal. However, to date such studies have relied mainly on window traps and, given results of Chapter 2, they should be conducted with direct habitat sampling methods (such as funnel extraction) to confirm that the beetles collected actually arise from the harvested stands and that they thus reflect the particular substrates available.

We know that spatial distribution and form of deadwood retention can influence biodiversity patterns. Fallen deadwood can be retained as single substrate entities dispersed evenly throughout a harvest block, as aggregations of many pieces of deadwood in piles, for example. Some forms of deadwood retention might be more beneficial than others for maintaining habitat quality for saproxylic organisms, but also their spatial distribution influences colonization of retained substrates. Ranius et al. (2011), for example, found that the colonization of log piles by specialists species of European aspen was influenced greatly by connectivity of

deadwood pools. In their study, some taxa responded to habitat connectivity at >1000 m spatial scale, suggesting that some species are influenced by large-scale landcape patterns in deadwood distribution. Sullivan and Sullivan (2012) found that windrows and piles were more effective than dispersed deadwood for encouraging use by small mammal populations. A linear configuration of windrows has the added benefit - over log piles- of forming continuous corridors of deadwood that can connect to intact forest features across harvest blocks. Future studies could examine whether saproxylic beetles fare better in response to certain forms of deadwood retention than to others, and at what spatial scale various species respond to deadwood distributions, in order to develop improved management practices. If the results of such studies show that saproxylic beetle diversity is influenced by large-scale deadwood connectivity, then entities and patterns of deadwood would best be managed across landscapes, rather than at a smaller (i.e., stand) scale.

As a beginning, the habitat-associations of saproxylic beetles outlined in this thesis will contribute to more effective biodiversity conservation. However, the quality of these habitats may be fundamentally altered by the surrounding environment in managed forests, rendering them useless for conservation of saproxylic beetles. For example, more extreme climatic conditions in exposed cut-blocks will likely influence the

saproxylic beetles using retained deadwood. Sun exposure has both positive and negative effects on saproxylic beetle species (Horak et al. 2011; Lindhe et al. 2005; Ranius et al. 2011). Furthermore, deadwood retained in open cut-blocks may be more susceptible to bark grazing by ungulates, and this has negative impacts on saproxylic diversity (Ranius et al. 2011). Thus, it will be important to study changes in habitat quality and habitat use by saproxylic organisms under different management scenarios. The concept of using deadwood habitats as biodiversity surrogates in managed stands needs to be tested, as important habitat qualities of retained deadwood may be altered by the conditions of harvested forests, thus impacting its utility for biodiversity conservation.

5.4.2. Additional Habitats, Host Species, and Forest Ecosystems

This study is far from an exhaustive treatment of habitats used by saproxylic beetles in aspen. Certainly, many more species and distinct assemblages likely reside within twigs and small branches, roots, cavities, or canopy portions of the trunk. These would be valuable habitats to target in future studies. Furthermore, effects of host species need more attention. Although few saproxylic species are truly host-tree-specific (Stokland et al. 2012), many strongly discriminate between coniferous and deciduous tree species. Saproxylic beetles have been studied in snags of white spruce (Jacobs et al. 2007a, b) and trembling aspen (Hammond et

al. 2004), as well as black spruce (*Picea mariana* [Miller] Sterns & Poggenburg) and balsam fir (*Abies balsamea* [Linné] Miller) (Janssen et al. 2011). It could be valuable to study saproxylic communities associated with logs of black spruce and balsam fir. Also, balsam poplar (*Populus balsamifera* Linné) snags are quite dominant in boreal stands (Lee 1998) and deserve study. Large diameter balsam poplar snags and logs have much thicker and harder bark than trembling aspen (C. Wood, pers. obs.) and thus the subcortical insects inhabiting these substrates could differ from that of aspen. It is possible that deadwood of balsam poplar would have more stable microclimate due to the greater persistence of this thick bark layer, and thus these substrates may support more sensitive species. Additionally, there are many forest ecosystems across North America in which the saproxylic fauna has not been examined. Research should be prioritized in rare or threatened ecosystems (e.g., Garry oak woodlands, red pine forests, and coastal temperate rainforests) in order to document the baseline biodiversity associated with these forest types.

5.4.3. Deadwood Dynamics and Succession

Understanding the natural dynamics and succession of deadwood habitats should be useful for developing forest management protocols. Deadwood recruitment and transition probabilities for various sizes and decay classes of aspen substrates might be helpful in long-term planning

to ensure adequate habitat provision in harvested areas. The transition rate of aspen trees into snags generally decreases with snag diameter in mature and old growth stands, such that small diameter (10 to 19 cm DBH) trees transition much more frequently (~5-8% per year) into snags than larger diameter (>20 cm DBH) trees (1-3% per year; Lee 1998). Some live trees also break, fall, and transition directly into logs, for which the estimated rate of transition is quite low. The transition of snags to logs appears similar between diameter classes (Lee 1998), with 10-20% of snags transitioning to logs per year in stands >80 years old (Figure 5.2). Overall, recruitment rates are much greater for small diameter substrates than large diameter deadwood, an observation about underlying process which corresponds to the observed low frequency of large diameter logs found during my study (Chapter 3).

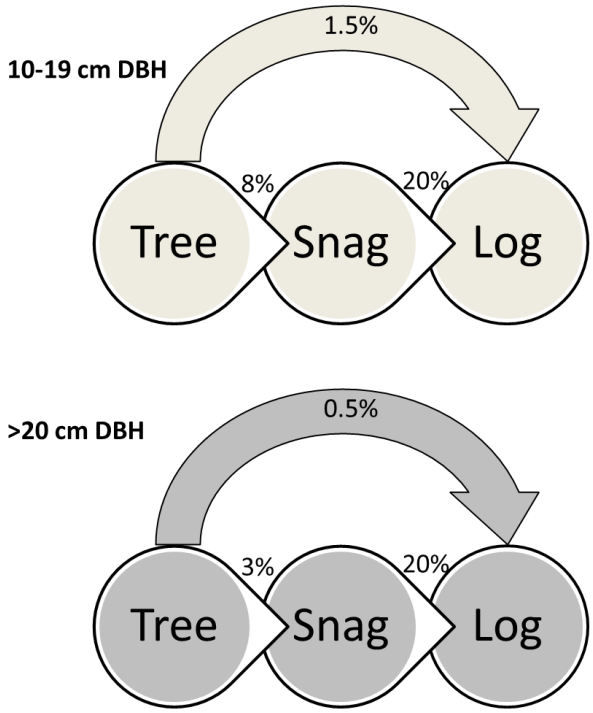

Figure 5.2 Transition probabilities for each substrate type in percent of stems per year (derived from Lee 1998), showing differential recruitment of small diameter deadwood than larger (>20 cm) diameter deadwood for old growth (100+ year old) aspen dominated stands of the boreal mixedwood forest of Alberta.

Unfortunately transition probabilities are not currently available for aspen deadwood decay classes. Knowledge of deadwood abundance and composition used in conjunction with decay succession rates would provide answers on how much (and what types) of deadwood are generated in natural and managed forests. It would be very interesting to observe transition rates between substrate types and decay classes of aspen, as log decay classes can arise from both live trees and snags at any point in decay succession (concept illustrated in Figure 5.3). Knowledge of such natural dynamic processes may be important for

developing management practices that effective provide a range of decay classes throughout time after harvest. From the transition probabilities summarized in Figure 5.2, we can see that 0.5-1.5% of live trees form fresh logs (decay class 1), which would then decay on the ground through the decomposition cycle. It is likely that most decay class 1 (DC1) logs might originate from trees (rather than DC1 snags). Interestingly, the results of Chapter 4 suggest that, indeed, saproxylic beetle assemblages are quite similar between DC1 snags and logs, suggesting that both transition from live trees. However, after DC1, assemblages within each substrate type diverged, suggesting quite separate decay trajectories. Perhaps assemblages of logs exhibited higher within group variability (Chapter 4, Figure 4.2), due to variable recruitment of later decay class logs from the succession of both snags and logs. Thus, questions remain about the influence of deadwood origin and previous decay history on resulting saproxylic beetle assemblages? Also, it would be useful to know the average transition rates between decay classes of snags and logs (i.e., how many DC3 logs arise from DC2 snags or DC2 logs)? These relationships could inform management strategies, allowing for more precise provisioning of required saproxylic beetle habitats through time.

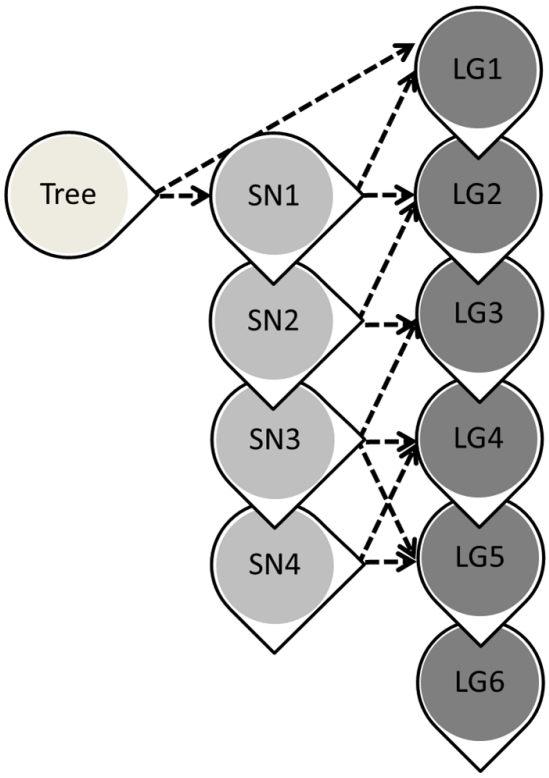

Figure 5.3 Theoretical transition dynamics for aspen substrate types and decay classes; direct transitions within substrate types are given by white arrows, while transitions between substrate types are given by black dashed arrows. The rate of succession between deadwood decay states has yet to be quantified.

5.4.4. The Influence of Stand Age

Limits to stand age and stand age distributions caused by truncation of replacement times that is inherent in bringing merchantable stands into harvest rotations could have large consequences on availability of the deadwood habitats discussed in this thesis. Deadwood size and decay class distributions are influenced by stand age, with more even distributions of size and decay classes in old stands than mature or young stands (Lee et al. 1997). Old growth deciduous stands have greater

volumes of large diameter (≥11 cm) logs than either young or mature stands, and less fine woody debris (Lee et al. 1997). Additionally, young stands have much higher densities of moderately decayed logs (decay class 3 and 4) and very low densities of early decay classes (Lee et al. 1997). Given that many saproxylic beetle species are associated with large diameter logs (Chapter 3) and that each decay class supports distinctive assemblages (Chapter 4), changes in the availability of deadwood habitats across the landscape could have serious repercussions for biodiversity.

Old stands are important for biodiversity. Hammond et al. (2004) showed that many saproxylic beetle species were exclusively found in old rather than mature aspen stands. Crites and Dale (1998) also found that the species richness of bryophytes and lichens was higher in old growth forests, and that stand age was important for determining species distributions in various decay classes of aspen logs. Clearly, habitat attributes such as decay class and position cannot be managed without consideration of the landscape context in which these habitats exist. Further research is needed to determine how forestry context influences habitat quality and to optimize deadwood habitat retention programs under different management scenarios.

5.4.5. Linking Ecological Processes to Community Patterns

Although saproxylic beetle assemblages of trembling aspen were described here, the ecological processes determining and including these organisms were not discussed in detail. Velland (2010) proposed that four key processes drive community dynamics: dispersal, drift, speciation, and selection. Species composition of assemblages may be thought of as arising from speciation and dispersal processes, with the relative abundances of these species being shaped by selection (fitness differences among species), drift (stochastic changes in species abundance), and ongoing dispersal (Velland 2010). When selection occurs under density-dependence individual fitness for a given species depends on the density of that species and other species playing similar roles in the community or connected through the trophic web. With knowledge of this, I believe it was important to consider the influence of predator and competitor density in examining size-class associations (Chapter 3), especially since beetle density did vary greatly among log size classes. Greater levels of within-substrate microhabitat heterogeneity in particular deadwood habitats (large diameter wood, heart-rotted wood) may also contribute to speciation processes, producing an increased opportunity for species to arise in heterogeneous substrates. For example, Speight (1989) documented the habitats of two click-beetle larvae within a large trunk cavity. *Ampedus cardinalis* (Schiödte) and *A. megerlei*

(Lacordaire) occupy different niches within the same cavity, with larvae inhabiting dry wood dust and wet, brown-rotted wood, respectively.

Differences in species dispersal ability and dynamics of source populations, will also contribute to the species diversity in habitats. For recently created deadwood habitat, dispersal is required to establish saproxylic assemblages; thus, habitat connectivity and proximity to source populations is important for primary deadwood colonizers. The stochastic effects of drift may be increasingly important in small communities (Velland 2010), and should then be considered for predicting species and community responses post-disturbance. Because neutral processes may dominate in small communities, such as those establishing habitats after a disturbance, extinction debts may be exacerbated (Orrock and Watling 2010). Although the details of these interactions is beyond the scope of this thesis, it is important to consider that any conditions (abiotic factors, species densities, biogeography) which affects the ecological processes underlying the patterns found here, will invariably result in different saproxylic communities.

However, it is fair to ask: when does it matter? Thus, futher attention should be given to link process to pattern in the study of saproxylic community ecology. This would, no doubt, require carefully preplanned experiments and ecological modelling, but such efforts will be

rewarded with a much greater depth of understanding for this subject than is currently available. Related questions include: how does species dispersal relate to habitat associations? How does the spatial distribution of deadwood (and particular habitat types) influence the inhabiting communities? How does community size and composition of retained deadwood habitats within harvest blocks compare to that of mature forests? From such additional studies we might be able to determine which species are most vulnerable to extinction and the conditions which perturb natural community dynamics beyond the acceptable range.

5.5. Conclusions

In addition to maintaining critical deadwood habitats, forest management practices would ideally aim to maintain the processes that create the natural range of deadwood habitat variability across the landscape. Under the concept of emulating natural disturbance, this is thought to mediate the negative effects of habitat alteration throughout time. Saproxylic species inhabiting rare deadwood habitats (e.g., large diameter and well-decayed logs and snags) are among those most likely to be negatively affected by boreal forest management (Siitonen 2001; Stenbacka 2009), and thus these habitats should be maintained as a starting point. In this thesis, the key deadwood qualities associated with saproxylic beetles in natural, mature aspen forests were: substrate type,

decay class, and diameter class. In addition, many species were associated with wood-decay fungi, bark cover, moss cover, and wood texture (Chapter 4), suggesting that these habitat features are also important to saproxylic biodiversity in aspen deadwood habitats.

Currently deadwood management in Alberta does not recognize the need for retaining particular deadwood characteristics for biodiversity conservation. Instead, the focus is on quantity of deadwood. Alberta's forest management protocols designate the amount of retained standing and downed deadwood as indicators of local/stand-scale biodiversity, however, this value is achieved by meeting the target of: "X% of harvest areas having downed woody debris (>1 cm diameter) retained on site", where X is variable and is determined during development of the Forest Management Plan (Alberta Sustainable Resource Development 2006). Thus, particular decay states, diameters, and qualities of deadwood are not ensured after harvest. It is clear that saproxylic beetles in these forest ecosystems need a range of deadwood diameters and decay classes to fulfill their habitat requirements; thus these critical habitats should retained for meeting conservation goals.

Given that ≥25 cm diameter logs were disproportionately important habitats to saproxylic beetles in my study (Chapter 3), retention of large diameter logs such as these will likely contribute to effective biodiversity

conservation. Large diameter substrates will not only support the many species associated with this size class, but will also persist for longer periods as habitat. Increased substrate persistence will no doubt better accommodate species with long developmental times, poor dispersal abilities, or those particularly sensitive to changes in the surrounding forest landscape. Additionally, as large diameter deadwood is more stable microclimatically (Boddy 1983), retaining these habitats may be even more valuable in harvested stands, to temper the impacts of altered stand microclimate.

The key to long-term conservation of biodiversity for saproxylic organisms will be in creating management scenarios that ensure steady recruitment of a range of deadwood habitats over time. Thus, the recruitment and decay rates of deadwood under various harvesting schemes should be measured and considered in planning. Low retention density (10% and 20% retention of live stems) contributes to a much greater mortality rate (28%) of aspen (Solarik 2010), than the natural rate (3.5-9.5%) in old growth stands (Lee 1998). Retention at the 50% and 75% level appears to maintain more natural deadwood recruitment rates (Solarik 2010), yet it may not be economically practical to employ such high retention levels in managed forests.

Overall, my work suggests that all size classes of logs supported particular species of saproxylic beetles and thus the range of sizes may be important habitats for the saproxylic community. Furthermore, a large variety of deadwood habitats seems to be required to accommodate the entire saproxylic fauna associated with trembling aspen. In conclusion, deadwood *quality* in addition to deadwood *quantity* must be taken into account in developing improved conservation measures for sustaining saproxylic biodiversity.

5.6. Literature Cited

Aitken, K.E.H. and K. Martin 2004. Nest cavity availability and selection in aspen–conifer groves in a grassland landscape. Canadian Journal of Forest Research 34: 2099-2109.

Alberta Forest Management Planning Standard, Alberta Sustainable Resource Development, Public Lands and Forests Division, Forest Management Branch v. 4.1, April 2006, 112 pp.

Boddy, L. 1983. The effect of temperature and water potential on the growth rate of wood-rotting basidiomycetes. Transactions of the British Mycological Society 80: 141-149.

Bourassa, S. and C.M. Wood. 2011. First record of *Diacheila arctica amoena* (Faldermann) (Coleoptera: Carabidae) in Alberta, Canada. The Coleopterists Bulletin 65(2): 144-145.

Cobb T.P., J.L. Morissette, J.M. Jacobs, M.J. Koivula, J.R. Spence, and D.W. Langor. 2011. Effects of Postfire Salvage Logging on Deadwood-Associated Beetles. Conservation Biology 25(1): 94-104.

Crites, S. and M.R.T. Dale. 1998. Diversity and abundance of bryophytes, lichens, and fungi in relation to woody substrate and successional stage in aspen mixedwood boreal forests. Canadian Journal of Botany 76: 641-651.

Fall, H.C. 1899. Revision of the Lathridiidae of Boreal America. Transactions American Entomological Society 26: 101-190, plates III-IV.

Hammond, H. E. J., D. W. Langor, and J. R. Spence. 2004. Saproxylic beetles (Coleoptera) using *Populus* in boreal aspen stands of western Canada: spatiotemporal variation and conservation of assemblages. Canadian Journal of Forest Research 34:1-19.

Hesselink, T.P. 2010. Increasing pressures to use forest biomass: A conservation viewpoint. The Forestry Chronicle 86(1): 28-35.

Hiratsuka Y, Stokes T, Chakravarty P, Morgan D. 1995. A field guide to classify and measure aspen decay and stain. Canadian Forest Service, Northwest Region, Northern Forestry Centre, Special Report 4.

Horák, J., A.A. Zaitsev and E. Vávrová. 2011. Ecological requirements of a rare saproxylic beetle *Cucujus haematodes* – the beetles' stronghold on the edge of its distribution area. Insect Conservation and Diversity 4: 81–88.

Hutchison, L.J. 1999. Wood-inhabiting microfungi isolated from *Populus tremuloides* from Alberta and northeastern British Columbia. Canadian Journal of Botany 77: 898-905.

Jacobs, J.M., J.R. Spence, and D.W. Langor. 2007a. Influence of boreal forest succession and dead wood qualities on saproxylic beetles. Agricultural and Forest Entomology 9(1):3-16.

Jacobs, J.M., J.R. Spence, and D.W. Langor. 2007b. Variable retention harvest of white spruce stands and saproxylic beetle assemblages. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 37(9):1631-1642.

Janssen, P., C. Hébert, and D. Fortin. 2011. Biodiversity conservation in old-growth boreal forest: black spruce and balsam fir snags harbour distinct assemblages of saproxylic beetles. Biodiversity Conservation 20: 2917-2932.

Lee, P.C., S. Crites, M. Nietfeld, H.V. Nguyen, and J.B. Stelfox. 1997. Characteristics and origins of deadwood material in aspen dominated boreal forests. Ecological Applications 7: 691-701.

Lee, P. 1998. Dynamics of snags in aspen-dominated midboreal forests. Forest Ecology and Management 105: 263–272.

Légaré, J.-P., C. Hébert and J.-C. Ruel. 2011. Alternative Silvicultural Practices in Irregular Boreal Forests: Response of Beetle Assemblages. Silva Fennica 45(5): 937-956.

Lindhe, A., A. Lindelow, and N. Asenblad. 2005. Saproxylic beetles in standing dead wood density in relation to substrate sun-exposure and diameter. Biodiversity and Conservation 14(12): 3033-3053.

Majka, C.G., D.W. Langor and W.H. Rücker. 2009. Latridiidae (Coleoptera) of Atlantic Canada: new records, keys to identification, new synonyms, distribution, and zoogeography. The Canadian Entomologist 141: 317-370.

Martikainen P., J. Siitonen, P. Punttila, L. Kaila and J. Rauh. 2000. Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biological Conservation 94: 199–209.

Nieto, A. and K.N.A. Alexander. 2010. European Red List of Saproxylic Beetles. Luxembourg: Publications Office of the European Union.

Orrock, J.L. and J.I. Watling. 2010. Local community size mediates ecological drift and competition in metacommunities. Proceedings of the Royal Society B 277: 2185-2191.

Pinzon, J.H. 2011. Composition and structure of spider assemblages in layers of the mixedwood boreal forest after variable retention harvest. Ph.D. Thesis. University of Alberta, Canada.

Pyper, M.P. 2009. Retention Patch Characteristics and Ground Dwelling Beetle Diversity: Implications for Natural Disturbance-Based Management. M.Sc. Thesis. University of Alberta, Canada.

Ranius, T. 2002. Influence of stand size and quality of tree hollows on saproxylic beetles in Sweden. Biological Conservation 103: 85–91.

Ranius, T., Martikainen, P., and J. Kouki. 2011. Colonisation of ephemeral forest habitats by specialised species: beetles and bugs associated with recently dead aspen wood. Biodiversity Conservation 20: 2903–2915.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecological Bulletins 49: 11–41.

Simila, M., J. Kouki, P. Martikainen, and A. Uotila. 2002. Conservation of beetles in boreal pine forests: the effects of forest age and naturalness on species assemblages. Biological Conservation 106(1): 19-27.

Solarik, K.A. 2010. Variable Retention Harvesting: Mortality of Residual Trees and Natural Regeneration of White Spruce. M.Sc. Thesis. University of Alberta, Canada.

Speight, M.C.D. 1989. Saproxylic invertebrates and their conservation. Nature and Environment Series 42 Council of Europe. Strasbourg, France.

Stenbacka, F. 2009. Response of saproxylic insect communities to forestry: Implications for Conservation. Ph.D. Thesis. Swedish University of Agricultural Sciences, Sweden

Stokland, J.N., J. Siitonen and B.G. Jonsson. 2012. Biodiversity in Dead Wood. Cambridge University Press, Cambridge, New York, xiv, 509pp.

Sullivan, T.P. and D.S. Sullivan. 2012. Woody debris, voles, and trees: Influence of habitat structures (piles and windrows) on long-tailed vole populations and feeding damage. Forest Ecology and Management 263: 189–198.

Velland, M. 2010. Conceptual synthesis in community ecology. The Quarterly Review of Biology 85(2): 183-206.

APPENDICES

Appendix 4-A

Distribution of saproxylic beetle species abundance in the main aspen substrate types sampled.

Family	Species		Sx	FG	Tr	Sn	Lg	∑
Anobiidae	*Caenocara scymnoides*	*	+	MYC	1	0	0	1
Anobiidae	*Dorcatoma pallicornis*	*	++	MYC	15	0	0	15
Anobiidae	*Hemicoelus carinatus*		++	XYL	40	0	2	42
Anobiidae	*Ptilinus lobatus*		++	XYL	47	0	5	52
Anthicidae	*Omonadus floralis*		+	OMN	0	0	1	1
Anthribidae	*Trigonorhinus limbatus*		+	MYC	0	0	1	1
Buprestidae	*Agrilus liragus*		++	XYL	1	0	6	7
Cantharidae	*Podabrus* sp. 1		+	ZOO	6	0	2	8
Cantharidae	*Podabrus* sp. 2		+	ZOO	22	0	21	43
Carabidae	*Agonum retractum*		+	ZOO	2	0	19	21
Carabidae	*Agonum sordens*	*	+	ZOO	1	0	0	1
Carabidae	*Bembidion fortestriatum*		+	ZOO	0	0	1	1
Carabidae	*Bembidion nigripes*		+	ZOO	1	0	1	2
Carabidae	*Bembidion timidum*		+	ZOO	0	0	1	1
Carabidae	*Perigona nigriceps*		+	ZOO	0	0	4	4
Carabidae	*Platynus decentis*		+	ZOO	97	0	25	122
Carabidae	*Platynus mannerheimi*	*	+	ZOO	4	0	0	4
Carabidae	*Pterostichus adstrictus*		+	ZOO	1	0	7	8
Carabidae	*Pterostichus pensylvanicus*		+	ZOO	0	0	4	4
Carabidae	*Trechus apicalis*		+	ZOO	0	0	1	1
Carabidae	*Trechus chalybeus*		+	ZOO	1	0	1	2
Cerambycidae	*Grammoptera subargentata*		++	XYL	26	0	1	27
Cerambycidae	*Neospondylis upiformis*	*	++	XYL	1	0	0	1
Cerambycidae	*Pogonocherus parvulus*	*	++	XYL	1	0	0	1
Cerambycidae	*Trachysida aspera aspera*	*	++	XYL	8	0	0	8
Cerambycidae	*Xylotrechus annosus annosus*		++	XYL	1	0	0	1
Cerylonidae	*Cerylon castaneum*		++	MYC	20	0	4	24
Ciidae	*Cis americanus*		++	MYC	3	0	16	19
Ciidae	*Cis fuscipes*	*	++	MYC	6	0	0	6
Ciidae	*Cis levettei*		++	MYC	1	0	1	2
Ciidae	*Cis maritimus*		++	MYC	0	0	1	1
Ciidae	*Dolichocis manitoba*		++	MYC	17	0	2	19

Family	Species		Sx	FG	Tr	Sn	Lg	∑
Ciidae	*Octotemnus laevis*	*	++	MYC	1	0	0	1
Ciidae	*Orthocis punctatus*	*	++	MYC	3	0	0	3
Ciidae	*Sulcacis curtulus*		++	MYC	7	0	2	9
Clambidae	*Clambus pubescens*	*	+	MYC	4	0	0	4
Cleridae	*Thanasimus undatulus*	*	++	ZOO	1	0	0	1
Coccinellidae	*Didion longulum*		+	ZOO	6	0	0	6
Corylophidae	*Clypastraea lugubris*		++	MYC	68	0	1	69
Corylophidae	*Orthoperus scutellaris*		++	MYC	7	0	4	11
Cryptophagidae	*Atomaria apicalis*		+	MYC	0	0	1	1
Cryptophagidae	*Atomaria diluta?*		++	MYC	0	0	2	2
Cryptophagidae	*Atomaria ephippiata*		+	MYC	0	0	2	2
Cryptophagidae	*Atomaria fuscata*		+	MYC	0	0	1	1
Cryptophagidae	*Atomaria lewisii*		+	MYC	0	0	8	8
Cryptophagidae	*Atomaria linearis*	*	+	MYC	1	0	0	1
Cryptophagidae	*Atomaria ochracea*		+	MYC	1	0	1	2
Cryptophagidae	*Atomaria* sp. 1		+	MYC	0	0	3	3
Cryptophagidae	*Atomaria* sp. 2		+	MYC	0	0	2	2
Cryptophagidae	*Atomaria* sp. 3	*	+	MYC	2	0	0	2
Cryptophagidae	*Atomaria* sp. 4	*	+	MYC	8	0	0	8
Cryptophagidae	*Atomaria stricticollis*	*	+	MYC	4	0	0	4
Cryptophagidae	*Atomaria subangulata*		+	MYC	1	0	62	63
Cryptophagidae	*Caenoscelis antennalis*		+	MYC	4	0	2	6
Cryptophagidae	*Caenoscelis ferruginea*		+	MYC	8	0	0	8
Cryptophagidae	*Cryptophagus actangulus*		+	MYC	1	0	9	10
Cryptophagidae	*Cryptophagus* sp. 1	*	+	MYC	1	0	0	1
Cryptophagidae	*Cryptophagus* sp. 2		+	MYC	20	0	4	24
Cryptophagidae	*Myrmedophila americana*		++	MYC	14	0	0	14
Cryptophagidae	*Pteryngium crenatum*	*	++	MYC	6	0	0	6
Cucujidae	*Cucujus clavipes*		++	ZOO	20	1	57	78
Cucujidae	*Pediacus fuscus*		++	OMN	1	0	5	6
Curculionidae	*Carphoborus carri*		++	PHL	0	0	1	1
Curculionidae	*Cossonus pacificus*		++	XYL	25	0	0	25
Curculionidae	*Magdalis* sp. 1		++	XYL	1	0	0	1
Curculionidae	*Phloeophagus canadensis*		++	XYL	0	0	1	1
Curculionidae	*Phloeotribus* sp. 1	*	++	PHL	1	0	0	1
Curculionidae	*Procyphalus mucronatus*	*	++	PHL	2	0	0	2
Curculionidae	*Rhyncolus brunneus*	*	++	XYL	1	0	0	1
Curculionidae	*Trypodendron lineatum*	*	++	AMB	3	0	0	3

Family	Species			Sx	FG	Tr	Sn	Lg	∑
Curculionidae	*Trypodendron retusum*			++	AMB	163	0	58	221
Dermestidae	*Dermestes lardarius*	*		+	DET	2	0	0	2
Dermestidae	*Megatoma cylindrica*			+	DET	4	0	0	4
Dermestidae	*Megatoma perversa*			+	DET	77	0	0	77
Elateridae	*Aeolus mellilus comis*			+	ZOO	1	0	1	2
Elateridae	*Ampedus apicatus*			++	OMN	1	0	1	2
Elateridae	*Ampedus deletus*			++	OMN	0	0	9	9
Elateridae	*Ampedus luctuosus*			++	OMN	0	0	2	2
Elateridae	*Ampedus nigricans*			++	OMN	21	0	0	21
Elateridae	*Ampedus* sp. 1			++	OMN	0	0	1	1
Elateridae	*Ampedus* sp. 2			++	OMN	0	0	1	1
Elateridae	*Ampedus* sp. 3			++	OMN	0	0	1	1
Elateridae	*Ampedus subtilis*			++	OMN	1	0	5	6
Elateridae	*"Ctenicera" nitidula*			+	OMN	7	0	1	8
Elateridae	*"Ctenicera" stricklandi*			+	OMN	8	0	1	9
Elateridae	*Denticollis denticornis*			+	ZOO	4	0	1	5
Elateridae	*Eanus decoratus*			+	ZOO	0	0	1	1
Elateridae	*Nitidolimonius resplendens*	*		+	ZOO	4	0	0	4
Elateridae	*Pseudanostirus propolus*			+	OMN	13	0	4	17
Erotylidae	*Triplax antica*	*		++	MYC	2	0	0	2
Erotylidae	*Triplax californica*			++	MYC	1	0	0	1
Erotylidae	*Triplax dissimilator*			++	MYC	29	0	0	29
Erotylidae	*Triplax thoracica*			++	MYC	16	0	0	16
Eucinetidae	*Eucinetus terminalis*	*		+	MYC	1	0	0	1
Eucnemidae	*Epiphanis cornutus*	*		++	MYC	5	0	0	5
Eucnemidae	*Isorhipis obliqua*			++	MYC	0	0	1	1
Eucnemidae	*Microrhagus pectinatus*	*		++	MYC	1	0	0	1
Histeridae	*Teretrius montanus*			++	ZOO	4	0	0	4
Hydrophilidae	*Cercyon herceus frigidus*			+	ZOO	0	0	1	1
Laemophloeidae	*Cryptolestes ferrugineus*			+	DET	0	0	1	1
Latridiidae	*Cartodere constricta*			+	MYC	0	0	178	178
Latridiidae	*Corticaria arctophila*	*		+	MYC	1	0	0	1
Latridiidae	*Corticaria elongata*			+	MYC	2	0	225	227
Latridiidae	*Corticaria ferruginea*			+	MYC	2	1	8	11
Latridiidae	*Corticaria* n. sp. 1 (WR)		†	+	MYC	82	0	0	82
Latridiidae	*Corticaria* n. sp. 2 (WR)		†	+	MYC	6	0	0	6
Latridiidae	*Corticaria* n. sp. 3		†	+	MYC	26	0	0	26

Family	Species			Sx	FG	Tr	Sn	Lg	∑
	(WR)								
Latridiidae	*Corticaria* n. sp. 4 (WR)		†	+	MYC	0	0	4	4
Latridiidae	*Corticaria* n. sp. 5 (WR)	*	†	+	MYC	1	0	0	1
Latridiidae	*Corticaria* n. sp. 6 (WR)		†	+	MYC	2	0	0	2
Latridiidae	*Corticaria orbicollis*			+	MYC	5	0	0	5
Latridiidae	*Corticaria rubripes*			+	MYC	25	0	12	37
Latridiidae	*Corticaria serrata*			+	MYC	0	0	2	2
Latridiidae	*Corticarina cavicollis*			+	MYC	0	0	2	2
Latridiidae	*Cortinicara gibbosa*			+	MYC	201	0	4	205
Latridiidae	*Dienerella filum*	*		+	MYC	1	0	0	1
Latridiidae	*Enicmus fictus*			+	MYC	1	0	1	2
Latridiidae	*Enicmus mimus*	*		+	MYC	1	0	0	1
Latridiidae	*Enicmus tenuicornis*			+	MYC	13	0	0	13
Latridiidae	*Latridius hirtus*			++	MYC	36	0	0	36
Latridiidae	*Latridius minutus*			+	MYC	8	0	23	31
Latridiidae	*Melanophthalma americana*			+	MYC	11	0	0	11
Latridiidae	*Melanophthalma helvola*	*		+	MYC	10	0	0	10
Latridiidae	*Melanophthalma inermis*			+	MYC	0	0	2	2
Latridiidae	*Melanophthalma pumila*			+	MYC	115	0	7	122
Latridiidae	*Stephostethus liratus*			+	MYC	13	0	2	15
Leiodidae	*Agathidium angulare*			+	MYX	1	0	1	2
Leiodidae	*Agathidium athabascanum*			+	MYC	0	0	1	1
Leiodidae	*Agathidium cavisternum*			+	MYX	4	0	2	6
Leiodidae	*Agathidium depressum*			+	MYC	4	0	3	7
Leiodidae	*Agathidium dubitans*			+	MYC	0	0	1	1
Leiodidae	*Agathidium maculosum*			+	MYX	0	0	1	1
Leiodidae	*Agathidium* n. sp. (?)1	*		+	MYC	2	0	0	2
Leiodidae	*Agathidium pulchrum*			+	MYC	0	0	6	6
Leiodidae	*Agathidium rotundulum*	*		+	MYC	1	0	0	1
Leiodidae	*Agathidium* sp. 1			+	MYC	4	0	0	4
Leiodidae	*Agathidium* sp. 2	*		+	MYC	1	0	0	1
Leiodidae	*Agathidium* sp. 3			+	MYC	0	0	1	1
Leiodidae	*Agathidium* sp. 4	*		+	MYC	1	0	0	1
Leiodidae	*Agathidium* sp. 5	*		+	MYC	2	0	0	2
Leiodidae	*Anisotoma amica*	*		++	MYX	2	0	0	2
Leiodidae	*Anisotoma globososa*	*		++	MYX	4	0	0	4

Family	Species			Sx	FG	Tr	Sn	Lg	∑
Leiodidae	*Catops basilaris*			+	MYC	0	0	1	1
Leiodidae	*Colon elongatum*			+	MYC	1	0	1	2
Leiodidae	*Platyhydnobius arizonensis*	*		+	MYC	1	0	0	1
Lucanidae	*Platycerus depressus*	*		++	XYL	1	0	0	1
Lyctidae	*Dictyoperus aurora*	*		++	XYL	1	0	0	1
Melandryidae	*Melandrya striata*			++	XYL	19	0	1	20
Melandryidae	*Orchesia castanea*			++	MYC	2	0	4	6
Melandryidae	*Orchesia* sp. 1			++	MYC	0	0	1	1
Monotomidae	*Monotoma longicollis*			++	MYC	0	0	1	1
Monotomidae	*Monotoma picipes*			++	MYC	0	0	1	1
Monotomidae	*Rhizophagus dimidiatus*			++	ZOO	2	0	0	2
Monotomidae	*Rhizophagus* n. sp. 1 (near pseudobrunneus-YB)		†	++	ZOO	337	0	1	338
Monotomidae	*Rhizophagus remotus*			++	ZOO	96	0	13	109
Mordellidae	*Mordellochroa scapularis*	*		++	MYC	2	0	0	2
Mycetophagidae	*Mycetophagus distinctus*			++	MYC	0	0	1	1
Mycetophagidae	*Mycetophagus serrulatus*	*		++	MYC	1	0	0	1
Mycetophagidae	*Typhaea stercorea*			+	MYC	0	0	9	9
Nitidulidae	*Colopterus truncatus*	*		++	MYC/SAP	23	0	0	23
Nitidulidae	*Epuraea avara*	*		+	MYC/SAP	1	0	0	1
Nitidulidae	*Epuraea flavomaculata*			+	MYC/SAP	210	8	12	230
Nitidulidae	*Epuraea linearis*			+	MYC/SAP	4	0	0	4
Nitidulidae	*Epuraea planulata*			+	MYC/SAP	22	0	2	24
Nitidulidae	*Epuraea populi*	*		+	MYC/SAP	4	0	0	4
Nitidulidae	*Epuraea rufa*	*		+	MYC/SAP	1	0	0	1
Nitidulidae	*Epuraea* sp. 1			+	MYC/SAP	0	3	2	5
Nitidulidae	*Epuraea* sp. 2	*		+	MYC/SAP	1	0	0	1
Nitidulidae	*Epuraea terminalis*			+	MYC/SAP	4	9	4	17
Nitidulidae	*Epuraea truncatella*			+	MYC/SAP	0	3	1	4
Nitidulidae	*Glischrochilus moratus*			+	MYC/SAP	3	0	0	3
Nitidulidae	*Glischrochilus sanguinolentus*			+	MYC/SAP	30	0	0	30
Nitidulidae	*Glischrochilus siepmanni*			+	MYC/SAP	11	0	0	11
Nitidulidae	*Glischrochilus vittatus*			+	MYC/SAP	22	1	0	23
Ptiliidae	*Acrotrichis* sp. 1			+	MYC	19	0	27	46
Ptiliidae	*Pteryx* sp. 1			+	MYC	2	1	55	58
Pyrochroidae	*Dendroides canadensis*	*		++	MYC	1	0	0	1
Pyrochroidae	*Dendroides testacea*	*		++	MYC	5	0	0	5
Pyrochroidae	*Schizotus*			++	MYC	4	0	26	30

Family	Species		Sx	FG	Tr	Sn	Lg	∑
	cervicalis							
Salpingidae	*Rhinosimus viridiaeneus*		++	MYC	2	0	0	2
Scirtidae	*Cyphon confusus*	*	+	OMN	1	0	0	1
Scirtidae	*Cyphon variabilis*		+	OMN	44	0	8	52
Scraptiidae	*Anaspis rufa*		++	OMN	0	0	1	1
Scraptiidae	*Canifa pallipes*		++	OMN	58	0	0	58
Silvanidae	*Ahasverus advena*		+	MYC	0	0	2	2
Silvanidae	*Dendrophagus cygnaei*		++	MYC	1	0	3	4
Sphindidae	*Odontosphindus clavicornis*	*	++	MYX	13	0	0	13
Staphylinidae	*Anotylus sobrinus*		+	ZOO	2	0	1	3
Staphylinidae	*Atrecus macrocephalus*		++	ZOO	1	0	39	40
Staphylinidae	*Baeocera humeralis*		++	MYC	0	0	12	12
Staphylinidae	*Baeocera* sp. 1		++	MYC	1	0	0	1
Staphylinidae	*Bolitobius horni*		+	ZOO	1	0	2	3
Staphylinidae	*Carphacis nepigonensis*		+	ZOO	102	0	0	102
Staphylinidae	*Coproporus ventriculus*		++	MYC	0	0	1	1
Staphylinidae	*Dinothenarus pleuralis*		+	ZOO	0	0	1	1
Staphylinidae	*Euplectus duryi*		+	ZOO	12	0	0	12
Staphylinidae	*Gabrius brevipennis*		+	ZOO	0	0	7	7
Staphylinidae	*Hapalaraea hamata*	*	+	ZOO	9	0	0	9
Staphylinidae	*Ischnosoma splendidum*		+	ZOO	2	0	5	7
Staphylinidae	*Lathrobium fauveli*		+	ZOO	0	0	11	11
Staphylinidae	*Lathrobium washingtoni*		+	ZOO	1	0	14	15
Staphylinidae	*Leptacinus intermedius*		+	ZOO	0	0	1	1
Staphylinidae	*Lordithon bimaculata*		+	ZOO	27	0	0	27
Staphylinidae	*Lordithon fungicola*		+	ZOO	21	0	0	21
Staphylinidae	*Lordithon longiceps*	*	+	ZOO	5	0	0	5
Staphylinidae	*Megarthrus angulicollis*		+	MYX	0	0	1	1
Staphylinidae	*Mycetoporus americanus*		+	MYC	3	0	1	4
Staphylinidae	*Neohypnus hamatus*	*	+	ZOO	1	0	0	1
Staphylinidae	*Nudobius cephalus*		++	ZOO	1	0	2	3
Staphylinidae	*Olisthaerus megacephalus*	*	++	ZOO	2	0	0	2
Staphylinidae	*Orobanus* sp. 1		+	ZOO	0	0	1	1
Staphylinidae	*Oropus* sp. 1		+	ZOO	1	0	0	1
Staphylinidae	*Philonthus lindrothi*		+	ZOO	0	0	1	1
Staphylinidae	*Phloeostiba lapponica*		++	ZOO/SAP/OMN	39	4	7	50
Staphylinidae	*Phyllodrepa* sp. 1		+	ZOO	1	0	16	17

Family	Species			Sx	FG	Tr	Sn	Lg	∑
Staphylinidae	*Proteinus atomarius*			+	MYC	0	0	1	1
Staphylinidae	*Proteinus limbatus*			+	MYC	0	0	2	2
Staphylinidae	*Pseudopsis sagitta*			+	ZOO	0	0	6	6
Staphylinidae	*Quedius criddlei*	*		+	ZOO	7	0	0	7
Staphylinidae	*Quedius frigidus*			+	ZOO	0	0	3	3
Staphylinidae	*Quedius fulvicollis*			+	ZOO	0	0	2	2
Staphylinidae	*Quedius plagiatus*			++	ZOO	21	0	5	26
Staphylinidae	*Quedius rusticus*			+	ZOO	0	0	1	1
Staphylinidae	*Quedius velox*			+	ZOO	48	0	1	49
Staphylinidae	*Scaphium castanipes*			+	MYC	0	0	2	2
Staphylinidae	*Sepedophilus testaceaus*			+	MYC	0	0	1	1
Staphylinidae	*Siagonium punctatum*	*		++	OMN	10	0	0	10
Staphylinidae	*Stenichnus ovipennis*			++	ZOO	32	0	1	33
Staphylinidae	*Stenus austini*			+	ZOO	0	0	3	3
Staphylinidae	*Stenus maritimus*			+	ZOO	1	0	1	2
Staphylinidae	*Syntomium confragosum*			+	OMN	2	0	1	3
Staphylinidae	*Tachinus elongatus*			+	ZOO	12	0	1	13
Staphylinidae	*Tachinus frigidus*	*		+	ZOO	2	0	0	2
Staphylinidae	*Tachinus fumipennis*			+	ZOO	1	0	6	7
Staphylinidae	*Tachyporus borealis*			+	ZOO	1	0	15	16
Stenotrachelidae	*Cephaloon tenuicorne*	*		++	OMN	3	0	0	3
Tenebrionidae	*Neatus* sp. 1 (unnamed-WS)	*	†	++	MYC	1	0	0	1
Tenebrionidae	*Platydema americanum*			++	MYC	1	0	0	1
Tenebrionidae	*Scaphidema aeneolum*	*		+	MYC	2	0	0	2
Tenebrionidae	*Upis ceramboides*			++	DET	1	0	1	2
Trogossitidae	*Ostoma ferruginea*			++	MYC	0	0	1	1
Trogossitidae	*Thymalus marginicollis*			++	MYC	7	0	1	8
Grand Total						2831	31	1226	4088

*only collected in WTs, thus removed for analyses; †confirmed new species;

Sx=Saproxylic Class: ++obligate, +facultative; FG=feeding guild: SAP=sapping tree wounds, PHL=phloem, XYL=xylem, AMB=ambrosia fungus, MYC=fungus, MYX=slimemolds, DET=detritus, ZOO=invertebrate prey, OMN=mixed feeding strategies; Tr= live tree, Sn= snag, Lg= log; YB=Yves Bousquet pers. comm. to CW, WR=Wolfgang Rücker pers. comm. to CW, WS=Warren Steiner pers. comm. to Vassili Belov; CW=Charlene Wood.

Appendix 5-A

Summarized distributional and classification information for all beetle species collected.

FAMILY	COLLECTION METHOD						TYPE[ł]			DECAY[ψ]									SIZE[ł]			
Species	HC	FE	RD	ET	TWT	FWT	Tr	Sn	Lg	Sn1	Sn2	Sn3	Sn4	Lg1	Lg2	Lg3	Lg4	Lg5	Lg6	SC1	SC2	SC3	SC4
Anobiidae																							
Caenocara scymnoides LeConte [+ Myc]					100			100					100								100		
Dorcatoma pallicornis LeConte [r ++ Myc]					0.88	0.12		0.88		0.24	0.24	0.24	0.18								0.53	0.35	
Hemicoelus carinatus (Say) [++ Xyl]			0.27	0.27	0.41	0.05		0.91	0.05	0.05	0.07	0.16	0.64			0.05					0.59	0.36	
Ptilinus lobatus Casey [++ Xyl]	0.09		0.28	0.19	0.41	0.04		0.87	0.09	0.02	0.04	0.54	0.28			0.09					0.56	0.41	
Anthicidae																							
Omonadus floralis (Linné) [+ Omn]		100							100						100								100
Anthribidae																							
Trigonorhinus limbatus (Say) [+ Myc]	100								100					100							100		
Buprestidae																							
Agrilus liragus Barter & Brown [++ Xyl]	0.71		0.14		0.14			0.14	0.86	0.14				0.71		0.14				0.29	0.57		0.14
Byturidae																							
Byturus unicolor Say [- Her]				0.33	0.33	0.33		0.67			0.33	0.33									0.67		
Cantharidae																							
Podabrus sp. 1 [? + Zoo]	0.14			0.07	0.36	0.43		0.43	0.14	0.21	0.07		0.14		0.07		0.07				0.36	0.21	
Podabrus sp. 2 [? + Zoo]	0.03		0.27	0.09	0.23	0.39		0.31	0.30	0.07	0.14	0.06	0.04		0.01		0.13	0.10	0.06		0.46	0.16	
Carabidae																							
Agonum retractum LeConte [+ Zoo]	0.67	0.10	0.14		0.10			0.10	0.90		0.05		0.05	0.05	0.10	0.10	0.14	0.29	0.24	0.05	0.52	0.43	
Agonum sordens Kirby [+ Zoo]					100			100					100									100	
Agonum superioris Lindroth [+ Zoo]		100							100								100				100		
Amara patruelis Dejean [- Zoo]						100																	
Amara quenseli (Schonherr) [- Zoo]					100			100			100										100		
Bembidion fortestriatum (Motschulsky) [+ Zoo]		100							100								100						100
Bembidion nigripes (Kirby) [+ Zoo]		0.50			0.50			0.50	0.50		0.50						0.50			0.50	0.50		
Bembidion timidum (LeConte) [+ Zoo]		100							100							100					100		

Appendix 5-A *-continued-*

FAMILY	COLLECTION METHOD						TYPE‡			DECAY¥									SIZE‡			
Species	HC	FE	RD	ET	TWT	FWT	Tr	Sn	Lg	Sn1	Sn2	Sn3	Sn4	Lg1	Lg2	Lg3	Lg4	Lg5	Lg6	SC1	SC2	SC3	SC4
Carabidae *-continued-*																							
Calathus ingratus Dejean [- Zoo]	0.40	0.30			0.30		0.30	0.70		0.10	0.10		0.10		0.10		0.10	0.40	0.10	0.10	0.60	0.30	
Calosoma frigidum Kirby [- Zoo]					100		100			0.29	0.43	0.14	0.14								0.71	0.29	
Diacheila arctica amoena (Faldermann) [r - Zoo]					100		100			100											100		
Perigona nigriceps Lindroth [r + Zoo]		100						100								100							100
Platynus decentis (Say) [+ Zoo]	0.15		0.06	0.19	0.58	0.02	0.78	0.20		0.26	0.11	0.13	0.27		0.06	0.04	0.04	0.02	0.04	0.02	0.52	0.37	0.06
Platynus mannerheimi Dejean [+ Zoo]					100		100			0.25	0.25		0.50								0.25	0.75	
Pterostichus adstrictus Eschscholtz [+ Zoo]	0.63	0.13	0.13	0.13			0.13	0.88					0.13					0.75	0.13		0.13	0.50	0.38
Pterostichus pensylvanicus LeConte [+ Zoo]	100							100									0.75		0.25		0.50	0.25	0.25
Trechus apicalis Motschulsky [+ Zoo]	100							100										100				100	
Trechus chalybeus Dejean [+ Zoo]	0.50		0.50				0.50	0.50			0.50							0.50			0.50		0.50
Cerambycidae																							
Grammoptera subargentata (Kirby) [++ Xyl]	0.01				0.32	0.67	0.32	0.01		0.13	0.13	0.02	0.02		0.01						0.28	0.05	
Neospondylis upiformis (Mannerheim) [++ Xyl]					100		100						100								100		
Pogonocherus parvulus LeConte [++ Xyl]					100		100			100												100	
Trachysida aspera (LeConte) [++ Xyl]					0.29	0.71	0.29			0.04	0.07	0.11	0.07								0.21	0.07	
Xylotrechus annosus (Say) [++ Xyl]			100				100				100										100		
Cerylonidae																							
Cerylon castaneum Say [++ Myc]	0.04	0.13	0.04	0.46	0.33		0.83	0.17		0.46	0.29	0.08			0.13	0.04					0.67	0.25	0.08
Chrysomelidae																							
Phratora frosti Brown [- Her]						100																	
Phyllotreta sp. 1 [? - Her]		100						100							100								100
Ciidae																							
Cis americanus Mannerheim [++ Myc]	0.05	0.79			0.16		0.16	0.84		0.05	0.05	0.05			0.05	0.79					0.16	0.05	0.79
Cis fuscipes Mellié [++ Myc]					100		100			0.33	0.17		0.50								0.83	0.17	
Cis levettei (Casey) [++ Myc]		0.50			0.50		0.50	0.50		0.50						0.50					0.50		0.50
Cis maritimus Hatch [r ++ Myc]		100						100									100				100		
Dolichocis manitoba Dury [++ Myc]	0.10		0.05	0.25	0.55	0.05	0.85	0.10		0.15	0.25	0.30	0.15		0.10						0.60	0.35	
Octotemnus laevis Casey [++ Myc]					100		100					100										100	
Orthocis punctatus (Mellié) [++ Myc]					100		100			0.33			0.67								0.67	0.33	
Sulcacis curtulus (Casey) [++ Myc]		0.22		0.56	0.22		0.78	0.22		0.11	0.33	0.33			0.22						0.67	0.11	0.22

Appendix 5-A *-continued-*

FAMILY	COLLECTION METHOD						TYPE[ł]			DECAY[ψ]									SIZE[ł]			
Species	HC	FE	RD	ET	TWT	FWT	Tr	Sn	Lg	Sn1	Sn2	Sn3	Sn4	Lg1	Lg2	Lg3	Lg4	Lg5	Lg6	SC1	SC2	SC3	SC4
Clambidae																							
Clambus pubescens Redtenbacher [+ Myc]					0.29	0.71		0.29		0.14		0.14									0.21	0.07	
Cleridae																							
Thanasimus undatulus (Say) [++ Zoo]					100			100				100									100		
Coccinellidae																							
Adalia bipunctata (Linné) [- Zoo]						100																	
Calvia quatuordecimguttata (Linné) [- Zoo]				0.50	0.50			100			0.50		0.50									100	
Coccinella septempunctata Linné [- Zoo]					100			100		100												100	
Didion longulum Casey [+ Zoo]				0.67	0.33			100		0.83	0.17										0.67	0.33	
Psyllobora borealis Casey [- Myc]					100			100				100										100	
Corylophidae																							
Clypastraea lugubris (LeConte) [++ Myc]			0.01	0.45	0.48	0.05		0.93	0.01	0.77	0.12	0.03	0.01			0.01					0.29	0.66	
Orthoperus scutellaris LeConte [++ Myc]			0.33	0.25	0.33	0.08		0.58	0.33	0.42	0.08		0.08	0.08	0.08	0.17					0.83	0.08	
Cryptophagidae																							
Antherophagus ochraceus Melsheimer [- Det]					100			100		0.33	0.33		0.33								0.67	0.33	
Atomaria apicalis Erichson [r + Myc]			100						100									100			100		
Atomaria diluta ? Erichson [r? ++ Myc]			100						100						100						100		
Atomaria ephippiata Zimmermann [+ Myc]		100							100					0.50	0.50					0.50	0.50		
Atomaria fuscata [r + Myc]	100								100					100								100	
Atomaria lewisii [r + Myc]		100							100						100								100
Atomaria linearis Stephens [r + Myc]					100			100					100								100		
Atomaria melanica Hatch [r? + Myc]						100																	
Atomaria ochracea Zimmermann [r + Myc]		0.50			0.50			0.50	0.50		0.50						0.50				0.50	0.50	
Atomaria sp. 1 [? + Myc]			100						100						100						100		
Atomaria sp. 2 [? + Myc]		100							100									0.50	0.50		0.50	0.50	
Atomaria sp. 3 [? + Myc]					0.67	0.33		0.67				0.67									0.67		
Atomaria sp. 4 [? + Myc]					100			100		0.13	0.50	0.13	0.25								0.63	0.38	
Atomaria stricticollis Casey [r + Myc]					0.80	0.20		0.80			0.20	0.20	0.40								0.40	0.40	
Atomaria subangulata Sahlberg [r + Myc]			0.98		0.02			0.02	0.98	0.02					0.98						0.98	0.02	
Caenoscelis antennalis (Casey) [+ Myc]		0.17	0.17		0.67			0.67	0.33	0.33		0.17	0.17				0.17	0.17		0.17	0.67	0.17	
Caenoscelis ferruginea Sahlberg [r + Myc]				0.13	0.88			100		0.75	0.13	0.13									0.75	0.25	

Appendix 5-A *-continued-*

FAMILY	COLLECTION METHOD						TYPE‡			DECAYΨ									SIZE‡			
Species	HC	FE	RD	ET	TWT	FWT	Tr	Sn	Lg	Sn1	Sn2	Sn3	Sn4	Lg1	Lg2	Lg3	Lg4	Lg5	Lg6	SC1	SC2	SC3	SC4
Cryptophagidae *-continued-*																							
Cryptophagus acutangulus (Gyllenhal) [+ Myc]		0.90			0.10			0.10	0.90			0.10		0.10	0.20	0.20	0.30		0.10	0.20	0.30	0.30	0.20
Cryptophagus sp. 1 [? + Myc]					0.50	0.50		0.50					0.50								0.50		
Cryptophagus sp. 2 [? + Myc]		0.13			0.67	0.20		0.67	0.13	0.07	0.20	0.13	0.27		0.03	0.07		0.03			0.47	0.20	0.13
Myrmedophila americana (LeConte) [++ Myc]				0.07	0.93			100		0.14	0.29	0.29	0.29								0.93	0.07	
Pteryngium crenatum (Gyllenhal) [++ Myc]					100			100		0.17	0.50	0.17	0.17								0.50	0.50	
Salebius octodentatus (Mäklin) [+ Myc]						100																	
Cucujidae																							
Cucujus clavipes Fabricius [++ Zoo]	0.57		0.16	0.07	0.16	0.04	0.01	0.25	0.70	0.04	0.11	0.04	0.06	0.01	0.57	0.11		0.01		0.04	0.46	0.16	0.31
Pediacus fuscus Erichson [++ Omn]	0.17	0.67			0.17			0.17	0.83			0.17			0.33	0.50				0.67	0.17	0.17	
Curculionidae																							
Carphoborus carri Swaine [++ Phl]		100							100					100								100	
Ceutorhynchus distinctus ? Brisout de Barneville [r? - H					100			100			0.50	0.50									100		
Cossonus pacificus Van Dyke [++ Xyl]				0.12	0.88			100		0.12	0.28	0.32	0.28								0.72	0.28	
Dendroctonus rufipennis (Kirby) [++ Phl]						100																	
Dorytomus sp. 1 [- Her]		100							100										100		100		
Dorytomus sp. 2 [- Her]						100																	
Magdalis sp. 1 [++ Xyl]				100				100					100								100		
Otiorhynchus ovatus (Linné) [- Her]		100							100						0.25		0.25	0.50			0.50		0.50
Phloeophagus canadensis Van Dyke [++ Xyl]		100							100							100					100		
Phloeotribus sp. 1 [++ Phl]					100			100					100								100		
Phloeotribus sp. 2 [++ Phl]						100																	
Procryphalus mucronatus (LeConte) [++ Phl]					100			100		100											100		
Rhyncolus brunneus Mannerheim [++ Xyl]					100			100					100								100		
Trypodendron lineatum (Olivier) [++ Amb]					100			100		0.33	0.67										0.67	0.33	
Trypodendron retusum (LeConte) [++ Amb]	0.24	0.01	0.01	0.51	0.19	0.03		0.71	0.25	0.69	0.02			0.24	0.00	0.00					0.41	0.55	0.00
Tychius picirostris (Fabricius) [- Her]			0.50			0.50		0.50			0.50										0.50		
Tychius stephensi Schonherr [- Her]		100							100					0.50		0.50				0.50			0.50
Dermestidae																							
Dermestes lardarius Linné [+ Det]					100			100				0.50	0.50								0.50	0.50	
Megatoma cylindrica (Kirby) [+ Det]			0.25	0.25	0.50			100			0.25	0.50	0.25								0.75	0.25	
Megatoma perversa (Fall) [r + Det]			0.06	0.55	0.39			100		0.01	0.12	0.42	0.45								0.66	0.34	

Appendix 5-A *-continued-*

FAMILY	COLLECTION METHOD						TYPE[ł]			DECAY[ψ]									SIZE[ł]			
Species	HC	FE	RD	ET	TWT	FWT	Tr	Sn	Lg	Sn1	Sn2	Sn3	Sn4	Lg1	Lg2	Lg3	Lg4	Lg5	Lg6	SC1	SC2	SC3	SC4
Elateridae																							
Aeolus mellilus comis (Say) [+ Zoo]		0.33			0.33	0.33		0.33	0.33	0.33					0.33						0.33	0.33	
Agriotes ferrugineipennis (LeConte) [- Her]					0.67	0.33		0.67		0.33	0.17	0.17									0.67		
Ampedus apicatus (Say) [++ Omn]	0.50				0.50			0.50	0.50	0.50					0.50							1.00	
Ampedus deletus (LeConte) [++ Omn]	0.89	0.11							1.00								0.22	0.33	0.44		0.11	0.33	0.56
Ampedus luctuosus (LeConte) [++ Omn]	1.00								1.00									1.00				0.50	0.50
Ampedus nigricans Germar [++ Omn]				0.08	0.73	0.19		0.81		0.23	0.12	0.27	0.19								0.50	0.31	
Ampedus sp. 1 [? ++ Omn]			1.00						1.00										1.00		1.00		
Ampedus sp. 2 [? ++ Omn]	1.00								1.00									1.00				1.00	
Ampedus sp. 3 [? ++ Omn]	0.50					0.50			0.50									0.50				0.50	
Ampedus "subtilis" (LeConte) [++ Omn]	0.83				0.17			0.17	0.83	0.17								0.50	0.33			0.67	0.33
"Ctenicera" nitidulus (LeConte) [+ Omn]		0.11		0.22	0.56	0.11		0.78	0.11	0.22	0.11	0.22	0.22					0.11			0.67	0.11	0.11
"Ctenicera" stricklandi (Brown) [+ Omn]	0.08			0.08	0.58	0.25		0.67	0.08	0.33	0.17		0.17			0.08				0.08	0.67		
Denticollis denticornis (Kirby) [+ Zoo]			0.14		0.57	0.29		0.57	0.14		0.29	0.29				0.14					0.43	0.29	
Eanus decoratus (Mannerheim) [+ Zoo]	0.33					0.67			0.33							0.33				0.33			
Nitidolimonius resplendens (Eschscholtz) [+ Zoo]					1.00			1.00				1.00										1.00	
Pseudanostirus propolus (LeConte) [+ Omn]	0.10		0.03	0.10	0.34	0.41		0.45	0.14	0.28	0.03		0.14	0.03		0.03		0.07			0.45	0.14	
Pseudanostirus triundulatus (Randall) [+ Omn]						1.00																	
Erotylidae																							
Triplax antica LeConte [++ Myc]					1.00			1.00		0.50	0.50										1.00		
Triplax californica LeConte [++ Myc]				1.00				1.00			1.00										1.00		
Triplax dissimulator (Crotch) [++ Myc]				0.03	0.85	0.12		0.88		0.30	0.42	0.09	0.06								0.79	0.09	
Triplax thoracica Say [++ Myc]				0.12	0.82	0.06		0.94			0.65	0.29									0.94		
Eucinetidae																							
Eucinetus terminalis LeConte [r + Myc]					0.50	0.50		0.50		0.50											0.50		
Eucnemidae																							
Epiphanis cornutus Eschscholtz [++ Myc]					0.50	0.50		0.50		0.30	0.10		0.10								0.30	0.20	
Isorhipis obliqua (Say) [r ++ Myc]			0.50			0.50			0.50								0.50				0.50		
Microrhagus pectinatus LeConte [r ++ Myc]					1.00			1.00			1.00										1.00		
Histeridae																							
Teretrius montanus Horn [++ Zoo]			0.50	0.25	0.25			1.00				0.25	0.75									1.00	

Appendix 5-A *-continued-*

FAMILY	COLLECTION METHOD						TYPE[ǂ]			DECAY[ψ]									SIZE[ǂ]			
Species	HC	FE	RD	ET	TWT	FWT	Tr	Sn	Lg	Sn1	Sn2	Sn3	Sn4	Lg1	Lg2	Lg3	Lg4	Lg5	Lg6	SC1	SC2	SC3	SC4
Hydrophilidae																							
Cercyon herceus frigidus Smetana [+ Zoo]		100							100								100						100
Laemophloeidae																							
Cryptolestes ferrugineus (Stephens) [+ Det]		100							100							100							100
Latridiidae																							
Cartodere constricta (Gyllenhal) [+ Myc]	0.02	0.98							100					0.12	0.51	0.26	0.08	0.02	0.01	0.06	0.10	0.07	0.78
Corticaria arctophila Fall [r + Myc]					100			100		100											100		
Corticaria elongata (Gyllenhal) [r + Myc]	0.00	0.99			0.01			0.01	0.99	0.00	0.00			0.02	0.63	0.18	0.09	0.04	0.03	0.02	0.07	0.01	0.90
Corticaria ferruginea Marsham [+ Myc]		0.73	0.09	0.09	0.09		0.09	0.18	0.73	0.18				0.09	0.18	0.27			0.18	0.55	0.18	0.18	0.09
Corticaria n. sp. 1 [n + Myc]				0.84	0.16			100		0.52	0.34	0.12	0.01								0.67	0.33	
Corticaria n. sp. 2 [n + Myc]				100				100				0.67	0.33								0.67	0.33	
Corticaria n. sp. 3 [n + Myc]				0.65	0.35			100		0.12	0.15	0.65	0.08								0.65	0.35	
Corticaria n. sp. 4 [n + Myc]			100						100							100					100		
Corticaria n. sp. 5 [n + Myc]					0.33	0.67		0.33					0.33								0.33		
Corticaria n. sp. 6 [n + Myc]				0.50	0.50			100					100									100	
Corticaria orbicollis (Mannerheim) [r + Myc]			0.60	0.40				100			0.20	0.40	0.40								100		
Corticaria rubripes Mannerheim [r + Myc]	0.03	0.27	0.14	0.49	0.08			0.68	0.32	0.05	0.16	0.27	0.19	0.03	0.14	0.11		0.03	0.03	0.05	0.57	0.22	0.16
Corticaria serrata (Paykull) [+ Myc]		100							100						0.50		0.50			0.50			0.50
Corticarina cavicollis (Mannerheim) [r + Myc]		100							100						100								100
Cortinicara gibbosa (Herbst) [+ Myc]			0.01	0.02	0.58	0.39		0.60	0.01	0.16	0.22	0.11	0.12	0.01							0.49	0.12	
Dienerella filum (Aubé) [r + Myc]					100			100			100										100		
Enicmus fictus Fall [+ Myc]		0.50		0.50				0.50	0.50			0.50					0.50			0.50		0.50	
Enicmus mimus Fall [+ Myc]					100			100			100										100		
Enicmus tenuicornis LeConte [+ Myc]				0.31	0.69			100		0.08	0.15	0.54	0.23								0.46	0.54	
Latridius hirtus Gyllenhal [++ Myc]				0.64	0.36			100		0.19	0.36	0.39	0.06								0.72	0.28	
Latridius minutus (Linné) [+ Myc]	0.03	0.13	0.59	0.09	0.13	0.03		0.25	0.72		0.03	0.16	0.06	0.09	0.03	0.03	0.56				0.78	0.13	0.06
Melanophthalma americana (Mannerheim) [r + Myc]			0.09	0.05	0.36	0.50		0.50		0.18		0.14	0.18								0.45	0.05	
Melanophthalma helvola Motschulsky [r + Myc]					0.22	0.78		0.22			0.11	0.04	0.07								0.15	0.07	
Melanophthalma inermis Motschulsky [r + Myc]		0.22				0.78			0.22						0.11	0.11						0.11	0.11
Melanophthalma pumila (LeConte) [+ Myc]			0.03	0.01	0.40	0.56		0.41	0.03	0.10	0.13	0.06	0.12	0.03							0.36	0.08	
Stephostethus liratus (LeConte) [+ Myc]		0.03	0.03		0.43	0.50		0.43	0.07	0.17	0.17	0.03	0.07		0.03				0.03		0.40	0.10	

Appendix 5-A *-continued-*

FAMILY	COLLECTION METHOD						TYPE[ǂ]			DECAY[ψ]									SIZE[ǂ]			
Species	HC	FE	RD	ET	TWT	FWT	Tr	Sn	Lg	Sn1	Sn2	Sn3	Sn4	Lg1	Lg2	Lg3	Lg4	Lg5	Lg6	SC1	SC2	SC3	SC4
Leiodidae	.					.			.										.				
Agathidium angulare Mannerheim [r + Myx]	.		0.50			0.50		.	0.50	0.50	.			0.50					0.50	.		1.00		
Agathidium athabascanum Fall [+ Myc]	.	1.00						.		1.00	.					1.00				.				1.00
Agathidium cavisternum Fall [r + Myx]	.	0.14	0.14			0.57	0.14	.	0.57	0.29	.		0.29	0.14	0.14			0.14	0.14	.	0.14	0.71		
Agathidium depressum Fall [+ Myc]	.		0.20		0.13	0.13	0.53	.	0.27	0.20	.	0.13	0.07	0.07				0.07	0.13	.	0.07	0.33	0.07	
Agathidium dubitans Fall [r + Myc]	.		1.00					.		1.00	.								1.00	.				1.00
Agathidium maculosum Brown [+ Myx]	.	1.00						.		1.00	.							1.00		.				1.00
Agathidium n. sp. (?) 1 [n? + Myc]	.					1.00		.	1.00		.		1.00							.		0.50	0.50	
Agathidium pulchrum LeConte [r + Myc]	.		0.86				0.14	.		0.86	.						0.14	0.71		.				0.86
Agathidium rotundulum Mannerheim [r + Myc]	.					1.00		.	1.00		.			1.00						.		1.00		
Agathidium sp. 1 [? + Myc]	.				0.40	0.40	0.20	.	0.80		.	0.20	0.60							.		0.80		
Agathidium sp. 2 [? + Myc]	.					1.00		.	1.00		.			1.00						.		1.00		
Agathidium sp. 3 [? + Myc]	.		1.00					.		1.00	.							1.00		.				1.00
Agathidium sp. 4 [? + Myc]	.					1.00		.	1.00		.				1.00					.		1.00		
Agathidium sp. 5 [? + Myc]	.					1.00		.	1.00		.	0.50	0.50							.		0.50	0.50	
Agathidium sp. 6 [? + Myc]	.						1.00	.			.									.				
Anisotoma amica Brown [r ++ Myx]	.					1.00		.	1.00		.	0.50	0.50							.		1.00		
Anisotoma globososa Hatch [++ Myx]	.					0.57	0.43	.	0.57		.			0.29	0.29					.		0.14	0.43	
Catops basilaris Say [+ Myc]	.	1.00						.		1.00	.								1.00	.			1.00	
Colon elongatum Notman [r + Myc]	.		0.20			0.20	0.60	.	0.20	0.20	.			0.20					0.20	.			0.40	
Platyhydnobius arizonensis (Horn) [r + Myc]	.					1.00		.	1.00		.		1.00							.		1.00		
Lucanidae	.							.			.									.				
Platycerus depressus LeConte [++ Xyl]	.					1.00		.	1.00		.	1.00								.		1.00		
Lyctidae	.							.			.									.				
Dictyopterus aurora (Herbst) [++ Xyl]	.					1.00		.	1.00		.		1.00							.		1.00		
Melandryidae	.							.			.									.				
Melandrya striata Say [++ Xyl]	.			0.05	0.23	0.64	0.09	.	0.86	0.05	.	0.23	0.36	0.18	0.09		0.05			.		0.86	0.05	
Orchesia castanea (Melsheimer) [++ Myc]	.			0.50		0.25	0.25	.	0.25	0.50	.				0.25			0.50		.		0.75		
Orchesia sp. 1 [? ++ Myc]	.	1.00						.		1.00	.							1.00		.			1.00	

Appendix 5-A *-continued-*

FAMILY	COLLECTION METHOD						TYPE[‡]			DECAY[ψ]									SIZE[‡]			
Species	HC	FE	RD	ET	TWT	FWT	Tr	Sn	Lg	Sn1	Sn2	Sn3	Sn4	Lg1	Lg2	Lg3	Lg4	Lg5	Lg6	SC1	SC2	SC3	SC4
Monotomidae																							
Monotoma longicollis Gyllenhal [r ++ Myc]		100							100						100						100		
Monotoma picipes Herbst [++ Myc]		100							100							100					100		
Rhizophagus dimidiatus Mannerheim [++ Zoo]				0.50	0.50			100		100												100	
Rhizophagus n. sp. 1 [n ++ Zoo]		0.00		0.01	0.96	0.03		0.97	0.00	0.57	0.33	0.04	0.03						0.00		0.54	0.43	
Rhizophagus remotus LeConte [++ Zoo]		0.01	0.12	0.59	0.26	0.02		0.86	0.12	0.47	0.38		0.02	0.02	0.09	0.01					0.67	0.32	
Mordellidae																							
Mordellochroa scapularis (Say) [++ Myc]					0.67	0.33		0.67			0.33		0.33								0.67		
Mycetophagidae																							
Mycetophagus distinctus Hatch [++ Myc]	0.50					0.50			0.50							0.50						0.50	
Mycetophagus serrulatus (Casey) [++ Myc]					100			100				100									100		
Typhaea stercorea (Linné) [r + Myc]		100							100					0.11	0.11	0.44	0.22	0.11			0.22	0.22	0.56
Nitidulidae																							
Colopterus truncatus (Randall) [++ Myc/SR]					0.53	0.47		0.53		0.12	0.09	0.09	0.23								0.35	0.19	
Epuraea avara (Randall) [r + Myc/SR]					100			100			100										100		
Epuraea flavomaculata Mäklin [+ Myc/SR]	0.05		0.03	0.50	0.36	0.05	0.03	0.87	0.05	0.73	0.11	0.02	0.01		0.05						0.41	0.53	0.01
Epuraea linearis Mäklin [+ Myc/SR]				0.25	0.75			100		0.25	0.50	0.25									0.75	0.25	
Epuraea planulata Erichson [+ Myc/SR]			0.08	0.31	0.54	0.08		0.85	0.08	0.69	0.15			0.04	0.04						0.54	0.38	
Epuraea populi Dodge [+ Myc/SR]					0.80	0.20		0.80		0.80												0.80	
Epuraea rufa (Say) [r + Myc/SR]					100			100			100										100		
Epuraea sp. 1 [? + Myc/SR]	0.20		0.80				0.60		0.40						0.20	0.20					0.80	0.20	
Epuraea sp. 2 [? + Myc/SR]					100			100		100											100		
Epuraea sp. 3 [? + Myc/SR]						100																	
Epuraea terminalis Mannerheim [+ Myc/SR]	0.05	0.05	0.52		0.19	0.19	0.43	0.19	0.19	0.05	0.05	0.10		0.05		0.05	0.05	0.05			0.76	0.05	
Epuraea truncatella Mannerheim [+ Myc/SR]			100				0.75		0.25					0.25							100		
Glischrochilus moratus Brown [+ Myc/SR]				0.33	0.67			100		0.67	0.33										0.33	0.67	
Glischrochilus sanguinolentus (Olivier) [+ Myc/SR]				0.03	0.46	0.51		0.49		0.16	0.16	0.03	0.13								0.41	0.08	
Glischrochilus siepmanni Brown [+ Myc/SR]				0.05	0.21	0.74		0.26		0.02	0.02	0.12	0.09								0.14	0.12	
Glischrochilus vittatus (Say) [+ Myc/SR]			0.04	0.42	0.42	0.12	0.04	0.85		0.50	0.31		0.04								0.42	0.46	
Meligethes canadensis Easton [- Pal]					100			100			100										100		
Orsodacnidae																							
Orsodacne atra (Ahrens) [- Her]				0.01	0.18	0.82		0.19		0.06	0.06	0.04	0.03								0.15	0.04	

Appendix 5-A *-continued-*

FAMILY	COLLECTION METHOD						TYPE[ł]			DECAY[ψ]										SIZE[ł]			
Species	HC	FE	RD	ET	TWT	FWT	Tr	Sn	Lg	Sn1	Sn2	Sn3	Sn4	Lg1	Lg2	Lg3	Lg4	Lg5	Lg6	SC1	SC2	SC3	SC4
Phalacridae	.						.			.										.			
Stilbus apicalis (Melsheimer) [r + Myc]	.					100	.			.										.			
Ptiliidae	.						.			.										.			
Acrotrichis sp. 1 [? + Myc]	.	0.13		0.49	0.02	0.20	0.16	.	0.35	0.49	.	0.05	0.18	0.07	0.04	0.04	0.05	0.07	0.02	0.20	0.11	.	0.71		0.13
Pteryx sp. 1 [r + Myc]	.	0.03		0.97			.	0.02	0.03	0.95	.	0.03				0.05	0.05	0.02	0.64	0.14	0.05	.	0.43	0.57	
Pyrochroidae	.						.			.										.			
Dendroides canadensis Latreille [r ++ Myc]	.				100		.	100		.	100									.	100		
Dendroides testaceus LeConte [++ Myc]	.				0.63	0.38	.	0.63		.	0.38	0.25								.	0.63		
Schizotus cervicalis Newman [++ Myc]	.	0.58	0.06	0.19		0.13	0.03	.	0.13	0.84	.	0.10	0.03			0.13	0.52	0.16	0.03	.	0.03	0.58	0.29	0.06
Salpingidae	.						.			.										.			
Rhinosimus viridiaeneus (Randall) [++ Myc]	.				0.33	0.33	0.33	.	0.67		.	0.33		0.33							.		0.33	0.33	
Scarabaeidae	.						.			.										.			
Aphodius fossor (Linné) [- Cop]	.					0.67	0.33	.	0.67		.	0.33		0.33							.	0.67		
Aphodius haemorrhoidalis (Linné) [- Cop]	.						100	.			.									.			
Aphodius leopardus Horn [- Cop]	.						100	.			.									.			
Scirtidae	.						.			.										.			
Cyphon confusus Brown [r + Omn]	.					100		.	100		.		100							.	100		
Cyphon variabilis (Thunberg) [+ Omn]	.	0.01	0.06	0.07	0.13	0.49	0.24	.	0.65	0.12	.	0.25	0.13	0.03	0.24	0.03	0.03		0.01		0.04	.	0.26	0.44	0.06
Scraptiidae	.						.			.										.			
Anaspis rufa Say [++ Omn]	.	0.14					0.86	.		0.14	.							0.14			.			0.14	
Canifa pallipes (Melsheimer) [++ Omn]	.			0.02	0.62	0.26	0.11	.	0.89		.	0.06	0.28	0.32	0.23							.	0.62	0.28	
Silphidae	.						.			.										.			
Nicrophorus defodiens Mannerheim [- Nec]	.					0.50	0.50	.	0.50		.	0.17			0.33							.	0.50		
Silvanidae	.						.			.										.			
Ahasverus advena (Waltl) [r + Myc]	.		100				.			100	.							100			.				100
Dendrophagus cygnaei Mannerheim [++ Myc]	.	0.75				0.25		.	0.25	0.75	.				0.25	0.25	0.50					.	0.50		0.50	
Sphindidae	.						.			.										.			
Odontosphindus clavicornis Casey [++ Myx]	.					100		.	100		.	0.23	0.62	0.08	0.08							.	0.92	0.08	
Staphylinidae	.						.			.										.			
Acidota crenata (Fabricius) [- Zoo]	.					100		.	100		.		100							.	100		
Acidota quadrata (Zetterstedt) [- Zoo]	.					100		.	100		.			100						.		100	
Anotylus sobrinus (LeConte) [+ Zoo]	.		0.20	0.20		0.20	0.40	.	0.40	0.20	.	0.20	0.20					0.20			.	0.60		
Atrecus macrocephalus (Nordmann) [++ Zoo]	.	0.15	0.13	0.70		0.03		.	0.03	0.98	.			0.03		0.03		0.08	0.35	0.40	0.13	.	0.05	0.75	0.10	0.10

Appendix 5-A *-continued-*

FAMILY	COLLECTION METHOD						TYPE‡			DECAYΨ										SIZE‡			
Species	HC	FE	RD	ET	TWT	FWT	Tr	Sn	Lg	Sn1	Sn2	Sn3	Sn4	Lg1	Lg2	Lg3	Lg4	Lg5	Lg6	SC1	SC2	SC3	SC4
Staphylinidae *-continued-*																							
Baeocera humeralis Fall [++ Myc]	0.08	0.92							100								0.08	0.92					100
Baeocera sp. 1 [r ++ Myc]				100				100					100									100	
Bolitobius "horni" Campbell [+ Zoo]	0.33		0.33		0.33			0.33	0.67		0.33								0.67		0.67		0.33
Carpelimus sp. 1 [? - Myc]		100							100							100							100
Carphacis nepigonensis (Bernhauer) [+ Zoo]				0.12	0.85	0.03		0.97		0.62	0.26	0.05	0.05								0.61	0.36	
Coproporus ventriculus (Say) [++ Myc]		100							100										100		100		
Dinothenarus pleuralis (LeConte) [+ Zoo]	100								100										100				100
Eucnecosum tenue (LeConte) [+ Zoo]						100																	
Euplectus duryi Casey [+ Zoo]				0.25	0.75			100		0.25	0.17	0.25	0.33								0.83	0.17	
Eusphalerum pothos (Mannerheim) [- Pal]				0.01	0.52	0.48		0.52		0.15	0.22	0.07	0.08								0.44	0.08	
Gabrius brevipennis (Horn) [+ Zoo]		0.71	0.29						100								0.43	0.43	0.14		0.57	0.43	
Hapalaraea hamata (Fauv.) [+ Zoo]					100			100		0.44	0.22	0.22	0.11								0.56	0.44	
Ischnosoma splendidum (Gravenhorst) [+ Zoo]	0.29	0.14	0.29	0.14	0.14			0.29	0.71			0.14	0.14				0.14	0.14	0.43		0.43	0.29	0.29
Lathrobium fauveli Duvivier [+ Zoo]	0.36	0.55	0.09						100								0.09	0.55	0.36	0.45	0.18	0.09	0.27
Lathrobium washingtoni Casey [+ Zoo]	0.20	0.40	0.33		0.07			0.07	0.93				0.07			0.07	0.13	0.33	0.40	0.13	0.53	0.07	0.27
Leptacinus intermedius Donisthorpe [+ Zoo]		100							100							100					100		
Lordithon bimaculatus (Schrank) [+ Zoo]				0.30	0.60	0.10		0.90		0.10	0.37	0.33	0.10								0.80	0.10	
Lordithon fungicola Campbell [+ Zoo]				0.81	0.19			100			100										100		
Lordithon longiceps (LeConte) [+ Zoo]					100			100			0.40	0.40	0.20								0.60	0.40	
Megarthrus angulicollis Mäklin [+ Myx]		0.50				0.50			0.50									0.50					0.50
Mycetoporus americanus Erichson [+ Myc]	0.17				0.50	0.33		0.50	0.17	0.17	0.17		0.17				0.17				0.50	0.17	
Neohypnus hamatus (Say) [+ Zoo]					100			100		100											100		
Nudobius cephalus (Say) [++ Zoo]	0.50				0.25	0.25		0.25	0.50	0.25					0.50							0.50	0.25
Olisthaerus megacephalus (Zetterstedt) [++ Zoo]					100			100		0.50			0.50								0.50	0.50	
Ontholestes cingulatus (Gravenhorst) [- Zoo]						100																	
Orobanus sp. 1 [r + Zoo]		100							100								100					100	
Oropus sp. 1 [r + Zoo]			100					100		100											100		
Philonthus lindrothi Smetana [r + Zoo]		100							100								100						100
Phloeostiba lapponica (Zetterstedt) [++ Zoo/SR]			0.25	0.33	0.38	0.04	0.08	0.75	0.13	0.56	0.15	0.02	0.02	0.10	0.04						0.56	0.40	
Phyllodrepa sp. 1 [? + Zoo]	0.18	0.76	0.06					0.06	0.94	0.06							0.06	0.88			0.06		0.94
Proteinus atomarius Erichson [r + Myc]			100						100										100		100		
Proteinus limbatus Mäklin [+ Myc]		100							100									0.50	0.50				100

Appendix 5-A *-continued-*

FAMILY	COLLECTION METHOD						TYPE‡			DECAYΨ										SIZE‡			
Species	HC	FE	RD	ET	TWT	FWT	Tr	Sn	Lg	Sn1	Sn2	Sn3	Sn4	Lg1	Lg2	Lg3	Lg4	Lg5	Lg6	SC1	SC2	SC3	SC4
Staphylinidae *-continued-*																							
Pseudopsis sagitta Herman [+ Zoo]		0.83	0.17						100						0.17			0.67	0.17	0.17	0.67	0.17	
Quedius criddlei (Casey) [+ Zoo]					100			100				0.14	0.86								0.71	0.29	
Quedius frigidus Smetana [+ Zoo]		100							100									100		100			
Quedius fulvicollis (Stephens) [+ Zoo]			100						100								0.50		0.50		100		
Quedius labradorensis Smetana [+ Zoo]						100																	
Quedius plagiatus Mannerheim [++ Zoo]	0.11		0.07	0.11	0.67	0.04		0.78	0.19	0.11	0.22	0.11	0.33		0.04	0.15					0.67	0.19	0.11
Quedius rusticus Smetana [+ Zoo]		0.50				0.50			0.50										0.50		0.50		
Quedius velox Smetana [+ Zoo]		0.02		0.08	0.72	0.18		0.80	0.02	0.18	0.20	0.23	0.18						0.02		0.53	0.27	0.02
Scaphium castanipes Kirby [+ Myc]	100								100							100							100
Sepedophilus testaceus (Fabricius) [+ Myc]		100							100							100				100			
Siagonium punctatum LeConte [++ Omn]					0.91	0.09		0.91		0.09	0.36	0.18	0.27								0.64	0.27	
Stenichnus ovipennis (Casey) [++ Zoo]			0.03	0.33	0.64			0.97	0.03	0.12	0.30	0.30	0.24				0.03				0.61	0.39	
Stenus austini Casey [+ Zoo]	0.33	0.67							100								0.67		0.33		0.33	0.33	0.33
Stenus maritimus Motschulsky [+ Zoo]	0.50				0.50			0.50	0.50		0.50								0.50			0.50	0.50
Syntomium confragosum Mäklin [+ Omn]		0.25			0.50	0.25		0.50	0.25		0.50					0.25					0.75		
Tachinus elongatus Gyllenhal [+ Zoo]	0.07			0.07	0.73	0.13		0.80	0.07	0.07	0.13	0.40	0.20				0.07				0.67	0.20	
Tachinus frigidus Erichson [+ Zoo]					100			100		0.50			0.50								100		
Tachinus fumipennis (Say) [+ Zoo]	0.25	0.38	0.13		0.13	0.13		0.13	0.75	0.13					0.25			0.13	0.38	0.25	0.13	0.13	0.38
Tachinus quebecensis Robert [+ Zoo]						100																	
Tachyporus borealis Campbell [+ Zoo]	0.19	0.44	0.31		0.06			0.06	0.94				0.06			0.06	0.19	0.31	0.38	0.25	0.31	0.25	0.19
Stenotrachelidae																							
Cephaloon tenuicorne LeConte [++ Omn?]					0.50	0.50		0.50		0.17	0.17	0.17									0.33	0.17	
Tenebrionidae																							
Neatus n. sp. 1 Steiner* [r ++ Myc]					100			100				100									100		
Platydema americanum (Castelnau & Brullé) [++ Myc]				100				100			100										100		
Scaphidema aeneolum (LeConte) [+ Myc]					100			100			0.50	0.50									100		
Upis ceramboides (Linné) [++ Det]	0.50				0.50			0.50	0.50				0.50		0.50						0.50		0.50
Trogossitidae																							
Ostoma ferruginea (Linné) [++ Myc]	100								100							100							100
Thymalus marginicollis Chevrolat [++ Myc]		0.13		0.38	0.50			0.88	0.13		0.38	0.50			0.13						0.63	0.25	0.13
TOTAL ABUNDANCE‡:	**292**	**631**	**423**	**823**	**2208**	**1142**	**31**	**3103**	**1243**	**1259**	**864**	**488**	**492**	**135**	**451**	**199**	**191**	**168**	**99**	**71**	**2496**	**1262**	**548**

Ecological information given in square brackets, as follows: n= confirmed new species, n? = likely new species (unconfirmed), r= new record for AB, r?= potential new record for AB (needs confirmation); ?= uncertain due to limited taxonomic revision or lack of

key characters for identification; ++= obligately saproxylic, += facultatively saproxylic, -= not saproxylic; Phl= phloeophagous, Xyl= xylophagous, Amb= ambrosia feeder, Myc= mycophagous, Myx= myxomycetophagous, Zoo= zoophagous, Omn= omnivorous or uncertain, Det= detritivorous, Pal= palnyvorous (pollin-feeder), Her= herbivorous, Cop= coprophagous, Nec= necrophagous, SR= also found feeding at sap runs of tree wounds; *name of this wide-ranging species is forthcoming from a revision in prep by W.Steiner (Majka & Johnson 2008); Levels of each factor are abbreviated as: HC= hand collection, FE= funnel extraction, RD= rearing drum, ET= emergence trap, TWT= trunk window trap, FWT= free-hanging window trap; Tr= live tree, Sn= standing dead tree (snag), Lg= fallen dead tree (Log); SC= size class: SC1= diameter ≥7 cm,<16 cm; SC2= diameter ≥16 cm, <25 cm; SC3= diameter ≥25 cm, <34 cm; SC4= diameter ≥34 cm, <43cm; Abundance calculations are proportions of total species abundance within each factor, with shading corresponding to greater relative abundances: ŀFWT (no substrate attachment) accounts for the remainder of species abundances, ψTr (live substrate) and FWT (no substrate) accounts for the remainder of species abundances; ĻTotal excludes abundance of some adult beetles (e.g., Staphylinidae: Aleocharinae, some female Latridiidae: Corticariinae, and some Ptiliidae) as well as larvae, as they were not determined at the species level.