Beetles and trees told me this story

University of Alberta

Fire history, landscape biodiversity and indicators for sustainable management of the boreal mixedwood forest

by

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En mémoire de mon grand-père,

Jacques Bergeron,

pour avoir partagé sa passion des mots et de la nature.

ABSTRACT

I examined the response of invertebrate assemblages to the forest mosaic established by past fire events, and tested the performance of trees as biodiversity surrogates in accurately reflecting relationships between fire history and invertebrate assemblages. Over 80 % of the studied landscape originated from three fire events; 35 % from 1895 (107 years before sampling), 20% from 1877 (125 years before sampling), and 30% from 1837 (165 years before sampling). Less than 8% of the forest originated before the earliest fire detected in 1837. Even in the absence of fire for over a hundred years, sites with different fire history exhibited major differences in beetle composition and diversity. Oldest sites supported the highest richness followed by sites originating from the most recent fire event. Sites originating from the intermediate fire events had the lowest species richness. Furthermore, the relationship between ground beetle assemblages and fire history corresponded to the directional succession shift from hardwoods to conifers described for the mixedwood boreal forest. I found that canopy tree composition was a good indicator of the relationship between fire history and carabid assemblage. However, comparison of biodiversity surrogacy models built from either ground survey of trees or data derived from aerial photography reveals that both confusion among tree species and inaccurate detection and estimation of less common trees species reduced the effectiveness of forest inventories as biodiversity surrogates. Ecosystem classification maps generated from multiple geo-referenced forest attributes performed better as biodiversity surrogates, especially in the detection of crucial old growth habitat. Composition and diversity of three invertebrate taxa (ground beetles, rove beetles, and spiders) were closely correlated to the ecosystem classification map. The use of many taxa improved the sensitivity of the biodiversity indicator to habitat parameters. Pitfall trapping biases were constant among forest types enabling a proper comparison of ground-dwelling invertebrate assemblages between different forests. However, consistent and proper installation of traps is required because catches of some taxa were drastically influenced by placement of the pitfall trap. Considering landscape history in the elaboration of conservation strategies for the extensively managed portion of the boreal forest will foster preservation of biodiversity.

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CHAPTER 1

Introduction

1.1 *Fires and biodiversity*

Boreal forest landscapes have evolved under the influence of natural disturbances such as wildfires and insect outbreaks (Bonan and Shugart 1989, Rowe and Scotter 1973). These natural phenomena maintain a mosaic of habitat associated with the persistence of boreal forest species adapted to such conditions (Danks and Foottit 1989, McCullough et al. 1998). Environmental properties of recently burnt areas are drastically different than those of the surrounding matrix (Pyne et al. 1996) and it is clear that early postfire successional communities are characterized by pioneer and often pyrophilous species (Cobb et al. 2007, Evans 1971, Hutto 1995, Koivula et al. 2006, Rowe 1983, Seaver and Clark 1910). Communities established in the first few decades of secondary succession are also distinct from the surrounding unburnt forest (Buddle et al. 2000, Fox 1983, Holliday 1991), and disparity between communities characteristic of late successional forests with different fires history is well documented for plants, mammals and birds (e.g., Bergeron 2000, DeGrandpré et al. 1993, Fisher and Wilkinson 2005). However, there is little evidence that this situation is also true for invertebrates (Hornberg et al. 1998, Paquin 2008, Segerström 1997, Spence et al. 1999), which comprise the major part of boreal forest biodiversity.

1.2 *Ecosystem management*

The present approach to ecosystem-based management is to plan resource exploitation based on efforts to create a forest mosaic inspired by natural disturbances

(Attiwil 1994, Bergeron et al. 2001, Hunter 1993, Johnson et al. 1998, Spence 2001). This procedure is thought to favor maintenance of native biodiversity that evolved together with these disturbances in managed landscapes (Franklin 1993). This requires basic knowledge of how natural disturbances influence biodiversity, and the development of corresponding landscape indicators that may be used in the planning process (Noss 1990), allowing the implementation of coarse filter approach to biodiversity conservation in managed landscape. Canopy tree species of the boreal mixedwood forest have the potential to be an excellent biodiversity surrogates because occurrence varies with fire history (Bergeron 2000), are generally related to local biodiversity (Work et al. 2004), are easily surveyed using remote sensing, and encompass the measure of a significant natural resource in high demand for industrial exploitation. Aerial photographs are important tools for ecosystem management and have been widely used to estimate stand composition in association with planning forest harvests (Morgan et al. 2010). Development of biodiversity surrogacy models based on these data is however at an early stage. Clearly, inaccurate landscape-level data about forest composition may have cascading effect in the ecological associations modeled, the consequent conservation strategies implemented, and in the final analysis, the efficacy of natural resource management plans (Thompson et al. 2007).

1.3 *Biodiversity*

The use of a wide array of taxa as biodiversity indicators is widely held to yield more accurate representation of the environment, and provide a sensitive indicator of integrity (Jonsson and Jonsell 1999, McGeoch 1998, Spence et al. 1999). Invertebrates are a group of choice for environmental assessment as survey methods yield high numbers of both individuals and species required to statistically quantify biodiversity. Beetles of the family Carabidae (Coleoptera; ground beetles) are well suited as biodiversity indicators in the boreal forest (Rainio and Niemela 2003, Work et al. 2008), given the well developed taxonomic resources to facilitate species-level identification, the simplicity of sampling them, and the microscale at which carabids interact with their environment rendering them sensitive to local change. In addition, epigaeic arthropods, including ground beetles, rove beetles and ground-dwelling spiders, are easily sampled using pitfall traps (Marshall et al. 1994). These taxa are also all known to respond to changes in forest structure and composition (Buddle et al. 2006, Work et al 2004). In this thesis, I describe the fire history of the EMEND landscape in northwestern Alberta, Canada, and focus on ground beetles and other epigaeics species to explore and test biodiversity surrogacy models and develop a base to implement the coarse filter approach to biodiversity conservation..

1.4 *Thesis organization*

In this dissertation, I present four chapters to demonstrate that biodiversity responds to the forest mosaic established by wildfires beyond the early successional stages, and that indicators of this process can be found in forest surveys developed for natural resource exploitation. I tie these ideas together in a fift synthesis and concluding chapter. All field work for this research was located at the EMEND (Ecological Management Emulating Natural Disturbance) study site in northwestern Alberta, about 90 km northwest of Peace River (Fig.1). In this introductory chapter, I explain the rationale supporting this research and present the structure of the dissertation. The second chapter describes the landscape relationship among fire history, forest structure and composition, and ground-beetle assemblages. The third chapter examines in detail the landscape patterns of association between ground-beetle assemblages and forest composition as established by fire. In the fourth chapter, I assess the performance of forest inventories and ecological land classification maps in depicting forest composition attributes that are related to ground beetle biodiversity. The fifth chapter explores whether the ecological patterns observed between biodiversity surrogates and ground beetles is applicable to a broader range of invertebrate taxa including rove beetles and epigaeic spiders. This chapter also tests the efficiency of pitfall trap sampling in different forest types. Finally, in the fifth chapter, I discuss the management implications of this work and indicate future research that may improve our understanding of this system and allow us to include biodiversity in a more dynamic approach to forest land management.

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Figure 1.1. Map of Canada showing the location of the EMEND study site in Alberta.

CHAPTER 2

Recent fire history and landscape patterns of ground beetle (Coleoptera: Carabidae) assemblages in mature boreal forest of northwestern Alberta, Canada

2.1 Introduction

Boreal forest landscapes have naturally evolved under the strong influence of wildfires (Johnson 1992, Payette 1992, Goldammer & Furyaev 1996). In fact, studies of fire history demonstrate that wildfires regulate the distribution of structural and compositional elements in this ecosystem (Heinselman 1973, Stokes and Dietereich 1980, Niklasson and Grandström 2000, Bergeron 2000, Basquil et al. 2001). As such, it is thought that the biodiversity characteristic of these forests is adapted to the conditions created by fires (Danks and Foottit 1989) and that fire regimes contribute to the maintenance of landscape scale biodiversity (Nilsson et al. 2001, Grandstrom 2001). Following this reasoning, it has been put forward that natural resource extraction should be planned to establish landscape mosaics inspired by fire so as to decrease the overall deleterious effect of anthropogenic activities on the biodiversity of managed woodlands (Hunter 1993, Attiwil 1994, Spence 2001, Johnson et al. 1998, Bergeron et al. 2001). Despite the rising implementation of natural disturbance paradigm in modern forestry, there is little direct evidence that biodiversity actually responds to the forest mosaic as established by wildfires, especially beyond the early stages of forest succession.

Scientific studies linking different post fire successional stages to conservation of the boreal fauna are generally implemented using a spatial chronosequence of stand types representing a theoretical succession pathway. For example, Work et al. (2004) and Jacobs et al. (2008) found strong effects of successional stage on the landscape assemblages of ground-dwelling beetles, but these and other studies have been based on the assumption that there is a directional shift from deciduous to coniferous dominated composition at all sites as the forest matures. European studies show that absence of fire for c. 200 years is associated with development of localized old forest, and faunal inventories of these sites support the hypothesis that such sites have a unique fauna, high in biological diversity, and including many rare and threatened species (Segerström 1997, Hornberg et al. 1998). Paquin (2008) provides the best evidence from North America directly linking the longer term fire history of the boreal forest to its faunal diversity. However, most studies have been implemented at either very local sites or along a defined chronosequence, therefore limiting the application of these findings to a landscape context.

Gandhi et al. (2001) found that fire residuals within recent burns (15 and 30 years) held ground-beetle (Carabidae) assemblages similar to surrounding mature and old growth forest. They suggested, based on tree age, that their fire residuals were repeatedly ’skipped’ by successive wildfires, introducing a landscape context for these dynamics. We now understand that despite the stochastic nature of fire regimes and annual areas burnt (Armstrong 1999), the occurrence of late successional forest attributes often result from landscape features that act as ‘fire breaks’ and lengthen the fire cycle locally (Cyr et al. 2005, 2007). In this context, fire residuals should not only support the fauna of mature forests while the surrounding burnt matrix regenerates, but these old growth elements may also exhibit a fauna distinct from that of the mature forest. Such local faunas may require structural and compositional elements developed by long-term absence of fire.

Despite the aforementioned evidence that local variation in fire regime contributes to the maintenance of old forest on the landscape, and that such habitats support a distinct fauna, no data known to us link the landscape context of fire history, stand structure and biological diversity. The main objective of the present study is to determine if the landscape fauna of ground beetles responds to local forest structure and composition as established by past fire events in a mosaic of mature and old growth forest. In this chapter, I focus on the age and composition of the forest and put it in a landscape context using a time-since-fire map. We also included drainage as environmental parameter because it is known to affect ground beetles (Lovei and Sunderland 1996) and affects fire history.

2.2 Methods

2.2.1 *Study area*

The study was conducted at the EMEND (Ecosystem Management Emulating Natural Disturbance; see Spence et al. 1999) research site located in the lower foothills ecoregion of the mixedwood boreal forest (Beckingham et al. 1996) in northwestern Alberta. The dominant tree species are *Picea glauca* (Moench), *Populus tremuloides* Michx. and *Populus balsamifera* L. on well drained sites and *Picea mariana* (Mill.) and

Larix laricina (Du Roi) K. Koch on poorly drained sites. The elevation varies between 677 and 880 meters in a catena-like topography of rolling hills, mostly consisting of morainal deposits with extensive valleys and depressions covered by lacustrine and organic deposits (Alberta Environmental Protection 1994).

2.2.2 *Sampling design*

In order to focus on local co-variation in fire history, forest composition and carabid assemblages, we established an intensive systematic grid of 200 sampling sites covering 84 km^2 of Boreal Mixedwood forest in 2002. At every site, we simultaneously assessed fire history, forest composition, and the carabid community. Sites were located roughly 640 m apart, with grid points adjusted locally within the nearest stand to include trees over 5 cm of diameter at breast height (dbh) and to be at least 40 m from any anthropogenic disturbance. This procedure allowed us to focus on mature and old forest, and minimize the edge effects on the catches of ground beetles. One potential sampling site was omitted from the grid because relocation of this site due to large harvested areas would have placed it within 40 m of the closest neighbouring site.

2.2.3 *Tree species composition*

We located a center point (corresponding to the predefined coordinates of our regular sampling grid) using GPS (Geographic Positioning System, GARMIN76 ™) and around this point, recorded the species identity [based on Moss (1983)] and diameter at breast height (dbh) of the 25 closest trees at every site. We also recorded these two measurements for one stem, within a 50 m radius, of any additional tree species not detected among the 25 regular sample trees. This allowed us to include tree species that might also contribute to explaining variation in ground beetle assemblages at each sampled site. This also allowed us to target the oldest tree of every species present locally. In order to obtain an appropriate measure that represents the influence of tree species at a particular site, we calculated the percent basal area for each species in every site as described in Bergeron et al. (2011).

2.2.4 *Fire history*

As a preliminary assessment in reconstructing fire history, we searched the Alberta historical fire database (ASRD 2010) for information relevant to our site. Only one fire event was recorded on our study site since records began in 1931. This 1995 fire was detected and extinguished by fire fighting crews before it burnt one hectare. As no sampling points were laid out within the burnt perimeter of this fire, and our study focuses on mature and old forest, we ignored this fire in further analysis.

We used a combination of fire-scarred trees and age structure (Bergeron and Charron 2010) to determine time since fire at all sites. This method combines the temporal resolution of fire scar events (Arno and Sneck 1977) and the spatial resolution of age distribution (Bergeron and Charron 2010). In every site, we used a chainsaw to sample a complete horizontal cross section (disc) at the root collar, as well as in the middle of the trunk, of the largest dominant tree of every species. Presence of macro-charcoal at the surface of the forest floor was recorded. Presence of such macro-charcoal in the forest floor was determined using two 0.5 X 0.5 m soil pits dug at 10 m east and west of the plot center, and down to the mineral soil. Furthermore, we established a system of 190 transects linking every site and covering 120 km along which we actively searched for fire scarred trees. We recorded a GPS position for every scar following Arno and Sneck (1977) and McBride (1983). We sampled one disc at the root collar for each scarred tree as described above for tree cross sections. Before counting the annual growth rings, all cross sections were polished using sanding paper of gradually increasing grit from 60 to 400 or 600, depending on what was required for accurate ring counts.

We counted the rings along two radii for each disc, and visually cross-dated (using the skeleton plot method, Stokes 1980) the four radii of each tree in order to accurately age the innermost ring of the basal disc. This age was considered as the year of tree establishment. For discs with fire scars, we counted and cross-dated the rings along three radii for each discs. We established a date for each fire scar encountered on living trees. We then used the fire rings as a ‘pointer year’ combined with the skeleton plot method to cross-date the fire events recorded on fire scarred trees that were dead at time of sampling.

2.2.5 *Drainage*

Soil drainage was measured in the same soil pits used to sample charcoal. A twelve-level classification scheme modified from Beckingham et al. (1996) was used to cathegorize dainage. The classification scheme varied from very rapidly drained to very poorly drained soils and considered height of the water table, water retention, soil texture, organic matter content, and soil type. We recorded an intermediate value when a site exhibited characteristics of two adjacent drainage categories.

2.2.6 *Ground beetle assemblages*

During the growing season immediately following the survey of the sites described above (2003), we used 3 pitfall traps at each site to sample ground beetle assemblages. A trap consisted of a plastic cup with an opening diameter of 11 cm and a depth of 13 cm, containing a plastic inner cup and a wooden roof supported over the trap by two nails (Spence and Niemelä 1994). Traps were installed 15 m from the center of the site at 0°, 120° and 240°. Silicate-free ethylene glycol (GM Dex-Cool®) in the inner cup was used as a killing agent and preservative. Traps were open from the second week of May until the third week of August for a maximum of 99 potential sampling days. This spanned most of the frost-free period. Trap contents were collected 4 times over this period. Five sites established in 2002 were harvested during the following winter and therefore were omitted for ground-beetle sampling. All carabid specimens were identified to the species level according to Lindroth (1961, 1963, 1966, 1968, 1969), with nomenclature following Bousquet (1991). Voucher specimens are deposited in the Spence laboratory collection and the Strickland Museum of Entomology at the University of Alberta.

2.2.7 *Statistical analysis*

As a first step in understanding the fire history of our landscape, we compiled the dates of fire events in a master fire chronology following Arno and Sneck (1977). We assumed that the age of the oldest tree at each site reflected the origin of the stand. We thus constructed a temporal stand origin distribution histogram with five-year intervals for the period between 1700-2000, and overlaid this distribution on the master fire chronology. We used the fire chronology and the pulses in tree recruitment to define 6 cohorts of sites originating from different fire or other disturbance events.

In order to present our fire history in a landscape context, and better understand the fire regime of the area, we produced a time-since-fire map (e.g., Heinselman 1973) of the EMEND study area by plotting the spatial distribution of the 6 cohorts previously determined. We included elevation contours and water bodies as determined by the Alberta Vegetation Inventory (http://www.srd.alberta.ca/MapsPhotosPublications/Maps/ResourceDataProductCatalogue/ForestVegetationInventories.aspx) to point out the potential fire breaks.

To evaluate the effect of fire history on the species richness of ground beetles, we plotted an individual based rarefaction curve (Simberloff 1979) for each of the 6 site cohorts of similar stand origin. For this analysis we combined the beetle samples from the two oldest cohorts because the number of individual beetles sampled from each was insufficient to generate an inflection in the rarefaction curve. This analysis was calculated using the function “rarefaction” (Jacobs 2006) in the R statistical package (R development core team 2010), and was based on the raw data.

Beetle samples from the three traps at each site were pooled and divided by the total number of effective trapping days to standardize for sampling effort. Samples from traps not operating at time of sample collection (disturbed by predators or flooded) were excluded from further analysis.

We performed a non-metric multidimentional scaling (NMS) ordination of 194 sites based on the standardized abundance of the beetle species in order to visualize how the fire history was related to the composition of ground beetle assemblages on the landscape. We used the Bray-Curtis dissimilarity index to build the distance matrix and chose the highest number of dimensions providing a reduction of five in the stress (McCune and Grace 2002). The NMS was calculated using a random start configuration, with a maximum of 20 iterations on the real data. We calculated centroids to represent average location of every cohort position in the ordination space. Centroids for the 13 most abundant beetle species, all the tree species, and each drainage class were also calculated and projected on the ordination diagram. Contribution of each site to centroid calculation for the beetles and the trees was weighted by the standardized abundance (or relative abundance in case of trees) of this species in each site. Calculations of the ordination and the centroids were performed using the R package vegan (Oksanen et al. 2011).

2.3 Results:

2.3.1 *Fire history*

We dated eight fire events from 105 fire scars distributed on 67 trees and determined the age of 405 trees. The age class distribution of the oldest tree in each site together with the fire chronology (Fig. 2.1) reveals that at least three of these fires were at the origin of the present forest mosaic. Fire events of 1895, 1877, and 1837 correspond to early pulses in tree recruitment on the EMEND landscape.

We divided the age distribution of sites in 6 cohorts, based on documented fire events and the pattern of tree recruitment illustrated by the density function of Fig. 2.1. The most recent cohort of sites is sparsely distributed over less than ten percent of the landscape (Fig. 2.2), and macrocharcoal was found at only 50% of these youngest fire sites (Table 2.1). A low number of fire scars are associated with the two fire events (1913 and 1917, 2 and 1 scars respectively) potentially at the origin of this cohort (Fig. 2.1) and they were spatially localized.

Over 34 % of the total number of sites originated in the second-most recent cohort (Table 2.1) and the pulse of tree recruitment corresponds to what appears to have been a large fire in 1895 recorded on 34 scars (Fig. 2.1). Most of these sites are spatially contiguous and are roughly distributed in two patches; one embracing the southwest corner of the landscape and one on the north side (Fig. 2.2). Macro-charcoal was found in 84% of the sites originating in this cohort (Table 2.1).

The third cohort originated from a fire (1877) that burnt 18 years before the fire of 1895 (Fig. 2.1), and 20 % of the sites were recruited over this period (Table 2.1). A high proportion (90%) of sites in this cohort contained macro-charcoal (Table 2.1) and the sites are contiguously grouped outside of the patches originating in the previous cohort (Fig. 2.2).

Sites originating in a fourth cohort are also spatially contiguous but patches are separated by sites originating from the fires of 1877 (third cohort) and 1895 (second cohort, Fig. 2.2). The two fires recorded during this recruitment period (1864 and 1854) with the highest number of fire scars (7 and 4 respectively) do not correspond to an observable pulse in tree recruitment. As the fire scarred trees for these two events were recorded on the limit of our study area, we conclude that the associated fires burt mainly outside of our study area. We therefore attribute the origin of this fourth cohort of sites to the fire event of 1837 recorded on two scars and corresponding to a tree recruitment pulse

(Fig. 2.1). Thirty percent of all sites considered here originated during this period and most of them (81%) contained macro-charcoal (Table 2.1).

Despite the absence of previous fire, Fig. 2.1 shows a tree recruitment pulse between 1805 and 1825. Macro-charcoal was found in a high proportion of the sites associated with trees of this age (82%, Table 2.1) and we attribute these sites to a fifth cohort. These sites, representing 5.5% of the total number of sites, are dispersed in the patches of sites originating from the 1837 fire (Fig. 2.2).

The oldest, sixth cohort, has originated between 1710 and 1805 (Fig. 2.1) and includes only 2.5% percent of the sites. Macro-charcoal was found in a low proportion of these sites (40%, Table 2.1), which are localized on the east side of the study landcape, between the two patches created by the fire in 1895, and neighboring sites originating from older fires (Fig. 2.1).

2.3.2 *Fire history and ground beetle assemblages*

Overall, 9776 ground-beetles representing 41 species were collected across the 194 sites (see Bergeron et al. *in press* for a detailed list). The two oldest cohorts identified in this study (between 177 and 300 years old at time of sampling) supported a higher species richness of carabid beetles than the younger forest stands when adjusted for the number of individuals by rarefaction (Fig. 2.3), as is required to interpret diversity measures calculated from unequal sample size (Buddle 2005). The sites originating from the 1895 fire (second cohort) had the second highest richness, followed by the sites from the first cohort. The sites originating from the 1877 and 1837 fires (third and fourth cohort) supported the lowest species richness.

NMS ordination of the beetle data provided a two dimensional solution with a stress of 15.01. Projection of centroids for each cohort revealed that the two oldest and the youngest cohorts were separated from the other stand cohorts along the first axis (Fig. 2.4). They are positioned in the third quadrant and are clearly associated with the centroids for the beetle species *Platynus mannerheimii* Dejean and *Agonum gratiosum* Mannerheim and for the larch tree (*Larix laricina*). Along the first axis, they also grouped close to the centroids for black spruce (*Picea mariana*) and *Pterostichus punctatissimus* (Randall) and are associated with very wet habitats with high values for drainage class (Fig. 2.4).

The three other cohorts of sites includes over 80% of all the sites (Table 2.1) and are distributed on the positive side of the first axis, with the centroids for dry and mesic drainage classes and numerous beetle and tree species. Fig. 2.4 shows a slight dispersion of these three cohorts along the y-axis, the centroid of the second cohort (1897 fire) being pulled toward negative values, together with the centroids for aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*). The centroids for the cohorts originating from the fire events of 1877 and 1837 are closer to the centroids for white spruce (*Picea glauca*) and balsam fir (*Abies balsamea* (L.) Mill.) along the y-axis.

2.4 Discussion

Old forest patches that have escaped fire over a long period of time (> 175 years) support a dramatically distinct (Fig. 2.4) and species-rich (Fig. 2.3) ground beetle assemblage compared to the surrounding matrix of pyrogenic mature forest. Paquin (2008), who characterized the ground beetle succession along a spatial chronosequence of black spruce sites established by fire also found a higher species richness in the oldest forest. Liebherr and Mahar (1979) suggest that high structural diversity encountered in such forest stands contributes to the high diversity of the fauna inhabiting these sites. Hornberg et al. (1998) propose that fire-free refugia nested in landscapes influenced by recurrent fires have the opportunity to develop an uncommon age class distribution characteristic of constant tree mortality and recruitment. This in turn favors the accumulation of dead wood over long periods of time and together with the slow decomposition rate at such wet sites, promotes development of a complex microscale mosaic of highly diverse microhabitats.

In our study, we denoted two species (*P. mannerheimii* and *A. gratiosum*) associated with forest patches older than 177 years old (Fig. 2.4). Interestingly, Paquin (2008) also found that *P. mannerheimii* was characteristic of forest older than 177 years old in the black spruce forest of eastern Canada. Despite the known affinity of this species for old forest (Niemelä 1997), its relation with deadwood is unclear (Biström and Väisänen 1988), even though the complex nature of the soil substrate is thought to contribute to the local maintenance of populations of this species (Niemelä 1987). *A. gratiosum* is also characteristic of wet productive lowlands (Larochelle and Lariviere 2003). In fact, these two species grouped together with high drainage classes (indicative of wet areas) and the centroid for larch, in the third quadrant of our ordination (Fig. 2.4) graphically indicate this association. In the lower foothills ecoregion, larch and black spruce typically occurs on wet sites and larch is especially indicative of high nutrient availability (Beckhingam et al. 1996). Our study demonstrates that this type of forest is prone to develop into old growth stage, likely because it burns infrequently.

Curiously, the centroid for the youngest cohort of sites also grouped in the third quadrant together with the two oldest cohorts (Fig. 2.4). The low occurrence of macro-charcoal in these sites (Table 2.1), their sparse distribution on the landscape (Fig. 2.2) and the low number of fire scars found for the most recent fires (Fig. 2.1) suggest that the age of the oldest tree may not reflect the true fire origin of these sites. It is possible, for example, that some of the forest at these sites originated from a previous fire event, but that regeneration was delayed by adverse conditions such as high water table or discontinuous permafrost. As the centroid of this cohort is close to centroids for high drainage classes (Fig. 2.4), it is also possible that flood events contributed to the origin of these sites (e.g, Bradshaw and Zackrisson 2009), or that these sites have escaped high-intensity fire for a long period of time and that senescence of older trees together with continuous recruitment of young stems, a dynamic characteristic of old forest (Payette 2010), prevented us from finding living trees that reflected the true origin of these stands (see Bergeron et al. 2001 and 2004 for similar cases). Whatever the historical basis, our results indicate that the invertebrate fauna inhabiting old forests on the EMEND landscape have affinities for hydric forest habitats.

Because the highest proportion of sites originated from the 1895 fire event (Fig. 2.1), we collected more specimens and species of ground beetle in stands of this cohort (Fig. 2.3). However, even after correction for the number of individuals sampled, this cohort still exhibited a much higher species richness than did the two older pyrogenic cohorts of 1877 and 1837 (Fig. 2.3). Composition of early post fire succession in the boreal mixedwood forest is quite variable with a high proportion of aspen dominated stands but also including coniferous dominated stands (Bergeron 2000). As this postfire environment matures, the proportion of conifers increases and the forest that was established within the perimeter of the fire becomes more homogeneous as a whole. Therefore, as the forest mature, the deciduous component is driven out of the system decreasing the diversity of habitat types available for biodiversity in later successional stages. This dynamic may contribute to our finding that the cohort originating from the most recent widespread fire supported higher carabid species richness than the cohorts of stands originating from older fires.

In support of the above argument, we also note that the centroid for the pyrogenic cohort of 1895 is located close to the centroid for aspen and many beetle species on the ordination of Fig. 2.4, and that the centroids for the older pyrogenic cohorts of 1877 and 1837 are closer to the white spruce centroid. These results must be interpreted carefully because we actually did encounter aspen dominated stands that originated from the 1837 fire event. Although the general theory predicts that proportion of conifer in the mixedwood forest will increase with time since fire (Bergeron 2000), local processes dictate the development of each stand (Oliver and Larsen 1996) and a high variability of successional pathways is encountered within a single fire perimeter. For example, it has been demonstrated that seed tree proximity is a major determinant of white spruce regeneration establishment (Solarik et al. 2010).

Despite the concordance of theory about mixedwood succesion with our beetle data, forest originating from the 1877 fire event only had 20 more years of evolution than the youngest pyrogenic cohort of 1895. However, it is more similar in beetle species richness and composition to the pyrogenic cohort originating from the 1837 fire event which occurred 40 years before (Figs. 2.3 and 2.4). It is possible that an event such as insect defoliation that I detected in tree rings initiated a sudden change in the forest structure making it more similar to an older successional stage. However, I believe that the spatial pattern of past fire events on our landscape may better explain the differences in beetle assemblages. The fire of 1895 burnt two distinct and relatively large patches, but seems to have skipped or burned more mildly the central and southwestern portion of our study landscape where the evidence of the two previous fires is still detectable (Fig. 2.2). The portion of the landscape burnt by this latest fire event may have fostered high heterogeneity in regeneration that included both deciduous and coniferous stands being within the perimeter immediately post-fire. The portion of the landscape not burnt by this latest fire event may have supported conditions that favored the establishment of mostly coniferous forest. Therefore, the ground beetle diversity and composition of the cohort originating from the 1877 fire is closer to that of the cohort originating from the 1837 fire than that originating from the 1897 fire (Fig. 2.3 and 2.4).

The presence of macro-charcoal in 80 % of the sites indicates that most of the landscape is of pyrogenic origin (Table 2.1). However, sites that are over 177 years old are always found nearby to older forest that did not burn in the most recent fire of 1897. We suggest that although extreme fire weather may allow a fire to spread across the whole landscape (Wein 1983), conditions in fire behavior and location of natural fire breaks may exclude the fires from certain sites, and these have higher probability of developing into old stands. Cyr et al. 2007 for example found that south facing slopes burn three times more frequently than the average site on their study landscape. Similarly, the proximity of fire breaks may also influence the chances of a site reaching older successional stages more quickly (Larsen 1997, Cyr et al. 2005). For example, late successional forest patches found in this study are associated with high drainage classes representing very wet conditions that may stop or lower the intensity of fire resulting in the maintenance of old forest attributes. Furthermore, the topographic and hydrographic features presented in Fig. 2.2 include north facing slopes, confluence of streams, and drainage headwalls, all of which have potential to slow or stop the propagation of forest fires (Camp et al. 1996).

Our study shows that sites hosting beetle species characterized as old forest specialists are small and irregularly distributed on the landscape and this has also been noted by Niemelä et al. (1993). They are characterized by wet soils (Fig. 2.4). Forest managers must pay special attention to wetter sites as they are more likely to host old forest attributes allowing the maintenance of stenotopic species. Fragmentation and continuous exploitation of the surrounding forest may further isolate old forest specialist populations by generally rarefying attributes of old forest available on the landscape, rendering dispersion of old forest specialists quasi impossible. We suggest that natural resources exploitation should try to minimize harvesting in such sites, and should also be planned in order to leave a connected network of these old forest on the landscape.

2.5 Conclusion

Our systematic and simultaneous characterization of fire history, forest composition and ground beetle assemblages over 8400 hectares of boreal mixedwood forest shows that old forest patches that have escaped fires for a long period of time support a distinct and species rich ground beetle assemblages compared to the surrounding matrix of mature forest. These fire refugia provide forest structure and composition different from those that exist under a regime of recurrent fires, and the species associated with such old forests need these conditions to thrive. Of special interest, we found that old forest inhabitants are well adapted to hydric conditions and that flooding and high soil moisture may be a characteristic of old forest. Understanding the landscape context in which these old forest develop is of upmost importance because the accurate detection, localization and estimation of the area of these patches on a landscape are required to dynamically include them in forest management planning.

My study demonstrates that *Platynus mannerheimii* is an old forest specialist in Alberta, as denoted in one other scientific study conducted in eastern Canada. In Europe, this species is considered in many countries as threatened because forest exploitation and associated peatland drainage eliminated most of its preferred habitat. A better understanding of the local variation in fire regime and application of precautionary principle in forested land management may help us to avoid such a situation and save other old growth species from extirpation.

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Table 2.1. Number of sites (n sites), proportion of total sites (% total sites), and proportion of sites with macrocharcoal (% char) for each cohort of stand origin.

Cohort	Year of origin	n sites	% total sites	% char
1	1910-1939	18	9.6	50
2	1895-1909	69	35	84
3	1875-1894	40	20.1	90
4	1835-1874	56	28.1	81
5	1805-1834	11	5.6	82
6	1710-1805	5	2.5	40
Total	1710-1939	199	100	80

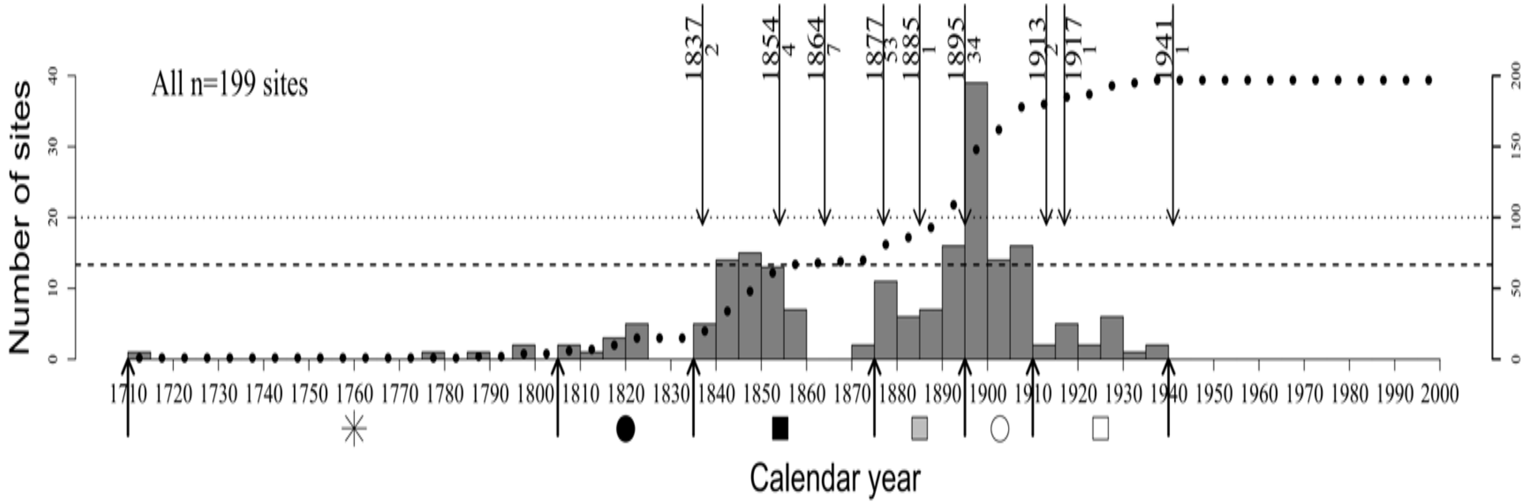

Figure 2.1. Number of sites in each five year period between 1710 and 2000 AC where the oldest tree originated. The top down arrows represent the fire events with the date and the number of scars associated. The bottom up arrows represent the limit of each period of recruitment. The dotted curve shows the density function of site accumulation, with the horizontal dotted line representing 50 % and the dashed line representing 33 %. Symbols below the x axis identify the recruitment cohort on all other figures.

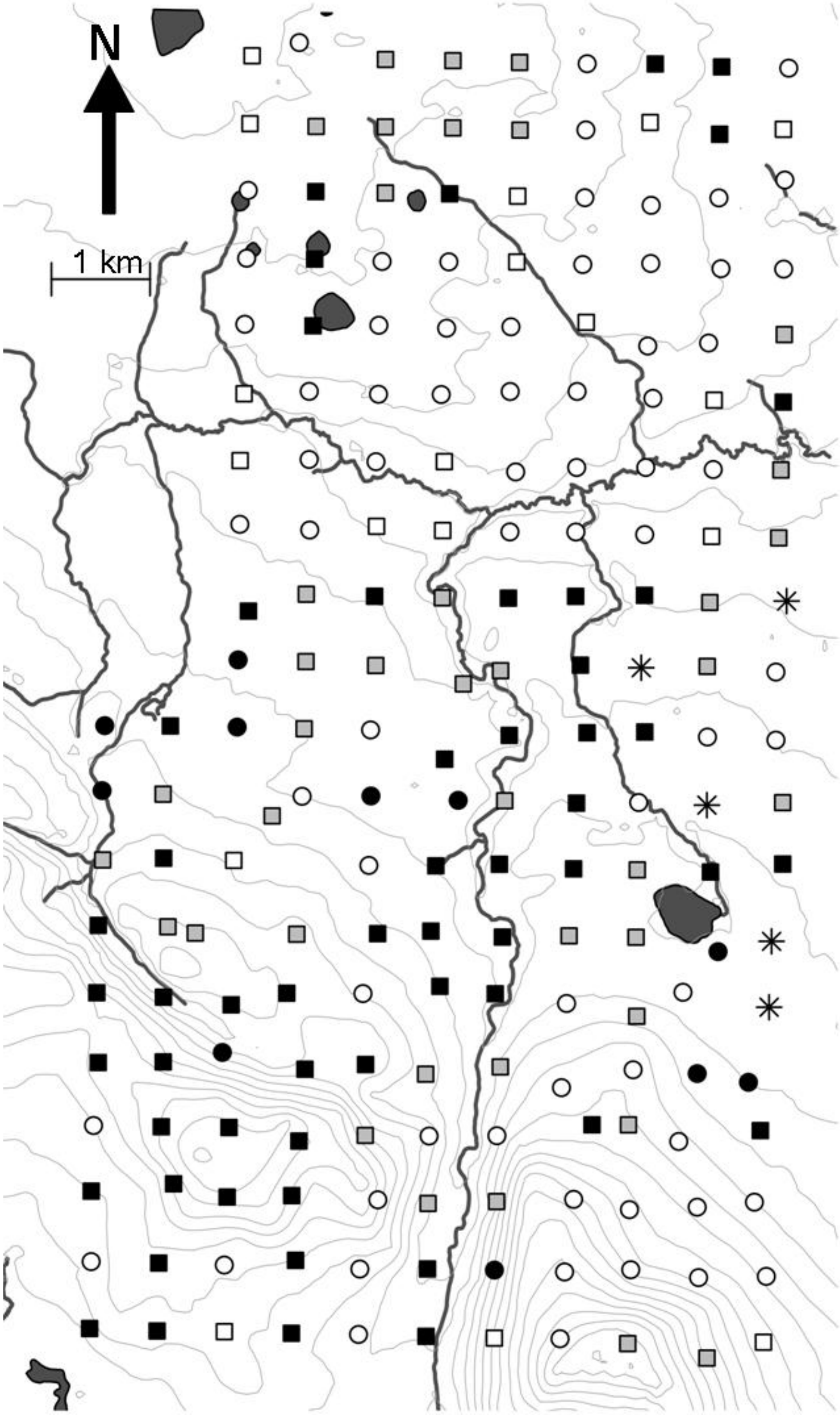

Figure 2.2. Time since fire map of the study landscape. Elevation contours for each 5 m interval are in light grey and water features in dark grey. The symbols for each site represent the different cohort of recruitment presented in Fig.2.1.

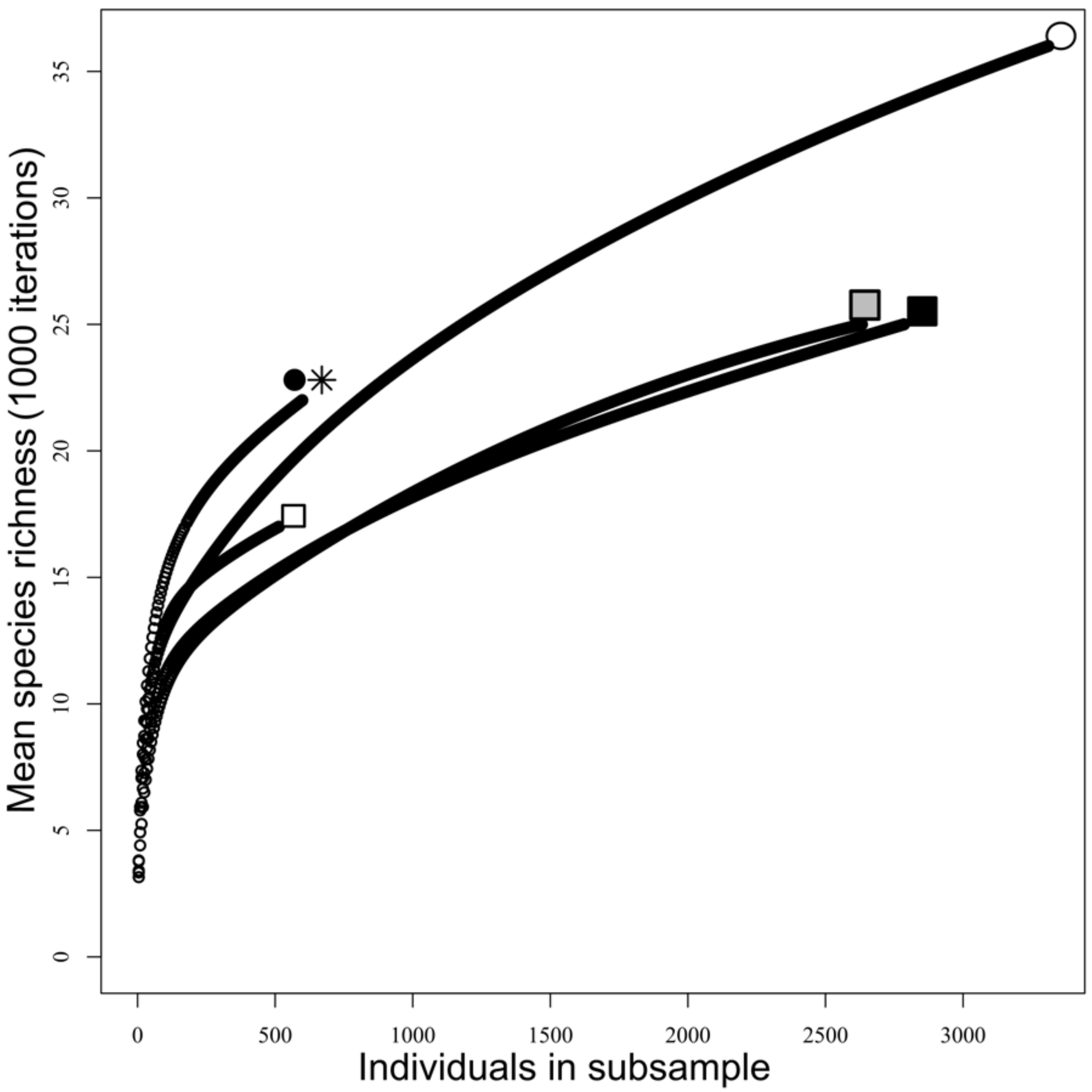

Figure 2.3. Rarefaction curves for the beetle specimens associated to each recruitment cohort of Fig.1. Beetle sampled from the two oldest cohorts were combined in order to obtain an inflection in the rarefaction curve. Cohort symbols as in Fig.2.1.

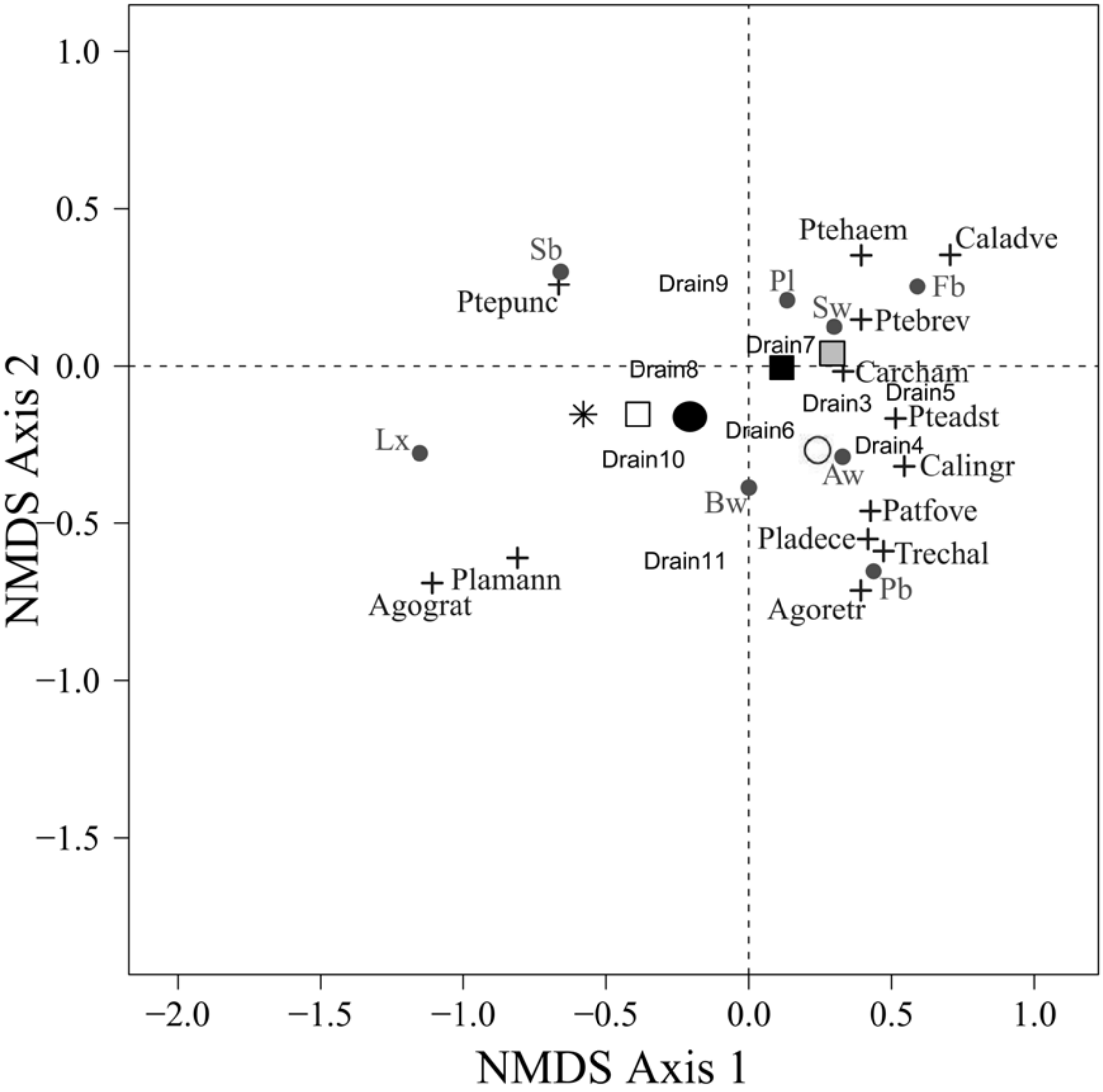

Figure 2.4. Non metric multidimentional scalling ordination of the 194 sites. The stress is 15.1 and the centroids for each cohorts are represented using the same symbols as Fig.2.1. Centroids for tree species are grey dots, centroids for the beetle species are black crosses, and centroids for the drainage classes are illustrated with text. The abbreviations for beetles are as follow: Agograt: *Agonum gratiosum*, Agoretr: *Agonum retractum*, Caladve: *Calathus advena*, Calingr: *Calathus ingratus*, Carcham: *Carabus chamissonis*, Patfove: *Patrobus foveocollis*, Pladece: *Platynus decentis*, Plamann: *Platynus mannerheimmi*, Pteads: *Pterostichus adstrictus*, Ptebrev: *Pterostichus brevicornis*, Ptepunc: *Pterostichus punctatissimus*, Stehaem: *Stereocerus haematopus*, Trechal: *Trechus chalybeus*. Abbreviations for the tree species are; Aw: *Populus tremuloides*, Fb: *Abies balsamea*, Lx: *Larix laricina*, Pb: *Populus balsamifera*, Sb: *Picea mariana*, and Sw: *Picea glauca*.

CHAPTER 3

Landscape patterns of species-level association between ground-beetles (Coleoptera: Carabidae) and overstory trees in boreal forests of western Canada

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3.1 Introduction

Although some ground-beetle species are recognized as forest habitat specialists (Lindroth 1961-69, Niemelä et al. 1992), the potential influence of ecological linkage between carabids and particular tree species has not been much studied. Adult or larval carabids may use deadwood as shelter, oviposition or overwintering sites (Goulet 1974). They may feed on prey or vegetative items that are associated with trees and the related forest floor (e.g., Koivula et al. 1992), or use particular understory forest plants as food or shelter. Some carabid species may require a certain amount of shade or specific forest floor conditions that are best provided by certain tree species. Ground-beetle assemblages are known to vary generally with stand canopy cover (Niemelä et al. 1992, Pearce et al. 2003, Gandhi et al. 2008, Work et al. 2010), and it is frequently assumed that this reflects strong relationships between tree cover and local edaphic conditions (Perry et al. 2008). Nonetheless, connections of these patterns of association to the indirect ecological interactions mentioned above remain largely undescribed. We do not know much about the specific elements of forest stands that affect the structure of carabid assemblages.

Associations between forest composition and ground-beetle species could involve a host of indirect processes, reflecting the ecological interactions of numerous forest ecosystem components (e.g., Allegro and Sciaky 2003). In a practical sense, modelling patterns of association between specific tree species and ground-beetles would reflect a more restricted subset of these processes but still include the state of many biotic and abiotic elements that are difficult or impossible to observe directly. Beetles of the family Carabidae are a group of choice for forest health assessment at local scales (Work et al. 2008), given the well developed taxonomic resources to facilitate species-level identification, the simplicity of sampling them, the fact that suitable habitat (i.e., the litter and upper soil layers) is not removed by forest harvest, and the microscale at which carabids interact with their environment making them sensitive indicators of change. Understanding their associations with particular trees species could increase their usefulness as indicators of human impact on forest landscapes. More importantly, as is our focus here, if such relationships between carabid and tree species can be defined, commonly available data about forest inventories could provide surrogates for at least this element of biodiversity. This, in turn, would be quite valuable in the context of monitoring requirements associated with forest certification and sustainable forest management.

As it is impossible to appropriately assess biodiversity of entire forested landscapes, implementation of practical conservation strategies must be based to some extent on biodiversity surrogates (Spence et al. 2008). Trees are easier to survey over large areas than are most of the small and often cryptic organisms that constitute the majority of biodiversity. Thus, trees have the potential to be excellent biodiversity surrogates for forest land, if their spatial arrangement shows concomitant variation with that of other living organisms. In fact, tight associations between tree and beetle species are central to the first well known scientifically based estimate of the global number of insect species (Erwin 1982) and community structure of herbivorous arthropods is well known to differ among tree species (Southwood et al. 1982). Knowing relationships between tree species cover and the ground-beetle community living in a forest may support useful broad-scale characterization of biodiversity and ecosystem function based on simple elaboration of tree species distribution. Mapping tree species distributions is easily achieved via remote sensing. Knowledge of relationships between these distributions and biodiversity could prompt more effective and efficient conservation efforts over wide areas by ensuring maintenance of suitable volumes of non-commercial and rare tree species on managed landscapes.

In the boreal forest, studies of carabid-tree relationships have been mainly based on stand-level categorization of canopy cover (e.g. conifer vs deciduous or spruce dominated vs aspen dominated) (e.g. Niemela et al. 1992, Pearce et al. 2003, Jacobs et al. 2008, Work et al. 2010) and thus do not consider the individual contribution of each tree species present. We hypothesize that many insects, including ground-beetles, perceive the forested landscape as a combination of multiple spatial gradients that supply the resources they require. As such, we predict that the structure of carabid assemblages should change along a forest transect in relation to the relative importance of every tree species included in providing resources or fostering conditions used by the beetles. In this context, ground-beetle assemblages might not be best viewed as Clementsian entities tightly associated to certain environmental conditions, but rather as one big Gleasonian community in which species abundances vary independently with environmental conditions. In this study, we assess patterns of association between ground-beetles and mature tree species on a northern forested landscape level using a systematic sampling design.

3.2 Methods

3.2.1 *Study area*

The study was conducted at the EMEND (Ecosystem Management Emulating Natural Disturbance) research site in the boreal mixedwood forest of northwestern Alberta, Canada. The approximate project centre is at 56° 46' 13" N and 118° 22' 28" W, ~90 km northwest of Peace River, (*see* Work et al. 2004 for the location of the site on Alberta map). The elevation varies between 677 and 880 m asl. The forest is a varying mixture of *Picea glauca* (Moench), *Populus tremuloides* Michx., *Populus balsamifera* L., combined with *Picea mariana* (Mill.) BSP and *Larix laricina* (Du Roi) K. Kock in wetter sites, with occasional *Abies balsamea* (L.) Mill., *Betula papyrifera* Marsh and *Pinus contorta* Loudon, representing the boreal-montane transitional nature of the lower foothill ecoregion. *Viburnum edule* (Michx.) Raf., *Rosa acicularis* Lindl., *Sherpherdia canadensis* (L.) Nutt., *Alnus crispa* (Ait.) Purch, *A. tenufolia* Nutt., and *Ledum groenlandicum* Oeder are common forest understory plants, and open meadows, fens, and bogs sometimes dominated by willow (*Salix* spp.) or alder (*Alnus* spp.) shrubs are interspersed on this typical boreal landscape.

3.2.2 *Sampling design*

In the summer of 2002, a systematic grid of 200 sites covering 84 km^2 (Fig.1) of forested land was established in order to describe landscape patterns of ecological association between ground-beetles and overstory trees. At every site, we recorded diameter at breast height (dbh) and species identity for the 25 stems over 5 cm dbh closest to our sample centre. We also documented the dbh and species of one stem for tree species present within a 50 meters radius but not recorded among the 25 stems encompassed in the original plots. This allowed us to consider the potential influence of proximal tree species on the beetle assemblages that were not included among the 25 stems. Drainage was recorded from two soil pits dug at 10 meters east and west from the plot centre. Drainage was categorized using a system of 11 classes, as modified from Beckingham et al. (1996), to classify sites that showed characteristics of two adjacent classes. In the systematic grid, sites were located approximately 640 m apart. However, grid position of sites was constrained by two conditions: all sites had to be at least 40 meters from any 1) anthropogenic disturbance or 2) natural area without trees larger than 5 cm dbh. These conditions focused our study on possible relationships between the epigaeic fauna and mature forest heterogeneity. As is typical of boreal landscapes, the EMEND site includes wet areas, peatlands and much local variation in forest cover. Therefore, in 57 cases where the above criteria were not met, the actual site location was moved further than 40 meters and placed in the nearest forest stand. Thus, the sampling grid illustrated in Fig. 3.1 is not perfectly regular. Two sites in an extensive harvest block were omitted because relocated sites would have been further from the original gridpoint than the nearest neighboring site.

The following summer (2003), we installed three pitfall traps in each of the same 200 sites (600 traps total). Traps were located at 0º (North), 120º, and 240 º on a circle 15 m in diameter centred on the previously established site. Pitfall traps were a plastic cup (11 cm diameter by 13 cm depth), containing a plastic inner collecting cup and covered by a 14 cm^2 of plywood supported over the trap by two nails (*see* Spence and Niemelä 1994). Traps were operated during the frost-free season (i.e., from early May until the end of August), providing a potential total of 100 trapping days. We also sampled the epigaeic fauna in the two grid sites omitted from tree samples that were located in large harvest blocks and established an extra trapping site in the only naturally burnt forest encountered on the landscape. Four sites established in year 1 were not sampled for beetles because they were harvested over the intervening winter. Hence, we collected beetle data in a total of 197 sites (Fig. 3.1). All beetles from the family Carabidae were identified to the species level using Lindroth (1960-1969). Nomenclature follows Bousquet (1991), and voucher specimens are deposited in the E. H. Strickland Entomological Museum (University of Alberta) in Edmonton, Canada and the Spence Laboratory Collection.

3.2.3 *Statistical analyses*

As a first step in linking within-stand canopy heterogeneity to ground-beetle assemblages, we calculated the relative basal area for each tree species in every site. Basal area is directly related to canopy cover (Spurr 1960) and, thus, appropriately represents the canopy influence of each tree species at a particular site. For each site, beetles from the three traps were pooled and their abundance divided by the sum of effective trapping days. This procedure allowed us to standardize beetle catches in relation to effective sampling effort. Although we report the abundance of beetle species collected in all 197 sites for entomological interest, the following statistical treatments were based only on the 194 grid sites located in forest with mature trees. This allowed us to focus on the effect of canopy heterogeneity on the beetle community.

In order to visualize how the assemblage of ground-beetles was arrayed on the EMEND landscape, we performed a non metric multidimentional scaling (NMS) ordination of 194 sites based on the standardized abundance of the beetle species. We used the Bray-Curtis dissimilarity index to build the distance matrix and chose the highest number of dimensions providing a reduction of five in the stress (McCune and Grace 2002). The NMS was calculated using a random start configuration, with a maximum of 20 iterations on the real data. Initial inspection of the resulting ordination showed that one site was a clear outlier and the ordination was recalculated without this site. This site was located in a small ellipse of trees left in a harvest block and had been disturbed in a similar way as the 3 other sites that had been previously removed from the analysis. For the 16 most abundant beetle species and all the tree species, we calculated centroids to represent average location of the species' position in the ordination space. Contribution of each site to centroid calculation was weighted by the standardized abundance (or relative abundance in case of trees) of this species in each site. The general relation between drainage and ground-beetle assemblage was illustrated by projecting vectors of influence on the ordination diagram.

Beetle assemblage response to forest canopy was more clearly illustrated by plotting the relative basal area of tree species for every site on the beetle ordination diagram. This procedure was undertaken because interesting ecological trends were obscured by the sole use of centroids or vectors. Centroid calculation, vector projection, and ordination were performed using the vegan package (Oksanen et al. 2011) within the R statistical language (R development core team 2010).

3.3 Results

We collected and identified 9,845 individual ground-beetles representing 48 species (Table 1). *Stereocerus haematopus* (Dejean), *Calathus advena* (LeConte) and *Pterostichus adstrictus* Eschscholtz accounted for over 70% of catches, and together with the next seven most abundant species [*Platynus decentis* (Say), *Calathus ingratus* Dejean, *Pterostichus punctatissimus* (Randall), *Agonum retractum* LeConte, *Trechus chalybeus* Dejean, *Patrobus foveocollis* (Eschscholtz), and *Pterostichus brevicornis* (Kirby)], accounted for 95% of the beetle catch. Nine beetle species (*Agonum cupreum* Dejean, *Amara laevipennis* Kirby, *Amara patruelis* Dejean, *Cymindis unicolor* Kirby, *Dyschirius hiemalis* (Bousquet), *Elaphrus clairvillei* Kirby, *Notiophilus semistriatus* Say, *Poecilus lucublandus* (Say) and *Trichocellus mannerheimii* (R.F. Sahlberg)) were trapped only in the 4 disturbed sites.

Among tree species, *P. glauca* was found in the highest number of sites followed by *P. tremuloides*, *P. mariana*, *P. balsamifera*, *A. balsamea*, and *L. laricina* (Table 3.2). *P. glauca* was also the most abundant species, and *P. mariana* was the second most abundant, accounting for twice as many stems as *P. tremuloides*, even if *P.mariana* was found in fewer sites. More modest but still notable numbers of *P. balsamifera, A. balsamea*, and *L. laricina* were encountered on the grid, but these species were found in a more restricted number of sites. *P. contorta* Loudon and *B. papyrifera* Marsh. were found in only 16 and 10 sites respectively and contributed to less than 1% of the total basal area on this landscape.

A two dimensional NMS solution arrayed the carabid assemblages collected from 193 sites in four quadrants (Fig. 3.2) with a stress of 15.1. One third of the sites clustered in the upper right quadrant in which values on both NMS axes were positive. The centroids for *S. haematopus*, *C. advena* and *P. brevicornis* were concentrated in this first quadrant of the ordination diagram, even though these species were captured at a broad range of sites. Centroids for the largest number of abundant species were concentrated in quadrant IV, which included about 25% of the sites. Species in quadrant IV were: *Carabus chamissonis* Fisher von Waldheim, *P. adstrictus*, *C. ingratus*, and with increasingly negative values on axis 2, *P. foveocollis*, *Pterostichus pensylvanicus* LeConte, *P. decentis*, *T. chalybeus*, *A. retractum* and *Agonum sordens* Kirby. Another 25% of the sites were distributed in quadrant II, along with the centroid for *P. punctatissimus* and the vector for increasing wetness of drainage classes. This vector indicates a concentration of sites with poorly drained soils in the second quadrant. Only 15% of the sites were located in the quadrant III along with the centroids for *Agonum gratiosum* (Mannerheim) and *Platynus mannerheimii* (Dejean). The centroid for *Trechus apicalis* Motschulsky was also placed in quadrant III, although sites with *T. apicalis* were also widely distributed in the second and fourth quadrant.

Despite the fact that this ordination was calculated strictly from the beetle data, relative basal area of each tree species is organized in an interpretable pattern when projected into the ordination space of Figure 3.2. A detailed depiction of the fit for each tree species is provided in Figures 3.3 to 3.8. For example, the highest values of relative basal area for the most abundant tree species, *P. glauca* (Fig. 3.3), were clearly concentrated in the first quadrant together with those for *A. balsamea* (Fig. 3.4), which was more restricted in relation to beetle sites. Sites with maximum values of relative basal area for *P. balsamifera* (Fig. 3.5) were concentrated mainly in the lower part of the fourth quadrant of the ordination, but some intermediate and low values were also encountered in the first quadrant. *P. tremuloides* was mostly distributed on the right side of the ordination biplot and seems to perform best when sites are defined by beetles that are characteristic of the first quadrant (Fig. 3.6). The highest values of relative basal area for *P. mariana* occurred toward the negative end of the x-axis, especially in the second quadrant (Fig. 3.7). A few wetter sites placed in the third quadrant were dominated by *P. glauca* (Fig. 3.3) and *L. laricina* (Fig. 3.8).

Fig. 3.9 provides a clear depiction of the drainage classes for each site on the ordination diagram. Sites on the right site of the ordination are generally better drained than sites on the left side of the ordination. Among the sites concentrated on the right side of the ordination, drier sites are mostly found below the x axis while mesic sites are found above the x axis.

3.4 Discussion

Ground-beetles were collected in all sites, and in numbers large enough to allow robust statistical analysis. This feature alone contributes to the suitability of this beetle family as useful biodiversity indicators for the mixedwood boreal forest mosaic (Rainio and Niemelä 2003). All of the species caught in more than 10 sites (Table 3.1) are common in and apparently well-adapted to boreal forest conditions; many of them are characteristic of mature and late successional forests (Niemelä et al. 1993, Spence et al. 1996, Jacobs et al. 2008) in Alberta. This result is to be expected, given our sampling design that focused on mature forest that has never been harvested. The ordination data presented here suggest that variation in composition of the forest-associated carabid community is structured by the same environmental factors that affect distribution of the trees, or perhaps is even by the trees *per se*.

Eight of the species were trapped only at the disturbed sites (all except *E. clairvillei*) are characteristic of open habitats (Lindroth 1961-69, Larochelle and Larivière 2003). We captured many additional species also characteristic of open habitats but which constituted less than 0.1% of the total beetle catch (Table 3.1). Thus, even on boreal landscapes that may be characterized as 'forested', ample source populations of these species are available to respond to natural forest gaps that become available through disturbance. The EMEND landscape is embedded in a mosaic of harvested and burnt sites that could support such populations, and it seems that individuals of these species even wander into areas that are mainly mature well developed forest.

The main ordination (Fig. 3.2) represents the landscape according to what portion of the overall beetle assemblage is found in each site. The fact that relative basal area of tree species shows a level of organization in ordination space (Fig. 3.2) suggests that as the ground-beetle assemblage shifts, the species included exploit different resources, and that availability of these resources vary with presence of particular tree species. It is also interesting to note that tree species group in the ordinations according to ecological similarities documented for these trees. Tree cover on the right side of the ordination, for example, is dominated by a combination of *P. glauca, P. tremuloides, P. balsamifera,* and *A. balsamea*. These species are characteristic of uplands in the lower foothills ecoregion of northwestern Alberta, occurring mainly in mesic to well-drained sites either in mixture or pure stands (Beckingham 1996). On the other hand, high relative basal areas of *P. mariana* and *L. laricina*, species that typically colonize wet lowlands, are found mostly on the left side of the ordination. The drainage vector projected on the ordination diagram (Fig. 3.2) confirms this major ecological difference between species on the right and left side of the ordination. All eleven carabid species representing over one percent of the collection (Table 3.1) have their centroids located on the right side of the ordination, except *P. punctatissimus* (Fig. 3.2). This underscores the general inhospitality of very poorly drained sites for ground-beetles, an interesting generalization from this study. Organization of the beetle community seems to follow general ecological requirements of tree species, and thus, soil drainage is one of the factor that drives the distribution of both tree and beetle species.

The distribution of carabids on the landscape may be explained in even more detail by isolating the connections to particular tree species in relation to what is known about habitat use of these carabids. For example, the beetle species arrayed around the centroid for *P. balsamifera* (*A. retractum, T. chalybeus*, *P. decentis*, *P. foveocollis,* and *P. pensylvanicus*; see Fig. 3.2) typically prefer moderately moist ground (Larochelle and Larivière 2003). In contrast, these authors note that beetle species located near the centroid for *P. tremuloides* (*C. ingratus* and *P. adstrictus*) in Fig. 3.2 prefer drier ground than the aforementioned species. Despite similar ecology, *P. balsamifera* occupies wetter sites than *P. tremuloides* (Burns and Honkala 1990) and this is reflected in the distribution of their relative basal areas according to beetle species (Fig. 3.2). Changes in the beetle assemblage along this gradient are strong enough to suggest differential influences on the structure of ground-beetle community by these two ecologically similar tree species.

C. ingratus and *P. adstrictus* are considered as habitat generalists in non-riparian areas of the boreal zone (Niemelä et al. 1993, Pearce and Venier 2006) and are found here along most of the deciduous-coniferous gradient on the right side of the ordination. The highest abundances of *C. chamissonis* are also found to occur on drier grounds. Being characteristic of mixed and coniferous forest (Larochelle and Larivière 2003), most *C. chamissonis* were trapped at transitions between the deciduous and coniferous components of this gradient (Fig. 3.2), a new finding in this study.

Sites located in the first quadrant are dominated by high values of relative basal area for *P. glauca* and *A. balsamea*, and are associated with high abundances of *S. haematopus, C. advena*, and *P. brevicornis* (Fig. 3.2). All three of these species are regularly associated with coniferous forest (Spence et al. 1996, Gandhi et al. 2001, Work et al. 2004). *C. advena* is most frequently trapped in the forest, but both *S. haematopus* and *P. brevicornis* may occur in more open spruce bogs or heaths with ericaceous vegetation characteristic of higher altitude and latitude (Lindroth 1966). This explains why in our ordination, the centroids for these two later species are located closer to the y-axis, where the presence of *P. glauca* and *P. mariana* overlap (Fig. 3.3 and 3.7). Despite the fact that *S. haematopus* and *P. brevicornis* may occur in habitat where black spruce grow, they are normally encountered on drier ground than is *P. punctatissimus*.

Highest abundances of *P. punctatissimus* are concentrated in the second quadrant together with the highest relative basal area values for *P. mariana* (Fig. 3.2). *P. punctatissimus*, *A. gratiosum*, and *P. mannerheimii* are all recognized to occur in coniferous forest (Lindroth 1966, Larochelle and Larivière 2003), especially that dominated by *P. mariana* (Holliday 1991, Niemelä et al. 1992, Pearce et al. 2003, Paquin 2008). However, both *P. mannerheimii* and *A. gratiosum* are especially common in wet productive sphagnum bogs, swamps and lowland forested sites dominated by *Picea* and *Larix* (Larochelle and Larivière 2003). In the lower foothills of northwestern Alberta, *L. laricina* tends to occur in lowlands together with *P. mariana*; however presence of tamarack indicates productive sites where nutrients are more available (Beckingham et al. 1996). Composition of the beetle assemblage seems to reflect this ecological difference as high abundances of *P. mannerheimii* and *A. gratiosum* are located in the third quadrant overlapping strongly with the highest relative basal area values of *L. laricina*.

Lindroth (1963) characterizes *T. apicalis* as a eurytopic species with affinities for *Sphagnum*. Although catches of this beetle are widely distributed on the ordination diagram, most catches occurred to the left side of the ordination (Fig. 3.2) together with *P. mariana,* the tree species that dominates *Sphagnum* bogs in the area (Beckingham et al 1996).

A. sordens is characterized as hygrophilous (Lindroth 1966), often occurring close to water especially eutrophic marshes. It was placed in the lower part of the fourth quadrant of the ordination together with beetle species characteristic of moist soils and significant cover of *P. balsamifera*. However, sites with *A. sordens* also occurred in the third quadrant together with populations of *A. gratiosum* and *P. mannerheimii* where beetle assemblage is more characteristic of wet areas. These sites also included beetles more characteristic of upland forest such as *P. decentis*, *T. chalybeus* and *P. brevicornis*. These species are characteristic of 'old growth' forest in Alberta (Spence et al. 1996, Niemelä 1997), and the fact that tree cover at these sites consists of a mix of *P. mariana*, *P. tremuloides* and *P. glauca* likely reflects that a fine-grained mix of upland mesic and lowland wet sites is common to boreal stands in this region. Such subtle local variation certainly contributes to the diversity of epigaeic invertebrates in naturally occurring boreal stands. Maintaining such subtle variation is not an obvious feature of silvicultural practices used to regenerate boreal stands. This also speaks to the need to account for variation in physiography within stands in designing systems to conserve biodiversity.

Despite the fact that ecological linkage between the beetle assemblage and the canopy trees is well depicted using species centroids projected on the beetle ordination (Fig. 3.2), much ecological information remains hidden. Examination of figures 3.3 to 3.6 reveals that *P. glauca*, *P. tremuloides*, *P. balsamifera*, and *A. balsamea*, each occupies a wide range of sites on the right side of the ordination corresponding to upland forest. In the boreal mixedwood forest, the beetle community seems not to respond to the habitat as a mixture of pure coniferous and deciduous stands, but rather, as stands supporting a gradual mixture of conifer and deciduous tree species. In the ordination space, sites for coniferous, mixed and deciduous forest are not tightly grouped according to these categories but are evenly dispersed along this gradient. This provides evidence that the ground-beetle community dynamics on this sort of landscape behaves more like one loosely integrated Gleasonian community instead of tight Clementsian species groups showing similar responses to resource distribution.

There is additional evidence that projecting centroids onto the ordination diagram fails to capture some significant ecological patterns. A few sites with high values of relative basal area for *P. glauca* also group together at the lowest values of the x axis of the NMS ordination (Fig. 3.3). This is intriguing as these sites seem to host a very different beetle assemblage than most sites with high relative basal area of white spruce. The beetle catches were dominated by *P. punctatissimus* and *A. gratiosum*, but did not include either *S. haematopus* or *C. advena*, species that were characteristic of all other sites with high relative basal area of *P. glauca* (Fig. 3.2). In these exceptional sites, *P. glauca* (Fig. 3.3) grows with *L. laricina* (Fig. 3.8) but the presence of *P. mariana* that generally supports a beetle community characteristic of wet sites is less important (Fig. 3.7). In these circumstances, the carabid community is more typical of wet productive sites. Figure 3.9 combined with the results shown in Figure 3.3 confirm that white spruce occurring in the most poorly drained sites support a different assemblage than white spruce occurring on moderately to well-drained sites. Following the widely used approach of projecting *P. glauca* distribution onto the ordination with a vector or, simply projecting the centroid for this species on the ordination diagram (Fig. 3.2), does not reveal this pattern. We suggest that this is evidence that non-linear gradients can affect arthropod community structure. Before such gradients can be studied and understood, they must be first revealed, something accomplished here by ordination in relation to basal area.

Patterns of association between beetle community structure and uncommon tree species having a restricted distribution on the landscape are of special interest in a conservation context. For example, *A. balsamea* is at the northwestern edge of its continental range at EMEND and stands are scattered and restricted to narrow habitats (Halliday and Brown 1943, Bakuzis and Hansen 1965), often located in areas “skipped” repeatedly by historical fires (Sirois 1997). The carabid assemblage associated with this tree is a subset of that characteristic of *P. glauca* stands (Fig. 3.3 and 3.4). Both of these tree species are shade tolerant and typical of late-successional forest (Burns and Honkala 1990). Accordingly, two species of beetle that occur together with *A. balsamea* in the first quadrant (*C. advena* and *P. brevicornis*, Fig. 3.2) are characteristic of old-growth forest (Niemelä et al. 1993, Jacobs et al. 2008). Furthermore, *P. brevicornis* appears to be restricted to moist and cool forest areas, such as the interior of sites skipped by fire (Spence et al. 1996). In our ordination, *A. balsamea* also occurs more marginally in the lower part of the fourth quadrant where the beetle assemblage is characteristic of sites dominated by *P. balsamifera* (Fig. 3.4). This may be attributed to the fact that *P. balsamifera* grows on moist sites (Burns and Honkala 1990), a feature rendering these sites more likely to escape fire and develop the specific edaphic conditions required by *A. balsamea*. It is interesting to note that these sites also support populations of *T. chalybeus* and *P. decentis*, species also recognized as typical of old forest (Spence et al. 1996). This interesting trend would also not have been detected simply by plotting centroids or projecting vectors.

A similar pattern of association appears between *L. laricina* and *P. mannerheimii* (Fig. 3.2), both of which are uncommon species of the EMEND landscape (Table 3.1 and 3.2). *P. mannerheimii* is generally recognized in both North America and Scandinavia as being an uncommon element of the boreal beetle community, having narrow microhabitat requirements and being locally restricted to mires, old wet forests and fire skips (Niemelä

1997, Haila et al. 1994, Niemelä et al. 1992, Paquin 2008, Gandhi et al. 2001). The strong association between uncommon tree and beetle species suggests that more careful consideration of the distribution and abundance of rare tree species on a landscape would be useful as a coarse-filter for conservation efforts to manage some elements of boreal biodiversity. Presence of these tree species should not be dismissed as ‘noise’ in managing a landscape mosaic of commercially important species valued for fiber.

In general, associations between carabid and tree species, as described previously, match species of the same rank order of abundance on the EMEND landscape (Table 3.1 and 3.2). For example, the beetle species collected in the highest number of sites (*S. haematopus* and *C. advena*) were associated with *P. glauca*, the tree species similarly recorded from the highest number of sites. This is also true for the association between the carabids *P. adstrictus* and *C. ingratus* and the tree species, *P .tremuloides* (second highest number of sites). *P. punctatissimus*, the sixth most common carabid, was associated with *P. mariana* (noted at the third highest number of sites). Likewise *A. retractum*, *T. chalybeus*, and *P. foveocollis* were associated with *P. balsamifera* (fourth highest number of sites), and *P. brevicornis* and *C. chamissonis* were predominately collected at sites with *A. balsamea* (fifth highest number of sites). As outlined above, *A. retractum* and *P. mannerheimii* were associated with *L. laricina* (recorded at the sixth highest number of sites). We suggest that each tree species indicates its own set of edaphic and perhaps even broader environmental conditions. If so, beetle species requiring conditions related to the most frequent tree encountered on a landscape will also be the most commonly encountered in systematic sampling efforts to the extent that beetle population sizes follow that of tree species. If a habitat is less frequent on a landscape, the beetle requiring this habitat should also be less frequently collected, and this is what we observed. Thus, including all tree species in stand-level forest inventories can have real practical value in developing regional conservation strategies.

3.5 Conclusion

Despite the indirect nature of potential links between distributions of tree and ground-beetle species, the ecological features associated with their distributions appear to be similar, allowing us to discern surprisingly clear patterns of association. Variation in carabid assemblages over this section of the boreal forest reflects the specific presence of all tree species present on this landscape. It is unknown at present the extent to which these associations simply reflect a response to common features or if, perhaps, the trees themselves contribute to conditions (e.g., through quality of litter) that promote success of particular invertebrate species. Furthermore, although associations between ground-beetle and tree species are strong and interpretable, the potential implication for predicting distribution of other invertebrate taxa remains to be investigated.

Nevertheless, these observations are of interest for regional conservation purposes. Because the boreal forest covers vast areas, it is impossible in cost-effective practice to assess biodiversity reliably, and thus surrogates are needed (Spence et al. 2008). Our results support developing an approach that uses details of forest inventory as a possible surrogate for arthropod biodiversity in conservation planning. Extensive Canadian forest surveys already include evaluation of canopy cover (Leckie and Gillis 1995), and this can be directly related to basal area (Spurr 1960) as used in this study. Our study emphasizes that accuracy of forest surveys and inventories is crucial to their use in conservation planning because uncommon carabid species are clearly associated with uncommon tree species. It will be important to include records of these uncommon tree species in all inventories and to ensure that methods employed in regeneration of forests managed extensively permit such trees to establish themselves in a rather natural manner, even when they are commercially unimportant.

3.6 Literature cited

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Table 3.1. Species of the family Carabidae collected in 197 sites during the summer of 2003 in boreal Alberta, Canada. n= sample size

Species	Catches	% catch	n sites
Stereocerus haematopus (Dejean)	2830	28.63	164
Calathus advena (LeConte)	2665	26.96	150
Pterostichus adstrictus Eschscholtz	1427	14.44	127
Calathus ingratus Dejean	607	6.14	118
Platynus decentis (Say)	529	5.35	114
Pterostichus punctatissimus (Randall)	421	4.26	100
Agonum retractum LeConte	349	3.53	78
Trechus chalybeus Dejean	285	2.88	78
Patrobus foveocollis (Eschscholtz)	223	2.26	76
Pterostichus brevicornis (Kirby)	172	1.74	71
Carabus chamissonis Fisher von Waldheim	159	1.61	69
Agonum gratiosum (Mannerheim)	48	0.49	20
Platynus mannerheimii (Dejean)	34	0.34	18
Pterostichus pensylvanicus LeConte	23	0.23	17
Trechus apicalis Motschulsky	14	0.14	12
Agonum sordens Kirby	11	0.11	6
Nebria gyllenhali Kirby	8	0.08	6
Bembidion grapii Gyllenhal	7	0.07	5
Agonum cupreum Dejean	7	0.07	4
Notiophilus directus Casey	6	0.06	4
Synuchus impunctatus (Say)	6	0.06	4
Trichocellus mannerheimii (R.F. Sahlberg)	5	0.05	4
Pterostichus riparius (Dejean)	5	0.05	3
Trichocellus cognatus (Gyllenhal)	5	0.05	3
Amara erratica (Duftschmid)	5	0.05	2
Patrobus septentrionis Dejean	4	0.04	2
Calosoma frigidum Kirby	3	0.03	2
Elaphrus clairvillei Kirby	2	0.02	2
Notiophilus borealis T.W. Harris	2	0.02	2
Cymindis unicolor Kirby	2	0.02	2
Loricera pilicornis (Fabricius)	2	0.02	1
Bembidion rupicola (Kirby)	2	0.02	1
Amara lunicollis Shiødte	2	0.02	1
Amara laevipennis Kirby	1	0.01	1
Agonum placidum (Say)	1	0.01	1
Agonum superioris Lindroth	1	0.01	1
Amara littoralis Mannerheim	1	0.01	1
Amara patruelis Dejean	1	0.01	1
Badister obtusus LeConte	1	0.01	1
Dyschirius hiemalis (Bousquet)	1	0.01	1
Elaphrus lapponicus Gyllenhal	1	0.01	1
Harpalus fulvilabris Mannerheim	1	0.01	1
Harpalus laevipes Zetterstedt	1	0.01	1
Miscodera arctica (Paykull)	1	0.01	1
Notiophilus semistriatus Say	1	0.01	1
Poecilus lucublandus (Say)	1	0.01	1
Sericoda quadripunctata (DeGeer)	1	0.01	1
Elaphrus americanus Dejean	1	0.01	1
Total	9885		
n species	48		

Table 3.2. Total and relative basal area for species of tree recorded in 194 sites for comparison with beetle assemblage in boreal Alberta, Canada. n= sample size

Tree species	Basal area (m^2)	% basal area	n trees	n sites
Picea glauca	82.2298	44.8	1720	133
Populus tremuloides	42.6206	23.2	831	91
Picea mariana	16.8314	9.2	1655	83
Populus balsamifera	36.4818	19.9	541	57
Abies balsamea	1.0901	0.6	103	20
Larix laricina	3.1918	1.7	86	17
Pinus contorta	0.9776	0.5	26	16
Betula papyrifera	0.2231	0.1	11	10

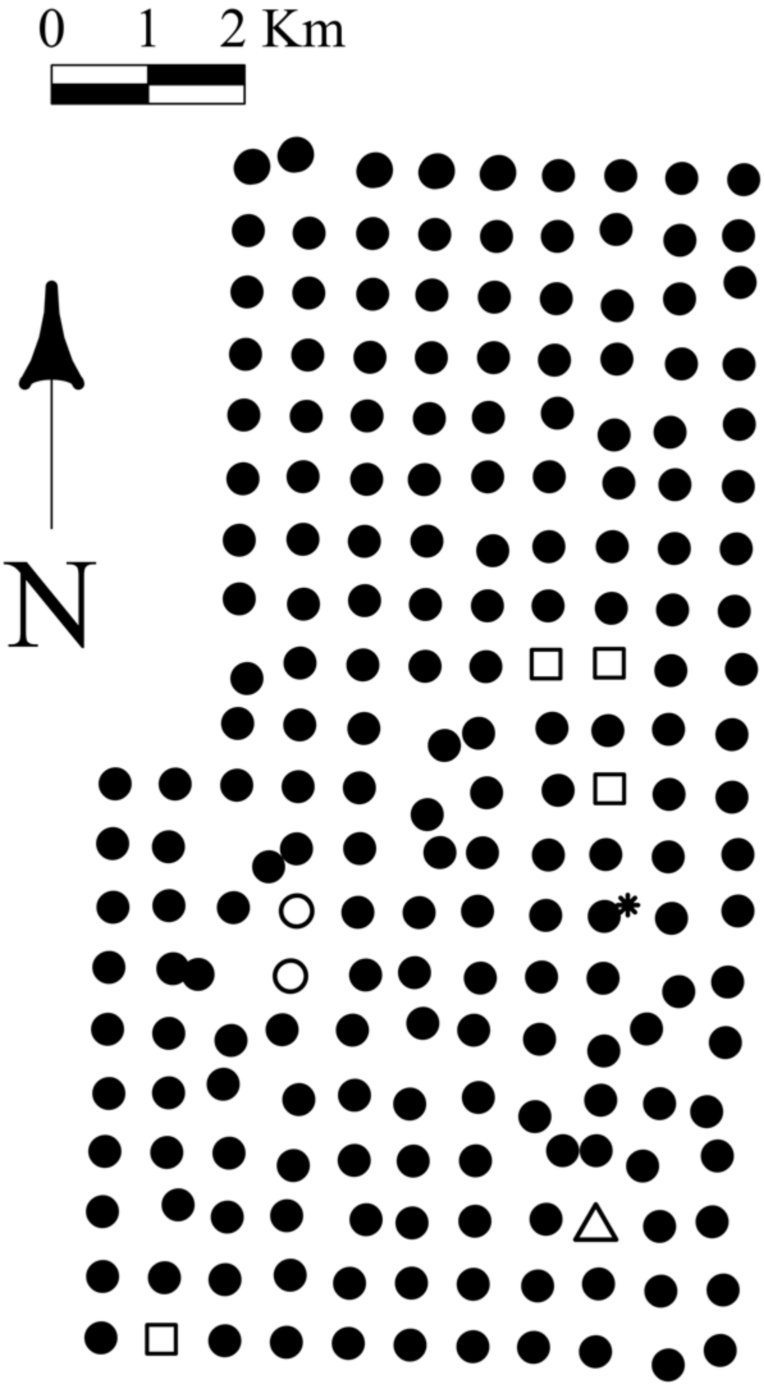

Figure 3.1. Map of the sampling sites. Squares represent destroyed sites, open circles represent harvested sites, triangle represents the outlier, and the star represents the burnt site.

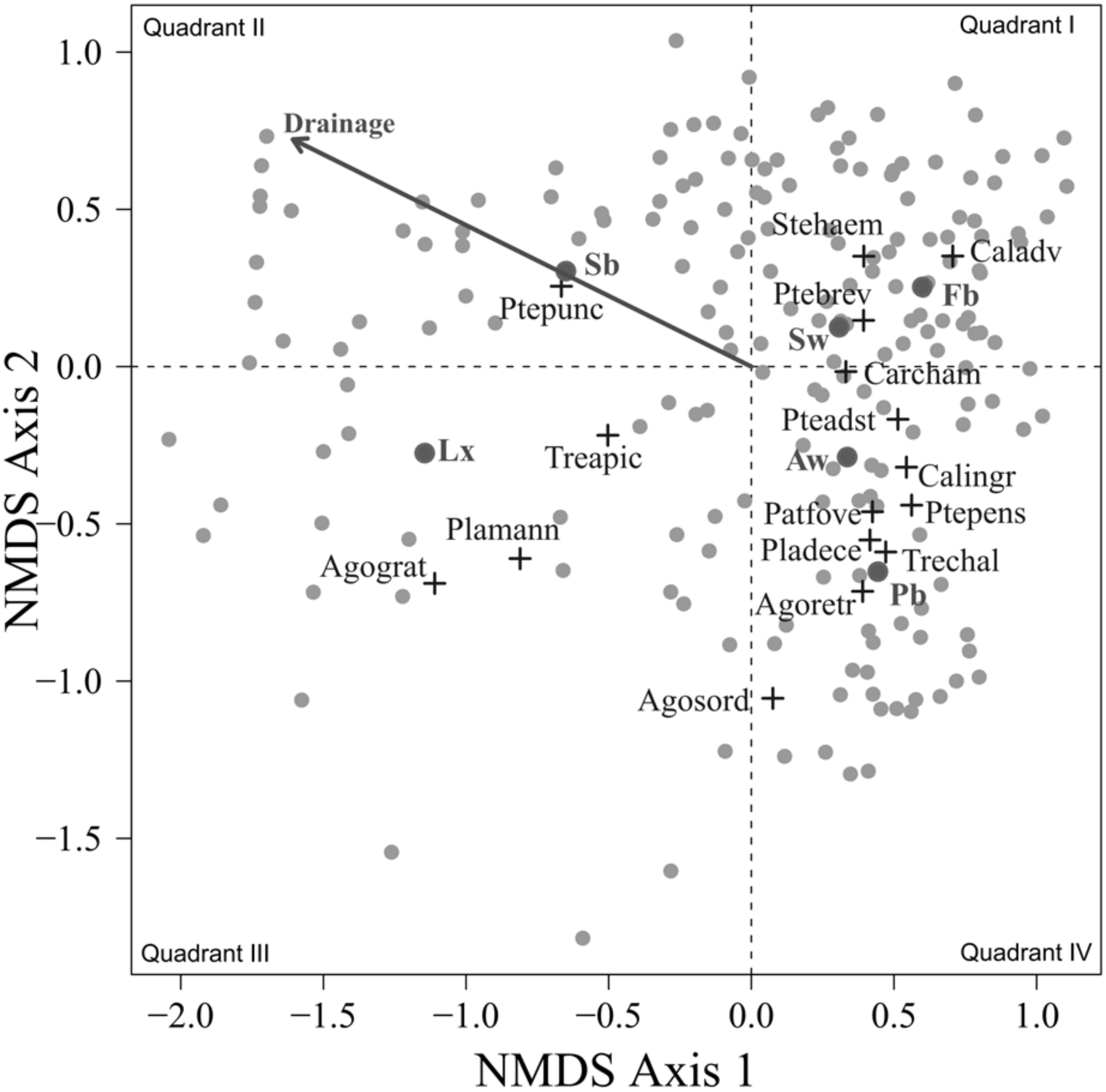

Figure 3.2. NMS ordination of the 193 sites (grey dots) with weighted centroid for beetle (crosses) and tree species (dark dots), stress = 15.1. Vector direction indicates sites with increasingly poor drainage. The abbreviations of the beetle species are as follow: Agograt: *Agonum gratiosum*, Agoretr: *Agonum retractum*, Agosord: *Agonum sordens*, Caladve: *Calathus advena*, Calingr: *Calathus ingratus*, Carcham: *Carabus chamissonis*, Patfove: *Patrobus foveocollis*, Pladece: *Platynus decentis*, Plamann: *Platynus mannerheimmi*, Pteads: *Pterostichus adstrictus*, Ptebrev: *Pterostichus brevicornis*, Ptepens: *Pterostichus pensylvanicus*, Ptepunc: *Pterostichus punctatissimus*, Stehaem: *Stereocerus haematopus*, Treapic: *Trechus* apicalis, Trechal: *Trechus chalybeus*. Abbreviations for the tree species are; Aw: *Populus tremuloides*, Fb: *Abies balsamea*, Lx: *Larix laricina*, Pb: *Populus balsamifera*, Sb: *Picea mariana*, and Sw: *Picea glauca*.

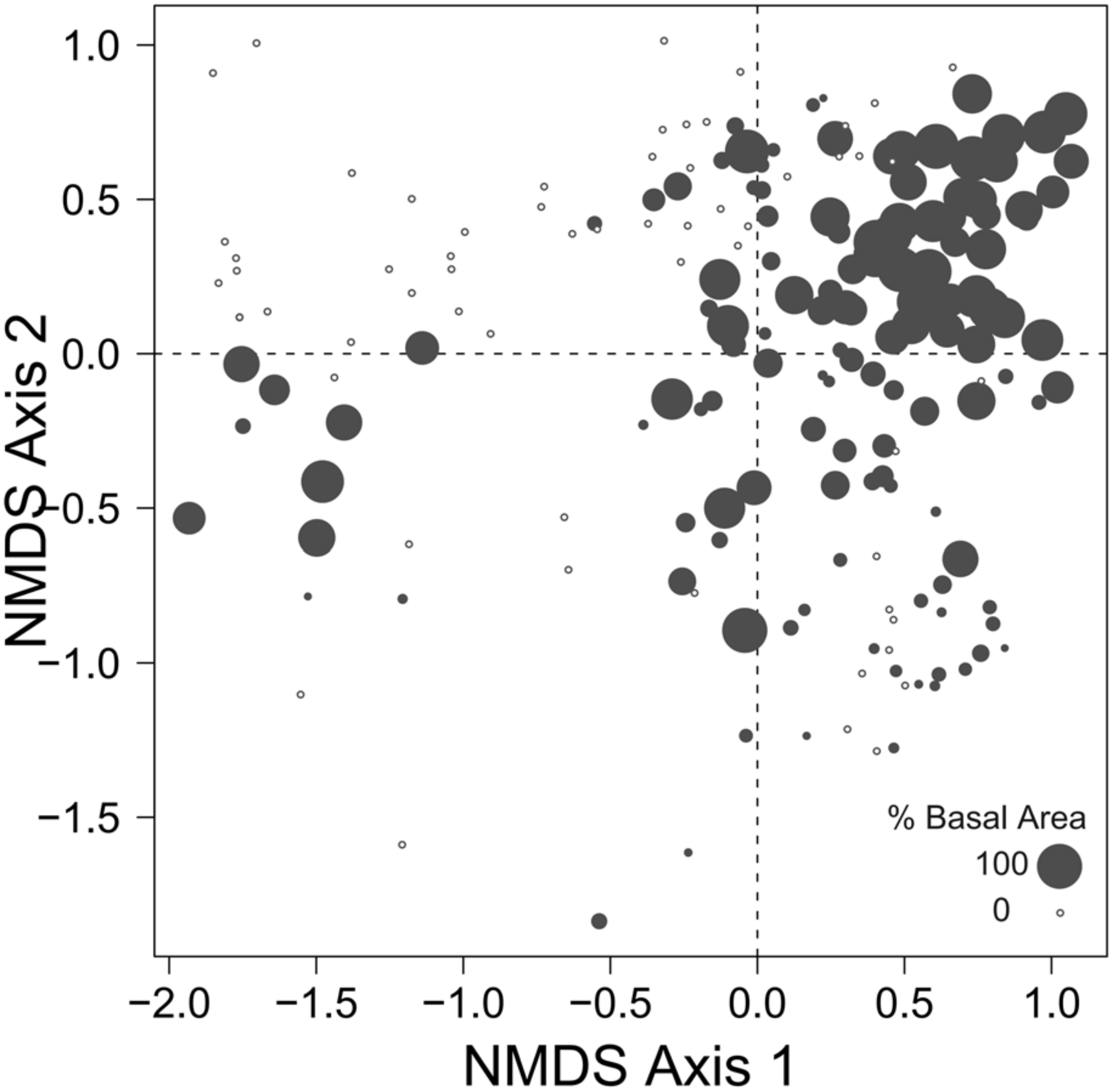

Figure 3.3. Relative basal area of *P. glauca* for the 193 sites plotted on the beetle ordination of figure 3.2.

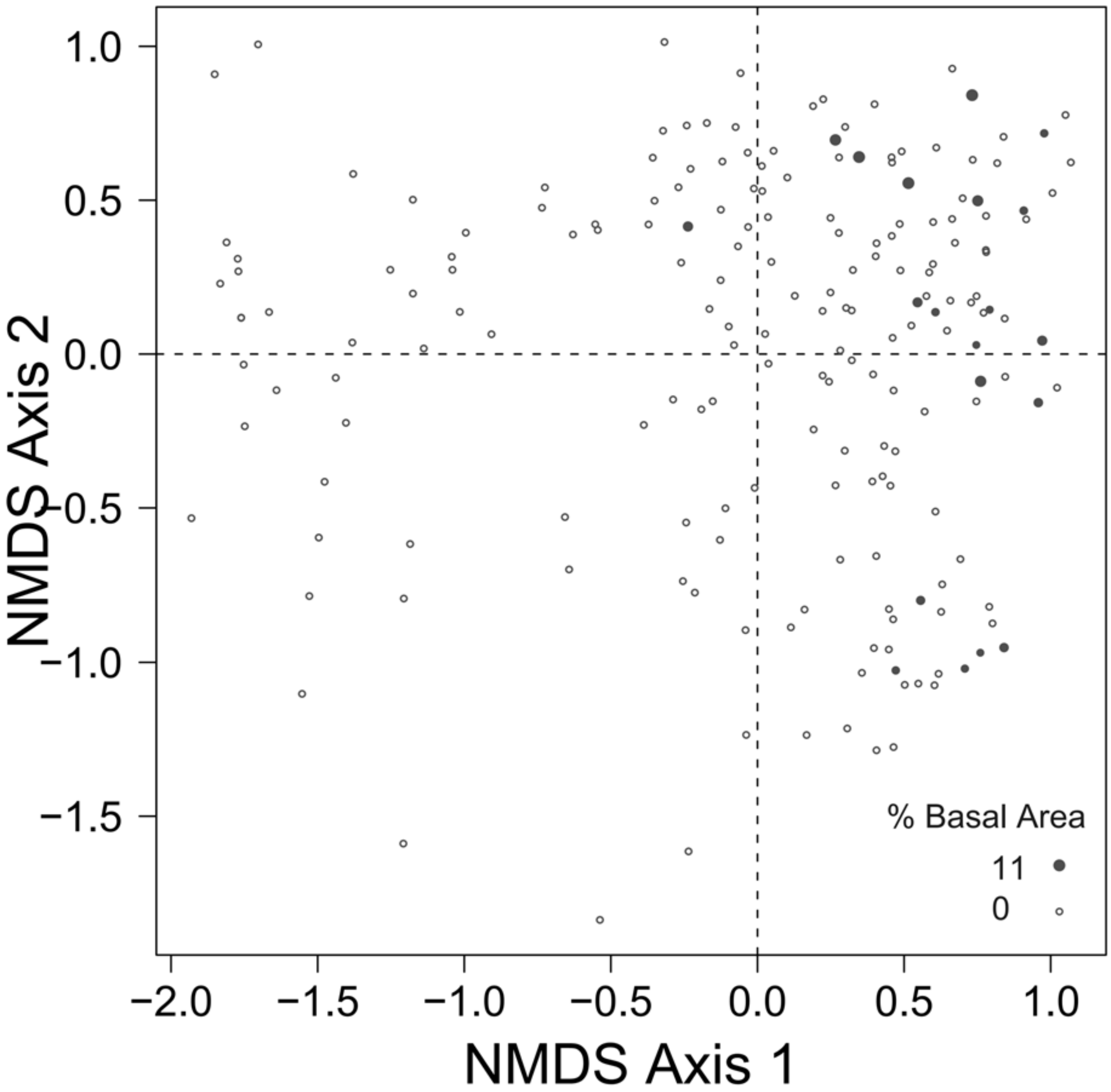

Figure 3.4. Relative basal area of *A. balsamea* for the 193 sites plotted on the beetle ordination of figure 3.2.

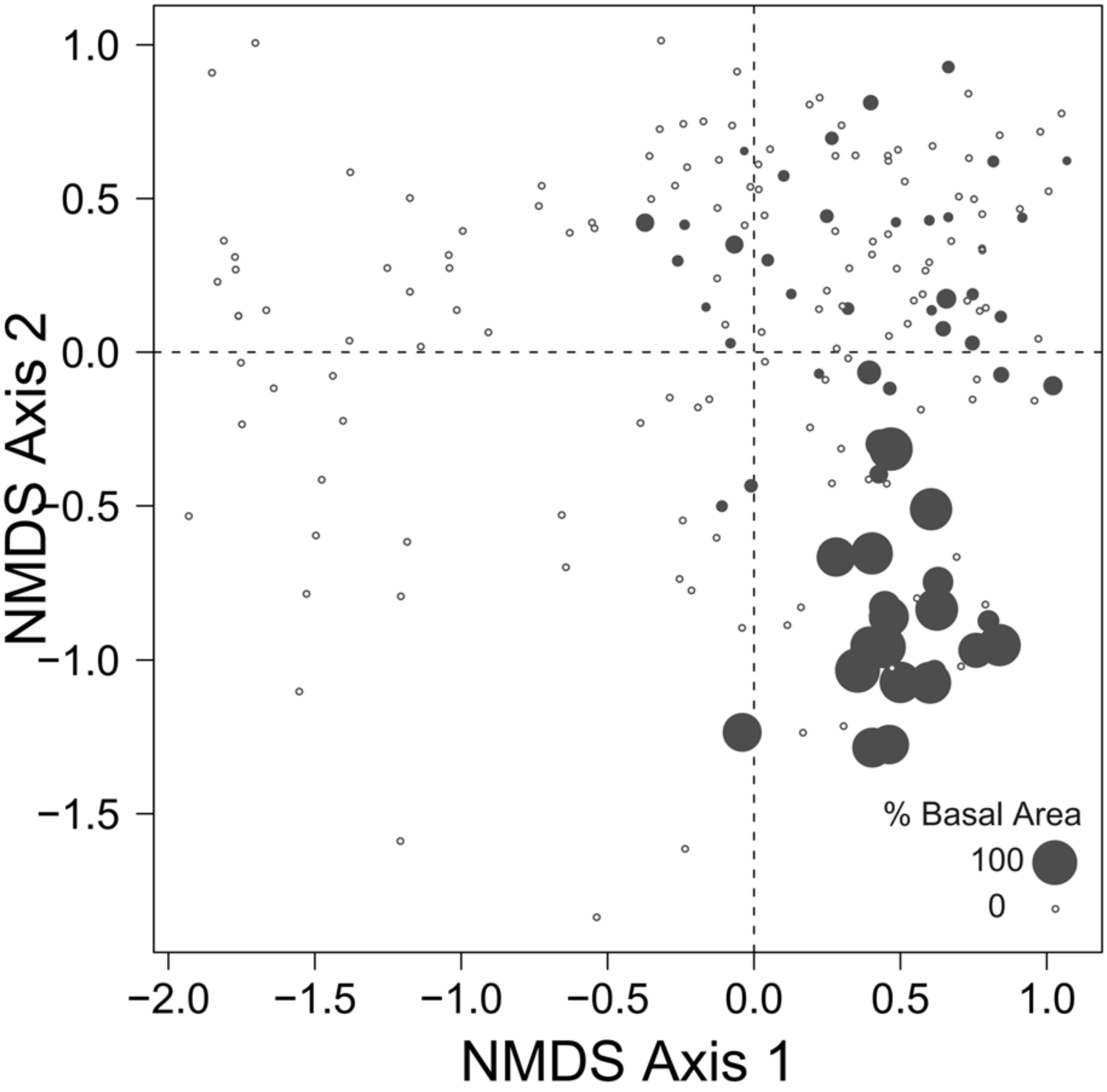

Figure 3.5. Relative basal area of *P. balsamifera* for the 193 sites plotted on the beetle ordination of figure 3.2.

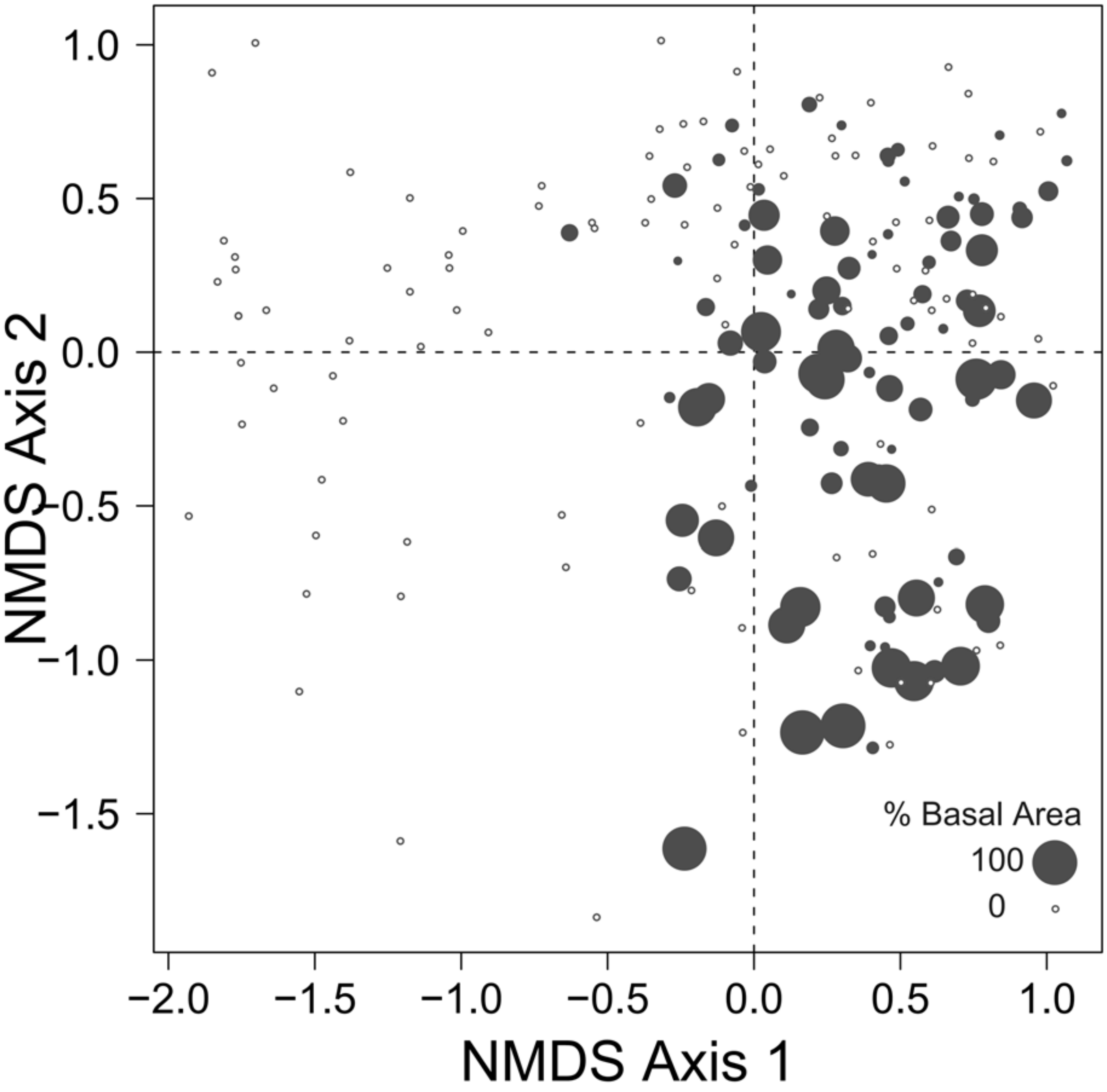

Figure 3.6. Relative basal area of *P. tremuloides* for the 193 sites plotted on the beetle ordination of figure 3.2.

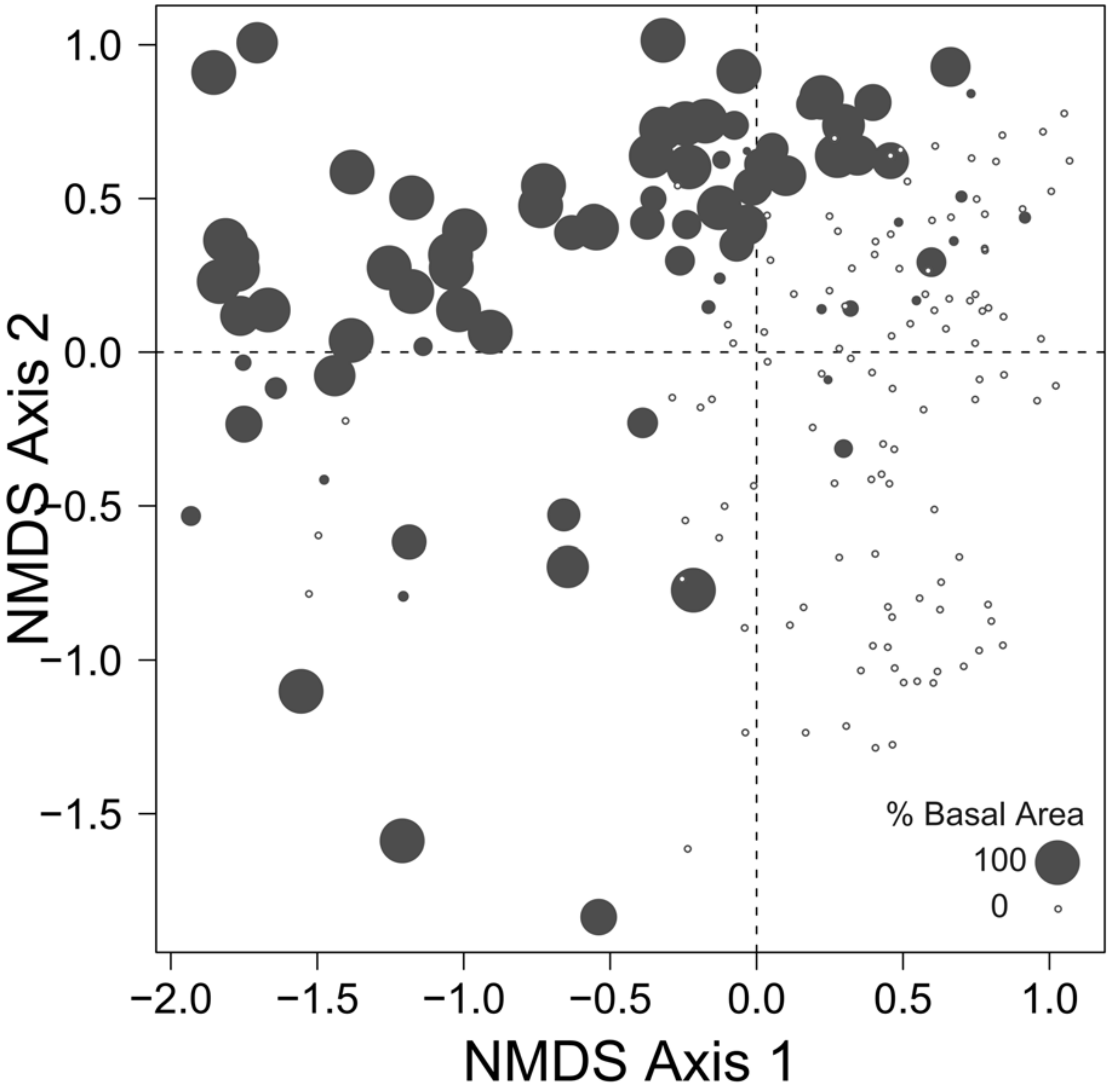

Figure 3.7. Relative basal area of *P. mariana* for the 193 sites plotted on the beetle ordination of figure 3.2.

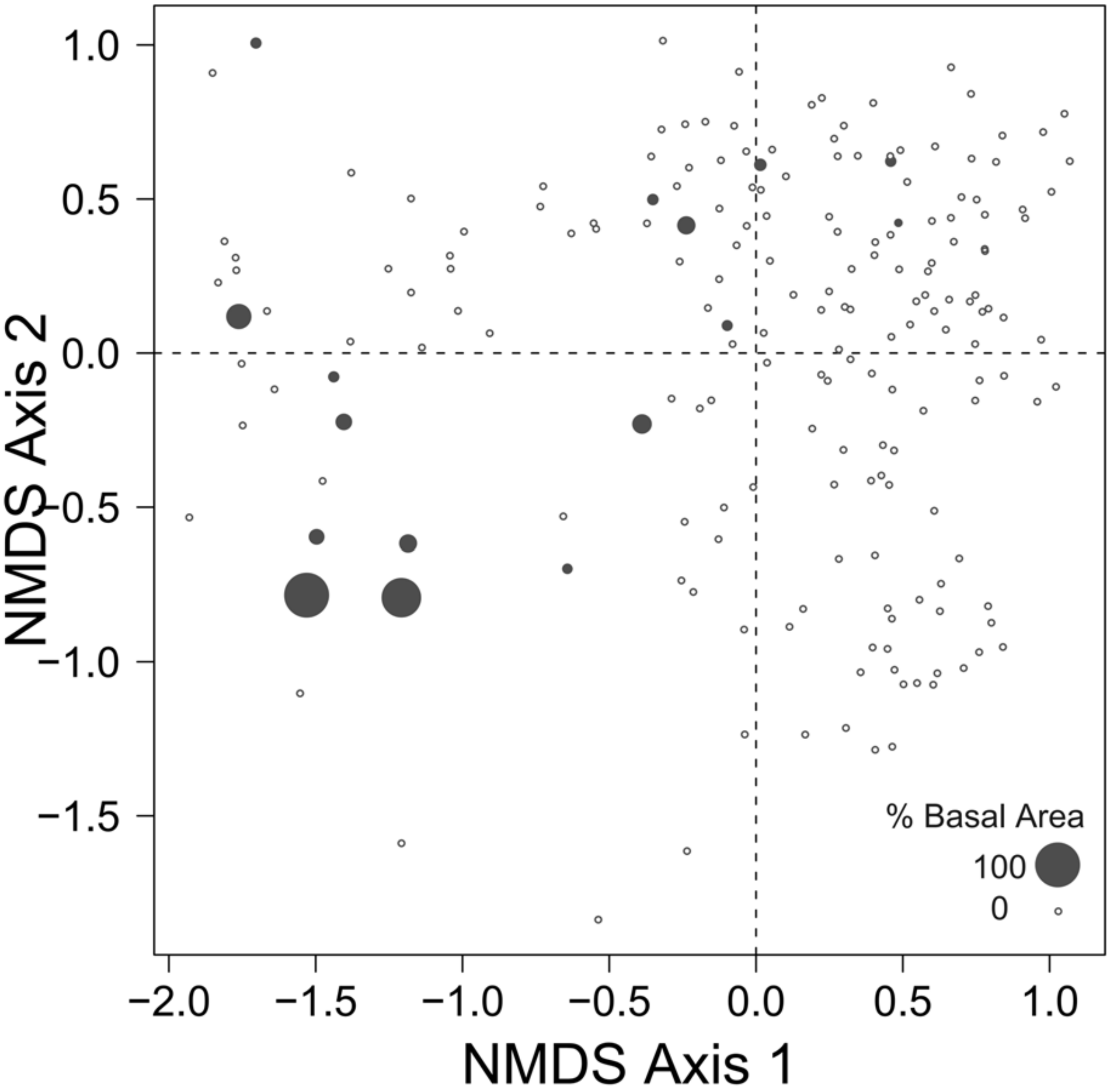

Figure 3.8. Relative basal area of *L. laricina* for the 193 sites plotted on the beetle ordination of figure 3.2.

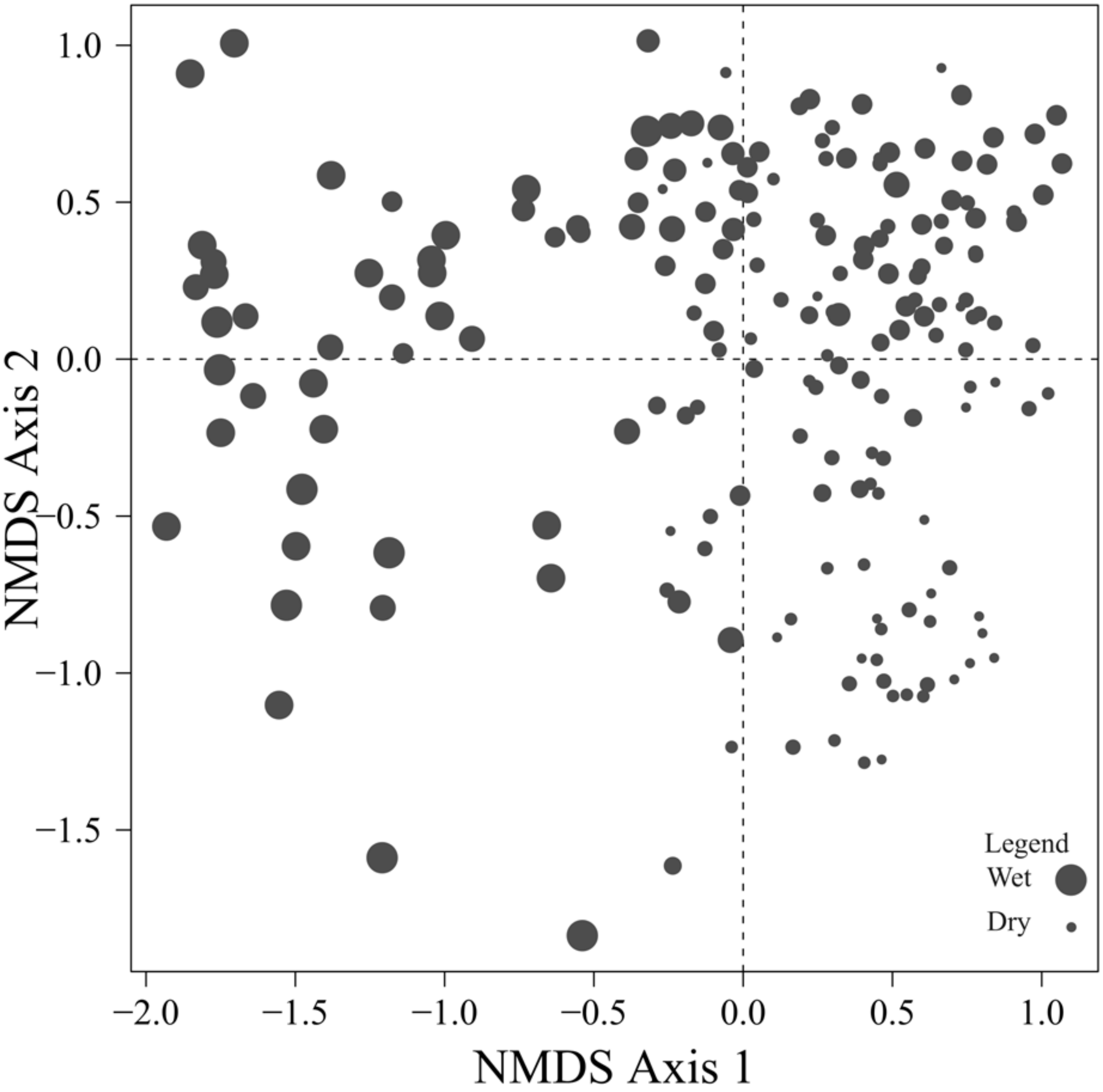

Figure 3.9. Drainage values for the 193 sites plotted on the beetle ordination of figure 3.2. High drainage values represent poorly drained sites.

CHAPTER 4

Ecosystem classification and inventory maps as surrogates for ground-beetle assemblages in boreal forest

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4.1 Introduction

Use of biodiversity surrogates provides a practical, realistic, and cost effective basis for landscape scale conservation strategies (Duro et al. 2007, Nagendra 2001, Turner et al. 2003). It offers a robust scientific basis to relate patterns of biodiversity to variation in managed ecosystems (Spence et al. 2008, Spence and Langor 2006), and does so in terms directly relevant to landscape planners. Coupled with remote sensing and geographical information systems, development of biodiversity surrogates can provide the high resolution maps needed to assist regional conservation planning and monitoring efforts (Ferrier 2002, Margules and Pressey 2000).

Given limited technical and financial resources for identifying and mapping the entire range of biodiversity over large areas, effective surrogates are essential for embracing a holistic ecosystem approach for maintenance of global and local biodiversity (Franklin 1993, Noss 1990, Wilson 1988). Of course, relationships between biodiversity and the surrogates employed must be monitored through detailed spot checks to ensure their fidelity over time (Spence et al. 2008). Nonetheless, because financial and technical support invested in large-scale bioinventories will always be insufficient to generate biodiversity maps with the grain size, extent, and species diversity level required for management planning, development of effective surrogates is our only hope. In this paper we show how vegetation and ecosystem classification might be employed to achieve this goal for the boreal mixedwood.

An array of remotely sensed data about landscapes on Earth is already available and widely used in land management (Richards and Jia 2006). There is compelling scientific evidence for mammal and bird species that remotely sensed environmental variables correlate with observed biodiversity patterns (Leyequien et al. 2007, Rodrigez et al. 2007). Furthermore, evidence for such correlations is now emerging for more cryptic groups such as invertebrates (Barbaro et al. 2007, Eyre and Luff 2004, Kerr et al. 2001, Müller and Brandl 2009), mosses and fungi (McMullan-Fisher et al. 2009). Research to date has concentrated on the detection, description and predictive modeling of relationships between biodiversity parameters and surrogates, but has largely ignored assessments of accuracy (Czaplewski 2003, Morgan et al. 2010). Failure to consider such error may have cascading effects on the ecological associations modeled, the consequent conservation strategies implemented and, in the final analysis, the efficacy of natural resource management plans (Thompson et al. 2007).

Aerial photography is especially well suited for ecological land management (Hall 2003, Morgan et al. 2010). For example, in Canada forest inventories are largely based on interpretation of aerial photographs ranging in scale from 1:10000 to 1:20000 (Leckie and Gillis 1995). These interpretations are the backbone of most forest management decisions and are used to inform the basal logic of many scientific predictive models (Avery and Berlin 2003, Paine and Kiser 2003). Stand level data interpreted from such photography are used to refine the spatial resolution of ecosystem classification frameworks (e.g. Beckingham et al. 1999, Nadeau et al. 2004) developed for national and international biodiversity conservation reporting (Bailey and Hogg 1986, Marshal et al. 1996, Olson et al. 2001). In addition to providing guidance for the establishment of biodiversity reserves on coarser scales (Margules and Pressey 2000), ecosystem maps with finer resolution have the potential to guide the detailed development of conservation strategies in operationally managed landscapes. The scale and the detail of the information contained in these maps provide the knowledge base used for stand level management and are therefore a crucial tool for linking these activities to biodiversity patterns across landscapes.

Most studies linking remote sensing to biodiversity generally focus on landscapes containing contrasting habitats such as farm lands, urban area, and forest (Barbaro et al. 2007, Eyre and Luff 2004, Kerr et al. 2001, McMullans-Fisher et al. 2009, Müller and Brandl 2009). Thus, by focusing on biodiversity patterns related to canopy heterogeneity, we assess the ability of remote sensing to detect biodiversity patterns in a rather homogeneous forest environment, as is directly relevant to addressing concerns about boreal biodiversity.

In this study, we compare performance of ecosystem classification maps (ecosite; Nielsen et al. 1999) and Alberta Vegetation Inventory (AVI) data (http://www.srd.alberta.ca/MapsPhotosPublications/Maps/ResourceDataProductCatalogue/ForestVegetationInventories.aspx) in reflecting biodiversity patterns for ground-beetles

(Coleoptera: Carabidae). We first assess how much variation in the beetle community can be explained by each of these data sets, and compare these results with data obtained through a detailed ground survey of trees. We then point out dissimilarities in the ecological models originating from remotely acquired data and ground survey. Finally, we assess the accuracy of data originating from air photo by directly comparing the AVI dataset with the ground survey data collected on a particular landscape for each tree species.

4.2 Methods:

4.2.1 *Study area*

The study was conducted at the EMEND (Ecosystem Management Emulating Natural Disturbance; see Spence et al. 1999) research site located in the lower foothills ecoregion of the mixedwood boreal forest (Beckingham et al. 1996) in northwestern Alberta. The dominant tree species are *Picea glauca* (Moench) (white spruce), *Populus tremuloides* Michx. (aspen), and *Populus balsamifera* L. (balsam poplar) on well drained sites and *Picea mariana* (Mill.) (black spruce) and *Larix laricina* (Du Roi) K. Kock (tamarack) on poorly drained sites. The elevation varies between 677 and 880 meters in a catena-like topography of rolling hills, mostly consisting of morainal deposits with extensive valleys and depressions covered by lacustrine and organic deposits (Alberta Environmental Protection 1994).

4.2.2 *Methods*

In the summer of 2002, we established a systematic grid of 200 sampling sites covering 84 km^2 of mixedwood forest. Sites were located roughly 640 m apart, with grid points adjusted locally within the nearest stand to include trees over 5 cm of diameter at breast height (dbh) and to be at least 40 m from any anthropogenic disturbance. In each site, we recorded the species (according to Moss 1983) and dbh for the 25 living trees, >5 cm dbh, closest to the site center. Dbh and species were also recorded for one stem of any additional tree species detected within 50 m of the center. This allowed us to include tree species absent from the 25 sampled stems that also contribute in explaining the ground-beetle biodiversity at the sampled site. Two sites were omitted from the grid because large harvested areas would have placed any sampling sites within 40 m from the next closest site.

Restricting the site selection to forest with well developed trees (>5 cm dbh) allowed us to focus on the surrogate variable “relative tree canopy cover”, as derived from aerial photography. It also allowed us to check the ability of remote sensing to depict biodiversity patterns that might be related to stand level boreal forest canopy heterogeneity.

During summer 2003, we used 3 pitfall traps at each site to sample the ground-beetle (Coleoptera: Carabidae) assemblage. A trap consisted of a plastic cup with an opening diameter of 11 centimeters and a depth of 13 centimeters, containing a plastic inner cup and a wooden roof supported over the trap by two nails (Spence and Niemelä 1994). Traps were installed 15 m from the center of the site at 0°, 120° and 240°. Silicate-free ethylene glycol (GM Dex-Cool®) in the inner cup was used as a killing agent and preservative. Traps were open from the second week of May until the third week of August for a maximum of 99 potential sampling days embracing most of the frost-free period. Trap contents were collected 4 times over this period. Five sites established in 2002 were harvested during the following winter and therefore were omitted from ground-beetle sampling. All carabid specimens were identified to the species level according to Lindroth (1961, 1963, 1966, 1968, 1969), with nomenclature following Bousquet (1991). Voucher specimens are deposited in the Spence laboratory collection and the Strickland Entomological Museum of the University of Alberta.

Data about relative tree canopy cover were obtained from the province wide AVI phase 3 for each site, using ArcView 3.4 software (ESRI ®). These data consist of photo interpretations of relative canopy cover in 10% classes for each tree species recorded in the delineated stand (polygon). Tree data collected on the ground were transformed into relative basal area and grouped into ten categories of 10% plus a 0% category in order to be comparable with the relative tree canopy cover based on AVI data. Continuous data about relative basal area included within plus or minus five percent of the category label were merged into this category to approximate the categorization of relative canopy cover made by air photo interpreters in developing the AVI data. The 0% category therefore includes values of relative basal area comprised between 0 and 5 percent, the 10% category includes values between 6 and 15 percent, and so on. We assumed that relative basal area of tree species is proportional to the relative canopy cover because of the linear correlation between diameter at breast height and crown diameter (Spurr 1960).

The ecosite classification data were acquired from a geo-referenced digital map generated by Nielsen et al. (1999) using the SiteLogix ecological mapping system

(Beckinghan et al. 1999), and following the ecological land classification system for west-central Alberta (Beckingham et al. 1996). This classification system includes four hierarchical levels: natural subregion (defined by climatic variation of reference physiographic sites), ecosite (defined by a nutrient-moisture gradient within subregions), ecosite phase (defined according to the main canopy cover within ecosites), and plant community (defined according to the understory plants within ecosite phases). We used the ecosite phase level because it provided the highest resolution available through the mapping procedure (Nielsen et al. 1999). To obtain ecosite phase variables for each site, we calculated the area in square meters for each ecosite phase within a 50 meters radius of the centre of the sampling site using ArcView 3.4 (ESRI ®).

4.2.3 *Statistical analysis*

Beetle samples from the three traps in each site were pooled and divided by the total number of effective trapping days to standardize for sampling effort. Samples from traps not operating (disturbed by animals or flooded) at time of sample collection were excluded from further analysis.

After a Hellinger transformation of the beetle species data (Legendre and Gallagher 2001), a variation partitioning procedure (Borcard et al. 1992, Legendre and Legendre 1998) was used to determine the proportion of variance in ground-beetle assemblages explained by AVI, ecosite map, and the ground survey data. These analyses were performed using the vegan (Oksanen et al. 2011) package within the R statistical language (R Development Core Team 2011) on the 193 sites from which beetle data were available.

Association between land cover variables from each survey method and the beetle assemblage was assessed by performing a canonical redundancy analysis (RDA, Legendre and Legendre 1998) on the transformed beetle data using the R package rdaTest (Legendre and Durand 2010). The Hellinger transformation minimizes the inward folding of the environmental gradient extremes (Legendre and Gallagher 2001), reducing the typically strong "horseshoe effect" in such data (Legendre and Legendre 1998).

Ordinations for each survey method were projected in the beetle assemblage (used as the response variable) space (Legendre and Legendre 1998) to facilitate comparison of the ability of alternative land survey data to explain biodiversity patterns. Vectors for the 13 most abundant beetle species and all tree species were added to help interpret drivers of the ordination results. Ordinal axes were judged as significant ($p<0.05$) predictors of beetle assemblages based on 999 random permutations. Forward selection (Blanchet et al. 2008) was performed on the ecosite data set in order to choose the variables explaining the most variation in the beetle assemblage, using the R package packfor (Dray et al. 2009).

Provincial AVI and ground data for the four most abundant tree species were compared for 198 sites, using misclassification matrices (Congalton 2001, Foddy 2002, Stehman and Czaplewski 1998, Wulder et al. 2006). We used all sites where tree data was available in order to increase the power of this analysis, instead of restricting our analysis to the 193 sites where beetle data was also available. AVI data classified within two categories (±20%) from the ground data were considered accurate. This range was determined based on the fact that many factors such as sampling design, positional error from our Global Positioning System unit, the loose linear relationship between basal area and crown diameter, and the methodological procedure of photo interpretation may all induce variability in the results. The average relative proportion of each tree species in misclassified sites was calculated for AVI and ground data in order to determine tree species biases in AVI. A *t*-test, performed with 999 permutations, was carried out for each tree species in misclassified sites to calculate significance of divergence in the relative proportion estimates between the two inventory methods.

4.3 Results

Overall, 9776 ground-beetles identified as representing 41 species were collected across the 193 sites. Although 5039 individual trees were sampled over the 198 sites, trees were represented by just eight overstory species: white spruce, aspen, black spruce, balsam poplar, balsam fir (*Abies balsamea* (L.)), tamarack, paper birch (*Betula papyrifera* Marsh.), and lodgepole pine (*Pinus contorta* Dougl. ex Loud). These same tree species were recorded on this landbase in the AVI. Twenty-three ecosite classification categories were detected in the study, all within a 50 m radius of at least one site where beetles were sampled (Table 4.1). Some records must be attributed to a combination of two ecosite phases originally described by Beckingham et al. (1996), because the mapping process could not unequivocally attribute a dominant ecosite class to the polygon (Nielsen et al. 1999).

4.3.1 *Relationships between beetles and forest composition*

Ecosite phase explained higher variance in the carabid assemblage (34%) compared to ground survey (32%) and AVI (22%, Fig. 1). The majority of variance in the beetle assemblage explained by the AVI data (18%) was congruent with the ground survey data, and was entirely included in the variance explained by the ecosite classification system. The ecosite phase and ground survey datasets mutually explained 23% of the variance in the beetle assemblage with ecosite phase explaining an additional 11% on its own.

The ecosite map does reflect ground beetle assemblage in a way that a specific pattern of association between ecosite phases and beetle species is discernable (Fig. 4.2). However, sites on the positive side of the first axis are dominated by ecosite phases characteristic of mesic sites, while the sites on the negative side of the first axis are dominated by ecosite phases characteristic of wetter areas (Beckingham et al. 1996). The deciduous dominated ecosites phases (e2, e2f2, f2, e?, and f6) are grouped in the third quadrant together with those for the beetles *Platynus decentis* (Say), *Agonum retractum* LeConte, *Trechus chalybeus* Dejean and *Patrobus foveocollis* (Eschscholtz). The vector for the mixed ecosite phase (e3) is oriented along the first axis at the edge of quadrant one and is closely aligned to the vectors for *Pterostichus adstrictus* Eschscholtz and *Calathus ingratus* Dejean, two of the most common carabids on this landscape. The vector for the white spruce dominated ecosite phase (e4) is in the first quadrant together with those for *Calathus advena* (LeConte), *Stereocerus haematopus* (Dejean) and *Pterostichus brevicornis* (Kirby). *Pterostichus punctatissimus* (Randall) is associated with ecosite phases having a poor nutrient regime and, despite its often stated affinity for wet ecosite phases (k1, l1k1, k1h1), the analysis shows that this beetle also occurs in ecosite phases typical of drier moisture regime (d1/e1, j1d1, Beckingham et al. 1996). *Agonum gratiosum* Mannerheim and *Platynus mannerheimii* Dejean are also associated with wet ecosites phases but these sites are generally richer in nutrient availability as reflected by the plant community composition (l2g1, l1).

The tree species vectors projected on the ordination for the AVI (Fig. 4.3) provide groupings that are generally similar to those in the ordination for the ground survey data (Fig. 4.4). For both ordinations, 1) the deciduous tree species group together in the fourth quadrant, 2) white spruce, lodgepole pine and balsam fir (*Abies balsamea*) are found on the positive side of the second axis, and 3) black spruce and tamarack group in the third quadrant. However, the relative positions of some tree species differ between these data sets. For example, the ground survey data achieve a greater differentiation between the aspen and balsam poplar vectors (cf. Figs. 4.4 and 4.5) than in the ordination based on the AVI data (Fig. 4.3). Similarly, differentiation between tamarack and black spruce is less pronounced in the ordination based on the provincial inventory data. We also noted that the angles between the white spruce vector and those for both aspen and balsam poplar are more acute for the ground survey data than for the AVI data. Furthermore, the relative position of vectors for balsam fir and lodgepole pine differ between data for AVI and ground surveys.

Positions of some beetle species also markedly differ relative to the tree vectors between ordinations based on the two tree survey techniques. In the ground survey data set, for example, *S. haematopus* seems to have an affinity for both white and black spruce (Figs. 4.4 and 4.5), while this beetle seems to be mostly restricted to white spruce stands in the ordination based on AVI (Fig. 4.3). Associations between presence of tamarack and *A. gratiosum* and *P. mannerheimmi* are more obvious for ordinations based on ground survey data than for those from the photography-based AVI. Similarly, the association between *P. brevicornis* and spruce-fir forest, and between *C. chammisonis* and the mixed forest (Fig. 4.4) is more obscure in the AVI ordination (Fig. 4.3).

4.3.2 ***Accuracy of inventory data derived from aerial photography***

Differences in local tree species composition are apparent between the AVI and ground data sets. Table 4.2, derived from the confusion matrices of Appendix 1, shows the proportion of sites in which the most abundant tree species were over-estimated, under-estimated, or accurately predicted from air photo interpretation when compared to ground truthed data based on the ground survey. For the relative amount of both aspen and white spruce, predictions based on interpretation of aerial photography are accurate in 70% of the sites; estimates are more often accurate for balsam poplar and black spruce. Abundance of aspen and white spruce, the most common tree species, are in general more frequently overestimated than underestimated when assessed by air photo, but the reverse is true for balsam poplar and black spruce. Thus, the AVI data tends to underestimate the abundance of these two tree species which are rarer in the forest.

In the sites where aspen is overestimated in AVI, balsam poplar and white spruce are both significantly underestimated (Fig. 4.6a). This same figure shows that in sites where aspen is underestimated, white spruce is significantly overestimated. AVI data also significantly underestimate the abundance of black spruce in sites where white spruce is overestimated, and relative abundance of *P .mariana* and aspen is overestimated in sites where white spruce is underestimated (Fig. 4.6b). In cases where black spruce is underestimated, white spruce is significantly overestimated, and in the less frequent cases where black spruce is overestimated, white spruce is significantly underestimated (Fig. 4.6c). The low number of sites with overestimation of balsam poplar in the confusion matrix does not allow the detection of trends in species bias. However, when this species is underestimated, abundance of aspen is significantly overestimated in the provincial data (Fig. 4.6d). Accuracy assessments for the four other tree species were not calculated because these trees are relatively rare on the landscape and the fact that we considered such a wide interval for accurate classification (±20% on each side of the value) makes any emerging patterns suspicious.

4.4 Discussion

4.4.1 *Source of Vegetation Data and Depiction of Biodiversity*

Forest vegetation patterns reflected in both the Canadian ecological land classification system (ecosite), as applied in west central Alberta (Beckingham et al. 1996), and the Alberta provincial forest inventory (AVI) data derived from aerial photography are clearly congruent with spatial patterns of ground-beetle biodiversity (Fig. 4.1). These sources of data about vegetation are broadly available in developed countries for use in landscape scale management of forested land. Analysis presented here suggests that they can provide a quantitative basis for development of coarse filter biodiversity conservation strategies and help guide efficient and effective biodiversity monitoring efforts.

This work reveals a net gain in predictive power (12%) when ecosite classification data are used, instead of maps of relative canopy cover available from AVI. Because the ecosite classification system integrates geospatial information about parent material, slope, aspect, elevation, soils, nutrients, moisture regime, and vegetation (Beckingham et al. 1999), beetle habitat is better modeled. This illustrates the advantage of using a composite georeferenced data base for modeling biodiversity patterns as suggested by Pressey (2004). It is imperative to include many relevant habitat variables in order to develop a surrogate system that adequately represents landscape biodiversity. Quality of input data about the taxa being modeled also contributes to the overall biodiversity predictive power of any surrogate system. Thus, it is of much interest to explore these relationships for other groups in which distribution and abundance varies at the stand level.

We found that accuracy of relative canopy cover estimated through interpretation of aerial photography varies between 70% and 86% (Table 4.2) and that we gained an additional 10% accuracy using tree species mix obtained from direct field survey in predicting ground beetle assemblages over data interpreted from aerial photographs (Fig. 4.1). This suggests that improvement in detection and estimation of tree species abundance on a landbase is crucial to the development of adequate biodiversity surrogates based on vegetation as small inaccuracies in tree species mixes may significantly impact the final classification (Nielsen et al. 1999).

Given the linear relation between tree basal area and canopy cover (Spurr 1960), a similar amount of variance in beetle assemblages should be explained by both datasets. Errors in the identification and estimation of tree species canopy cover inherent in air photo interpretation likely drives the discrepancy observed in these results. The AVI did nonetheless perform reasonably well at explaining the multivariate structure of ground beetle assemblages; 78.3% of the variance explained was congruent with what was explained by the data from ground surveys (18 of 23%).

Although similar patterns of association between vegetation and beetle diversity emerged using either the ground survey of trees or the AVI (Figs. 4.3 and 4.4), some differences were apparent. These differences may affect applicability of these data for conservation and biodiversity monitoring efforts. For example, in our study landscape, strong association between *P. mannerheimii* and tamarack is obvious using field survey data (Figs. 4.4 and 4.5) but more obscure when the association is modeled from the AVI data (Fig. 4.3). It is well understood that *P. mannerheimii* is characteristic of productive wet sites dominated by *Picea* and *Larix* (Larochelle and Larivière 2003). Furthermore, this carabid is recognized in both North America and Fennoscandia as being an uncommon faunal element, being locally restricted by a narrow microhabitat requirement to old wet forests and fire skips (Gandhi et al. 2001, Haila et al. 1994, Niemelä 1997, Niemelä et al. 1992, Paquin 2008). The ecosite classification map captures the distinct habitat occupied by *P. mannerheimmi*, even though the tree canopy cover estimated in AVI is included in developing the ecosite classification. Thus, the ecosite classification system increases the relevance of AVI data for prediction of biodiversity, reinforcing the use of composite geo-referenced databases for biodiversity mapping. Inclusion of many types of variables in the ecosite description compensates for other variables assessed with lower confidence.

Another interesting case is the contrast in associations of *S. haematopus* suggested by alternative descriptions of forest vegetation. The AVI data (Fig. 4.3) suggest a strong association with white spruce, although this species seems to occupy the zone of habitat overlap between white spruce and black spruce in the ordination based on the ground survey data (Fig. 4.4 and 4.5). Comparison of the datasets for the two spruce species (Appendix 4-A) reveals that white spruce is more often overestimated in the AVI while black spruce was more often underestimated when compared to the ground survey data (Table 4.2). This suggests that confusion between the two spruce species in the AVI data leads to an overestimation of the strength for the association between *S. haematopus* and white spruce and an underestimation of the association between this beetle species and black spruce. Although seemingly consistent with published accounts of *S. haematopus* being associated with drier conifer sites (Larochelle et Larivière 2003, Lindroth 1966), results presented here show that many upland stands of black spruce are mistakenly identified as white spruce (see also Spurr 1960). Thus, the association between *S. haematopus* and black spruce does not emerge in analyses based on the provincial inventory data.

There is a similar problem with estimation for two *Populus* species, with balsam poplar often misinterpreted as aspen in data from aerial photography (Table 4.2 and Fig. 4.6 a & d, Spurr 1960). Such misclassification also affects the depiction of associations between forest vegetation and the ground beetle fauna. In the ordination based on the ground survey (Fig. 4.4), the vector for balsam poplar is associated with *A. retractum* and *P. decentis* and the vector for aspen is closer to the vectors for *C. ingratus* and *P. adstrictus*. This is in accordance with the published information about habitat use in these species; i.e., aspen, *C. ingratus* and *P. adstrictus* occur generally on dryer grounds than balsam poplar, *A. retractum*, and *P. decentis* (Burns and Honkala 1990, Larochelle and Larivière 2003). However, in the ordination based on the AVI (Fig. 4.3), both *Populus* species are associated with *A. retractum* and *P. decentis*. Clearly, better differentiation of the fauna associated with each of these two deciduous tree species is achieved in the model based on ground surveys of stand composition (Figs. 4.3, 4.4, and 4.5).

Relative position of vectors for less abundant tree species, such as lodgepole pine and balsam fir, and the beetles *P. brevicornis* and *C. chamissonis*, differ greatly between the ground and AVI based model (Figs. 4.3 and 4.4). The methodology employed here does not allow us to effectively detect bias in air photo interpretation for these less abundant tree species. However, the discrepancy between the ecology modeled from ground survey and air photo data for the less common tree species implies that detection and estimation of less abundant tree species from air photo interpretation does not concur with what was found on the ground. We suggest that accurate detection of surrogate classes that are rare (in this case, less than 2% of the total basal area of all tree sampled by ground survey) on forested landscapes is an important part of an effective approach to employing forest vegetation as a surrogate system for biodiversity. This implies that accurate detection and location of these less abundant surrogate classes provide opportunity to manage landscapes in a manner that should conserve the unique biodiversity gradients associated with these rare trees and, as a consequence, the associated biota.

The use of ground data better represents the finer scale mixture of both deciduous and coniferous components than AVI data. This is based on, for example, by the narrower angle between the white spruce vector and the balsam poplar and aspen vectors in the field survey model (Fig. 4.4) compared to that seen in the model based on the AVI data (Fig. 4.3). Direct comparisons of relative tree species composition confirm that air photo interpreters tend to rarely assign intermediate relative canopy cover values (Appendix 4-A), perhaps reflecting a former provincial policy to manage forest landscapes in terms of either deciduous or coniferous stands. Fig. 4.6 also shows that deciduous species are underestimated in sites where coniferous species are overestimated, and vice versa. Landscape management based on this sort of air photo interpretation will indeed tend to “unmix” the mixedwood forest (Magnussen 1997) and thereby affect the distribution and relative abundances of species that depend upon the natural scale of the mix.

4.4.2 *Accuracy of inventory data interpreted from aerial photography*

For the four tree species common enough for investigation, overall agreement between AVI and ground survey varied between 70% and 86% (Table 4.2). These species composition accuracy values are comparable to those reported by Fent et al. (1995) for 1:500 photographic images of the Alberta mixedwood forest and correspond to the accuracy range of the best Canadian forest inventory maps (Leckie and Gillis 1995). However, only balsam poplar achieved the benchmark of 85% mapping accuracy generally accepted in the remote sensing literature for validating maps (Anderson 1971, Wulder et al. 2006). Thompson et al. (2007) demonstrated that such errors in estimation of relative tree canopy cover in Ontario forest inventory maps did affect temporal projection of wood supply and introduce serious inaccuracies in models and maps of wildlife habitat. Our results also suggest that inaccuracies in forest inventory obtained from air photo interpretation lead to erroneous modeling of ground-beetle habitat in the mixedwood boreal forest of north western Alberta, and may impede the use of remotely acquired data for biodiversity conservation.

The inaccuracies in ground beetle habitat models originating from errors in canopy cover estimation may partly be mitigated and bolstered by using a combination of multiple georeferenced layers representing many habitat variables. From the net gain of 12% in overall predictive power using ecosite classification data, five percent were gained by describing patterns detected by ground survey of trees but undetected by air photo interpretation (Fig. 4.1). Complementing the relative canopy cover derived from air photo with other land variables to produce an ecosystem classification map (ecosite; Nielsen et al. 1999) allowed us to capture some of the biodiversity patterns related to canopy cover that were undetected with the sole use of canopy cover from air photo interpretation. Despite the fact that ecosite classification may enhance our ability to model biodiversity patterns, the use of accurate data is essential to gain as much predictive power as possible and ultimately being able to include the most complete information on biodiversity in conservation on managed forest lands. Technological developments in computer assisted analysis of remotely acquired images promise improvement in tree species differentiation and relative amount estimation, as well as spatial-temporal consistency of the generated data set, and this will improve management for both biodiversity value and fiber resources.

Provincial forest inventory maps currently used in forest management weakly correspond to landscape patterns observed in ground-beetle assemblages. Use of such map data as a management surrogate for strategic implementation of biodiversity conservation on the landscape allocated for extensive harvest provides only minimal knowledge to represent regional biodiversity. Combining these maps with other biophysical geo-referenced databases to produce ecologically based land classification improved our ability to detect biodiversity patterns and should improve our strategic framework for managing biodiversity patterns.

Inaccuracies in the databases derived solely from remotely sensed images lead to biases in biodiversity habitat models, therefore limiting accurate spatial and temporal assessment of regional biodiversity patterns. Despite the general concordance of the ecological associations modeled from field or remotely sensed habitat characteristics, we found that divergence in estimates of relative canopy cover confused detection of ecological associations between distributions of beetle and tree species.

4.5 Conclusion

Implementation of effective conservation strategies for the extensively harvest portion of the boreal forest must start with an accurate, high resolution, wide ranging, and spatially explicit knowledge of relevant landscape habitat parameters. Field work to correlate biodiversity patterns with remotely sensed environmental parameters and assess the accuracy of the habitat maps will support development of biodiversity surrogates to meet conservation goals, as we show in this study. In the absence of such surrogates, resource constraints for conservation efforts presently mean that there is little effective protection of ‘biodiversity’ (as opposed, perhaps, to protection of a handful of charismatic species) for large areas of extensively managed forest. In fact, the Canadian ecosystem classification system has the potential to serve as framework for reporting biodiversity conservation requirements to public and governmental agencies. The possibility of including biodiversity along with other land values, such as ecosystem services and local community values (Naidoo et al. 2008), suggests that spatial databases can be developed as powerful decision tools for regional land management.

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Table 4.1. Code, total area, proportional area, and number of sites for every land classification category recorded within a 50m radius of our 193 sites. The names and codes follow nomenclature by Nielsen et al. (1999).

Ecosite phase	Code	Total area (m^2)	%	n sites
Low-bush cranberry Sw	e4*	423130	27.9	77
Low-bush cranberry Aw	e2*	249251	16.4	46
Low-bush cranberry Aw-Sw-Pl	e3*	241713	15.9	59
Treed bog	k1*	145549	9.6	35
Treed poor fen // treed bog	l1/k1*	91588	6.0	19
Low-bush cranberry Sw // bracted honeysuckle Sw	e4/f4	84896	5.6	16
Shrubby poor fen // shrubby meadow	l2/g1*	78144	5.2	21
Labrador tea/horsetail Sb-Sw // labrador tea-mesic Pl-Sb	j1/d1*	27740	1.8	5
Low-bush cranberry Aw // bracted honeysuckle Aw-Pb	e2/f2*	26874	1.8	4
Labrador tea/horsetail Sb-Sw // horsetail Sw	j1/i3	20278	1.3	6
Treed bog // labrador tea-subhygric Sb-Pl	k1/h1*	19044	1.3	4
Labrador tea-mesic Pl-Sb // low-bush cranberry Pl	d1/e1*	18358	1.2	5
Bracted honeysuckle Aw-Pb	f2*	18358	1.2	4
Low-bush cranberry (no tree canopy)	e?*	14178	0.9	3
Labrador tea-subhygric Sb-Pl // labrador tea/horsetail Sb-Sw	h1j1*	9790	0.6	3
Water	w1	9749	0.6	6
Low-bush cranberry Sw // labrador tea/horsetail Sb-Sw	e4j1	9152	0.6	3
Treed poor fen	l1*	7903	0.5	2
Bracted honeysuckle Sw // horsetail Sw	f4i3	6119	0.4	1
Anthropogenic	z1	5640	0.4	6
Low-bush cranberry Pl	e1	5002	0.3	1
Bracted honeysuckle willow	f6*	1857	0.1	1
Shrubby poor fen // forb meadow	l2g2	1635	0.1	1

Table 4.2. Accuracy estimation of relative canopy cover by Alberta Vegetation Inventory for the four most abundant tree species when compared to 198 ground surveyed sites.

	P.tremuloides		***P.balsamifera***		***P.glauca***		***P.mariana***	
	n sites	%	n sites	%	n sites	%	n sites	%
Accurate	138	70	170	86	137	69	148	75
Overestimated	45	23	2	1	36	18	8	4
Underestimated	15	7	26	13	25	13	42	21

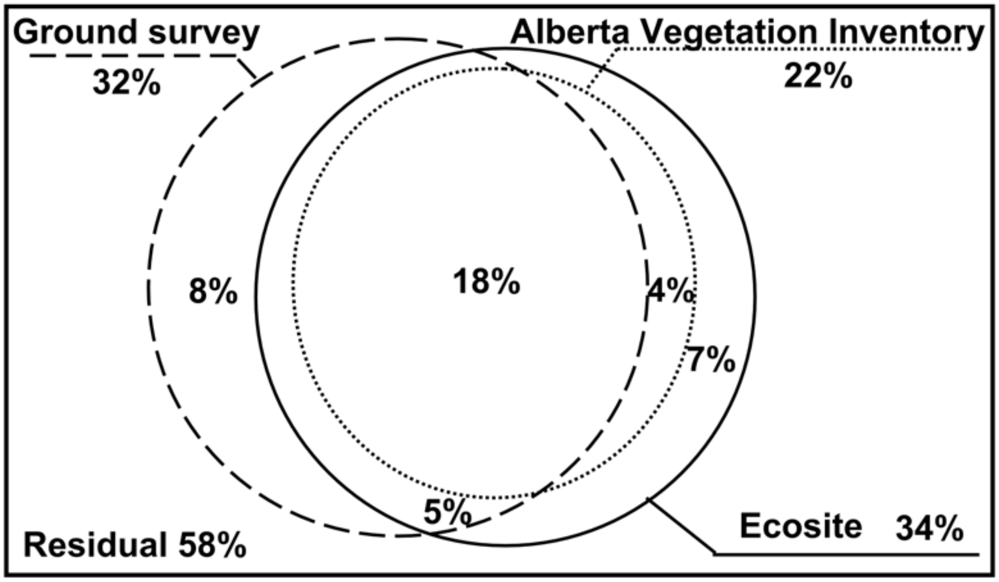

Figure 4.1. Venn diagram representing the proportion of the variation in the beetle community explained by the different datasets. Percentages are rounded to the closest unit.

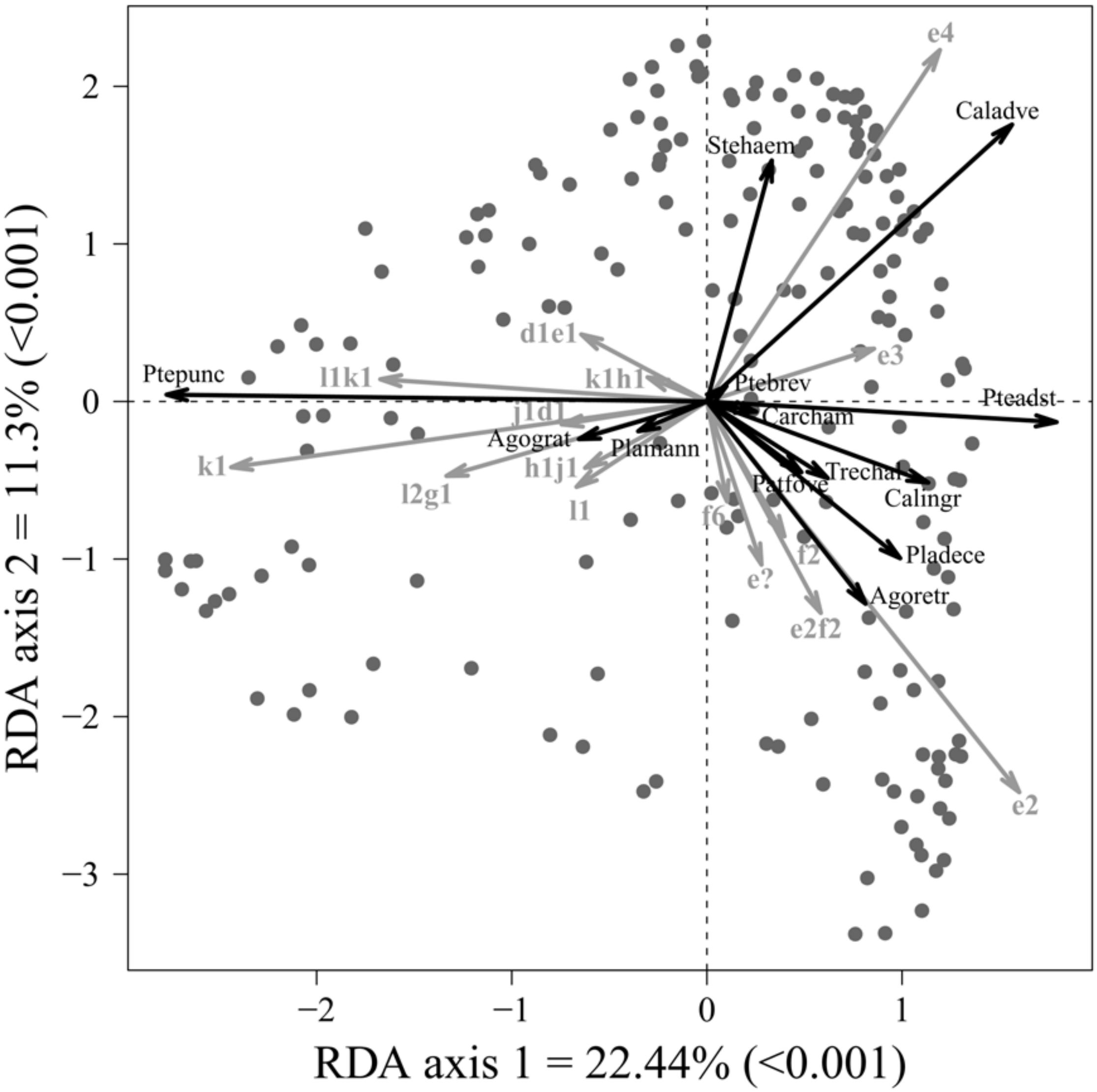

Figure 4.2. Ordination diagram resulting from a redundancy analysis between the beetle assemblage and the ecological classification map. Grey dots are the 193 sites. The ecological categories are in light grey and the beetles species are in black. Refer to table 1 for the code of the ecological categories. The abbreviations of the beetle species are as follow: Agograt: *Agonum gratiosum*, Agoretr: *Agonum retractum*, Caladve: *Calathus advena*, Calingr: *Calathus ingratus*, Carcham: *Carabus chamissonis*, Patfove: *Patrobus foveocollis*, Pladece: *Platynus decentis*, Plamann: *Platynus mannerheimmi*, Pteads: *Pterostichus adstrictus*, Ptebrev: *Pterostichus brevicornis*, Ptepunc: *Pterostichus punctatissimus*, Stehaem: *Stereocerus haematopus*, Trechal: *Trechus chalybeus*.

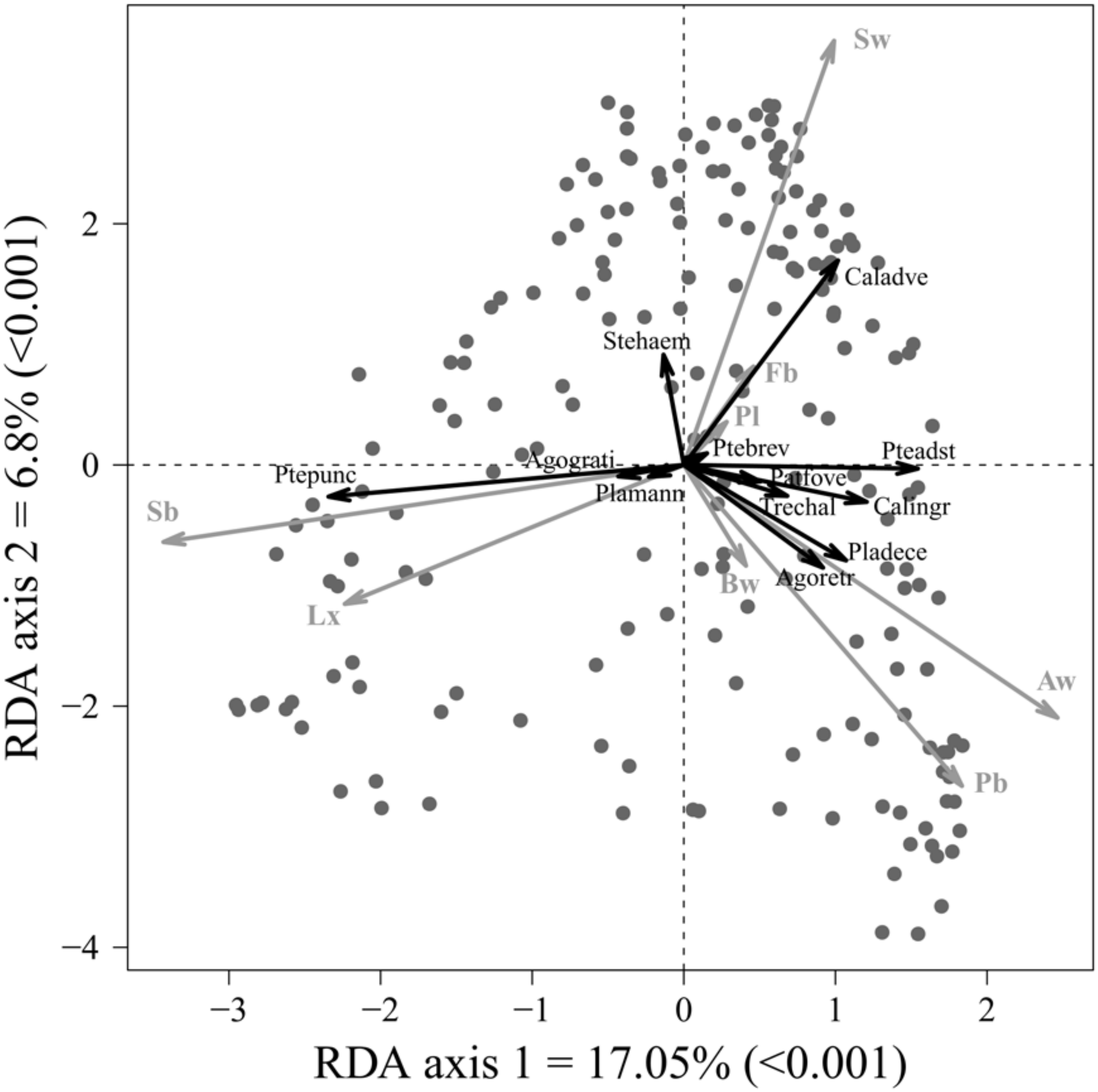

Figure 4.3. Ordination diagram resulting from a redundancy analysis between the beetle assemblage and the relative canopy cover of provincial forest inventory map. The abbreviations for beetle species are as in Fig. 2. The abbreviations for tree species are as follow: Aw: *Populus tremuloides*, Bw: *Betula papyrifera*, Fb: *Abies balsamea*, Lx: *Larix laricina*, Pb: *Populus balsamifera*, Pl: *Pinus contortae*, Sb: *Picea mariana*, Sw: *Picea glauca*.

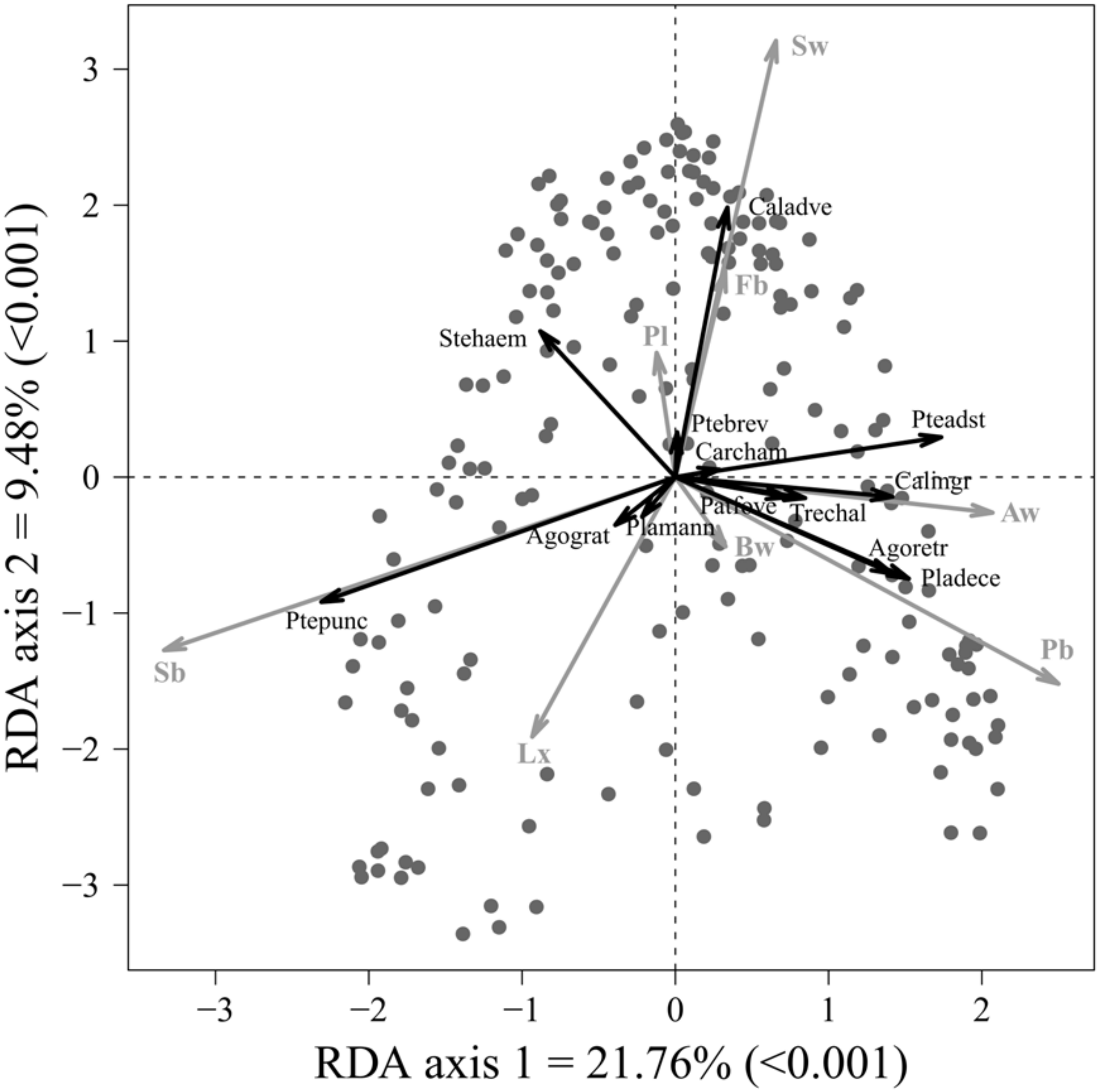

Figure 4.4. First and second axis of the ordination diagram resulting from a redundancy analysis between the beetle assemblage and the relative basal area of tree species recorded from ground survey. Abbreviations for the beetle species are as in Fig. 2 and those for the tree species are as in Fig. 4.3.

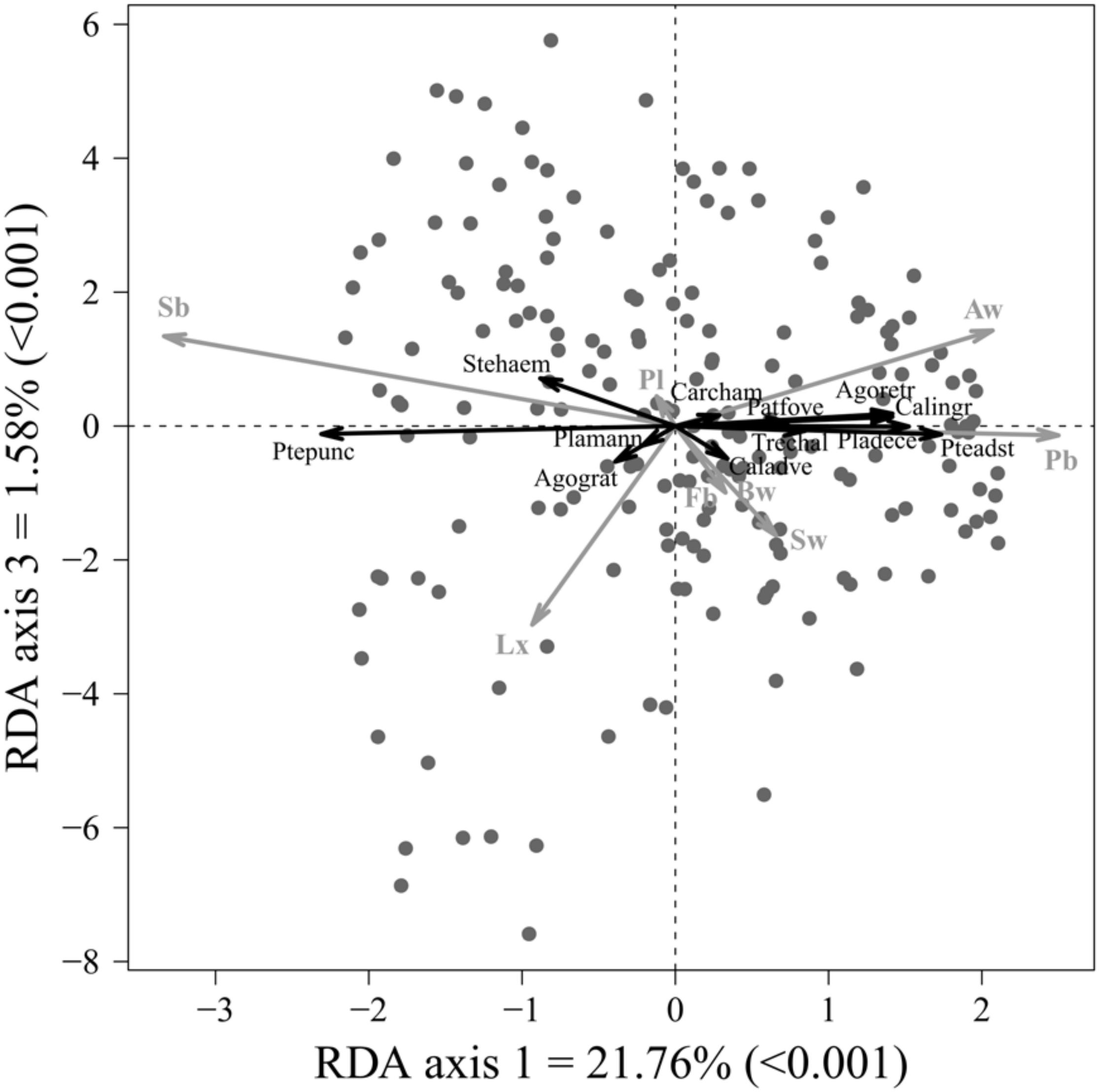

Figure 4.5. First and third axis of the ordination diagram resulting from a redundancy analysis between the beetle assemblage and the relative basal area of tree species recorded from ground survey. Abbreviations for the beetle species are as in Fig. 2 and those for the tree species are as in Fig. 4.3.

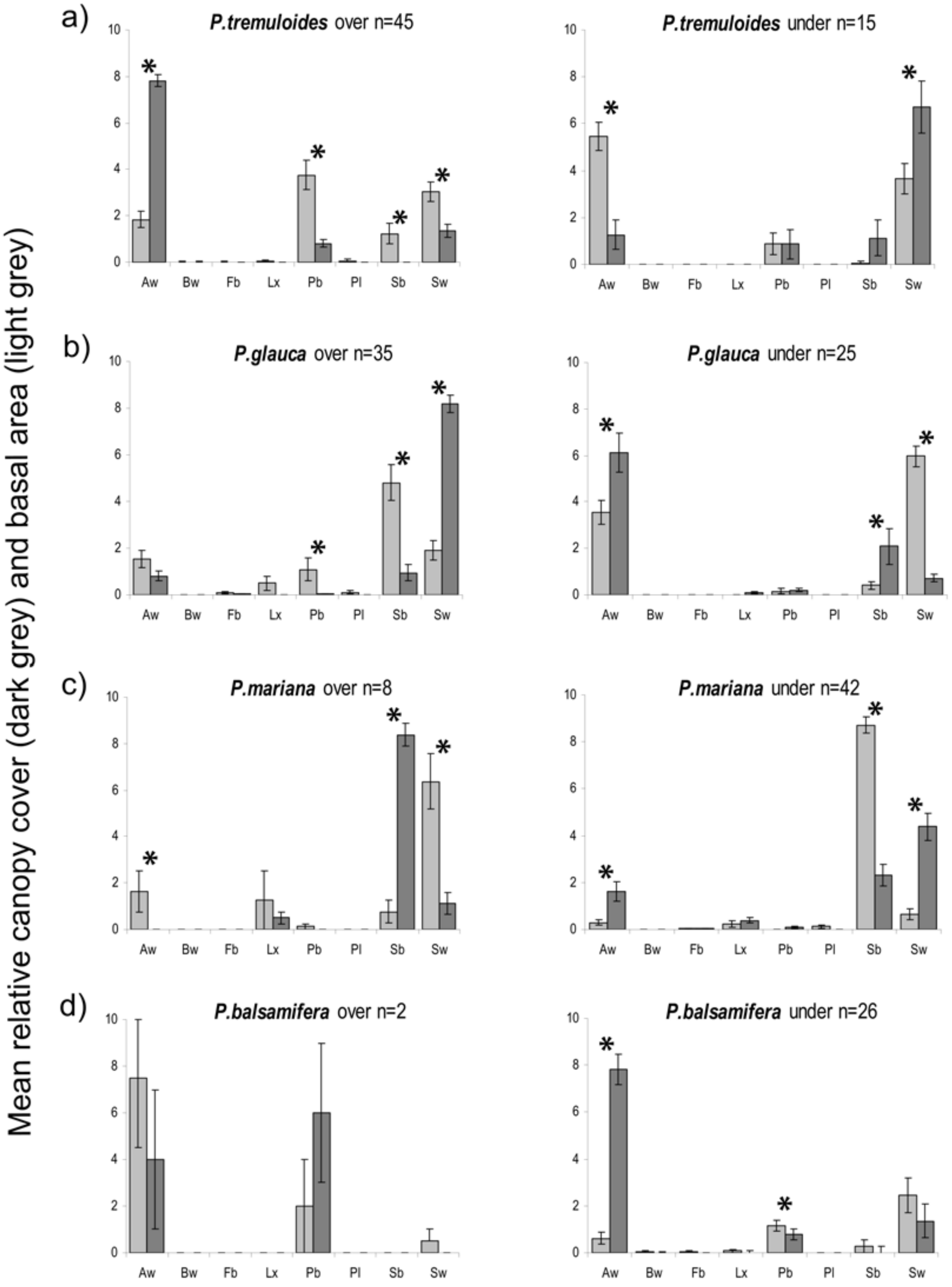

Figure 4.6. Average percentage (± SE) by tree species in misclassified sites estimated by air photo interpretation (dark grey) and ground survey (light grey). * indicates a significant ($p<0.05$) difference between provincial inventory and ground survey. Refer to Fig. 4.3 for abbreviations of tree species. Over = overestimated, under = underestimated.

Appendix 4-A: Confusion matrices of 198 sites between percentage of canopy cover evaluated by AVI and percentage of basal area assessed by ground survey for the most abundant tree species.

CHAPTER 5

Effect of habitat type and pitfall trap installation on boreal forest ground-dwelling arthropod assemblages

5.1 Introduction

Arthropods are gaining popularity as target organisms in environmental assessment studies (Kremen et al. 1993, McGeoch 1998, Taylor and Doran 2001, Langor and Spence 2006) but both the natural history and habitat associations of most species is still poorly known. These shortcomings hinder the capacity to provide a clear species-level picture of biodiversity variation on the scale of natural landscapes and in a way that parallels normal expectations for work with vertebrates. A crucial step toward such knowledge is to combine the results of local studies assessing species distribution in different habitats with the broader scientific literature about arthropod taxa to provide the most complete information possible about all species considered, including those that are uncommon, locally restricted and most in need of high priority attention (Nichols and Williams 2006). Using species as working unit supports development of relevant ecological knowledge not only at species level but also provides more accurate and comparable analyses of biodiversity patterns in terms of species richness and composition (Spence et al. 2008).

McGeoch (1998) and Jonsson and Jonsell (1999) suggest that combining many taxa yields a more accurate representation of the environment, and therefore possibly provides more sensitive indicator value. In an analysis of ground beetles, rove beetles and spiders, for example, Buddle et al. (2006) found clearer patterns of arthropod response to disturbance in the pooled data than from singular consideration of each individual taxon. Populations of these ground-dwelling arthropod taxa are easily and simultaneously well sampled using pitfall traps (Marshall et al. 1994), making them especially appealing as operational indicators of ecosystem response. Furthermore, because ground and litter habitats of some sort remain, even after the most severe disturbance, the response of epigaeic arthropods, including both specialist and generalist taxa (Niemelä et al. 1993), can be studied across any gradient of broad habitat change.

Useful association of ground-dwelling arthropod assemblages with different habitat types necessitates special attention to the sampling technique employed (Spence at al. 2008). Pitfall traps, well suited for sampling epigaeic arthropods, are known to yield biased estimates of species composition and population sizes (Greenslade 1964, Uetz and Unzicker 1976, Adis 1979, Franke et al. 1988, Topping and Sunderland 1992, Spence and Niemelä 1994, Esch et al. 2008). In addition to intrinsic trap and species specific factors (Luff 1975, Waage 1985, Halssall and Wratten 1988, Morill et al. 1990, Lemieux and Lindgren 1999, Work et al. 2002, Koivula et al. 2003), stand characteristics such as canopy openness (temperature, moisture; Briggs 1961, Honek 1997, Esch et al. 2008), vegetation structure (Greenslade 1964, Koivula et al. 2003, Phillips and Cobb 2005) and forest floor characteristics (Greenslade 1964) may all affect the catch of arthropods at the individual and species level.

Although largely unstudied, variation in placement of traps affecting exactly which forest floor level is sampled may cause bias in the pitfall trap samples. The organic soil layer (LFH horizons in the Canadian Soil Information System; Agriculture Canada Expert Committee on Soil Survey 1983) of coniferous mixed, or deciduous stands are characterized by quite different surface litter layers, originating from accumulation of curled leaves or needles, combined with feather mosses or sphagnum in lowlands. This variation in organic soil layer among forest stands provides different microhabitats for prey items, refuges from predators, and microclimatic environment that may drive differential behavior of ground dwelling arthropods and variation in composition of their assemblages. Furthermore, the three dimensional structure of the organic soil layer provide habitats beneath the surface in certain stands and thus alter the arthropod assemblages represented in pitfall trap catches. This particular problem has not been addressed although it could be important for studies that attempt to establish associations between ground-dwelling arthropods and ecological land classification systems.

In this study, we simultaneously investigated habitat associations of ground-dwelling spiders, rove and ground beetles in three different habitats of the Lower Foothill natural subregion of northwestern Alberta (Beckingham et al. 1996). We first looked at differences in number of species and number of individuals amongst different stand types and then further examined arthropod species level associations within these habitats comparing our results with studies conducted more broadly in the boreal forest. We also studied the effect of pitfall trap depth on catch by comparing assemblages from those with the lip at the surface of the organic soil with those having the lip at the top of the mineral soil.

5.2 Methods

5.2.1 *Study area*

The study was conducted at the EMEND (Ecosystem Management Natural Disturbance, Spence et al. 1999) research site in the boreal forest of northwestern Alberta, Canada. The study area is located in the Lower Foothills forest region on the border of the mixedwood forest region (Rowe 1972). The forest communities of the Lower Foothills natural subregion reflect the transition between the mixedwood boreal forest and the Rocky Mountain cordilleran ecosystem. Upland forest at EMEND is dominated by a mixture of *Picea glauca* (Moench) Voss, *Populus tremuloides* Michx. and *P.balsamifera* L. and the poorly drained sites by *Picea mariana* (Mill.) B.S.P. and *Larix laricina* (Du Roi) K Koch. Beckingham et al. (1996) identified 14 types of ecosite and 30 ecosite phases in this subregion. A number of understory plant community types are also associated with this classification system. However, there is no integrated information about the arthropods associated with any of these classes.

The three forest habitats types selected for this study represent three ecosite phases as described by Beckingham et al. (1996): low bush cranberry aspen dominated (e4; canopy cover > 80% *Populus tremuloides*), low bush cranberry white spruce dominated (e2; canopy cover > 80% *Picea glauca*), and tree bog (k1; canopy cover > 80% *Picea mariana*). We selected these three ecosite phases, drawn from two ecosites, in order to investigate whether data about arthropod assemblages reflects the hierarchical nature of the classification system. The low bush cranberry ecosite is the reference site for the Lower Foothills subregion and typically has a mesic moisture regime and a medium nutrient regime (Beckingham et al. 1996). The bog ecosite develops thick organic soils composed of slowly decomposing peat. It is characterized by a poor nutrient regime and poor drainage (Beckingham et al. 1996). The location of ecosite phases across the study sites was obtained from a map generated by Nielsen et al. (1999).

5.2.2 *Sampling design*

Three replicated groups of six pitfall traps were installed in each of the three ecosite phases designated above, for a total of 54 traps spread over nine sites. Each trap was a plastic cup with an opening diameter of 11 centimeters and a depth of 13 centimeters, containing a plastic inner cup and a wooden roof supported over the trap by two large nails driven through opposite corners (see Spence and Niemelä 1994). A 2 x 3 grid of six traps was put in the ground at each site with an inter-trap distance of five meters. Three randomly chosen traps were positioned in the grid with the lip flush with the forest floor (hereafter called surface traps) and the remaining three were set deeper, with the lip at the mineral soil level (hereafter called deep traps). Deep traps were 15 and 25 cm below the forest floor. Most black spruce sites had more than a vertical meter of sphagnum accumulation and the deep traps were therefore positioned 20 to 25 cm below the forest floor in order to position them above the water table. About 150 ml Ethylene gycol (GM Dex-Cool®) was added to each trap as a preservative and traps were serviced every third week between 24 May and 20 August 2005, giving a total of 89 trapping days. Replicates were located at least four kilometers from each other and the three sites within replicates were less than one kilometer apart.

Specimens were collected by decanting the trap contents into a piece of cheese cloth in the field and carabids, staphylinids and spiders were subsequently sorted from the samples and identified to species in the laboratory. Aleocharine staphylinids (excluding specimens from the genus *Lypoglossa*) could not be identified to the species level, given the time and resource constraints of this study. Thus, the 215 individuals placed in this sub-family were not considered in the following analyses. Voucher specimens are deposited in the Spence laboratory collection for further reference.

5.2.3 *Statistical analysis*

Data about annual abundances and number of species were pooled from the three traps run at the same depth in each site. These numbers were divided by the total number of trap days for these particular traps to adjust the data for differences in sampling effort resulting from trap disturbance. The following analyses were computed using R 2.9.0 (R Development Core Team 2009) using functions developed by authors as cited below.

Composition of ground-dwelling arthropod assemblages was compared among habitat types and between trap depths using a non-metric multi-dimensional scaling (NMDS) ordination (McCune and Grace 2002) calculated using the function ‘metaMDS’ from the vegan package for R (Oksanen et al. 2009). The Bray-Curtis dissimilarity measure was used to build the dissimilarity matrix and the optimal number of dimensions was determined using the five percent rule in stress reduction (McCune and Grace 2002). The final configuration was tested against random configuration through 999 permutations.

Permutational multivariate analysis of variance (perMANOVA, Anderson 2001, McArdle and Anderson 2001), calculated using the ‘adonis’ function from the vegan package for R (Oksanen et al. 2009) was used to assess differences in arthropod composition among habitats and trap depth. Each test was based on 999 permutations using the Bray-Curtis index as the distance metric. PerMANOVA was conducted on the three taxa separately as well as the pooled data, using habitat and trap depth as grouping variables. The effect of trap depth within habitats was assessed using a blocked perMANOVA calculated with depth as the grouping variable and habitat as the blocking variable.

In order to evaluate potential effects of habitat and trap depth on the number of individuals and the number of species, a two factorial permutational ANOVA (Anderson and Legendre 1999) was performed on each taxon separately as well as on the pooled data for all three taxa. Because estimates of species richness are sensitive to sample size (Buddle et al. 2005), species richness was compared among depths, habitats, and taxa, using individual based rarefaction curves (Simberloff 1979). This analysis, calculated using the function “rarefaction” (Jacobs 2006), was based on the raw data as the goal is to standardize the number of species by the number of individuals.

Species-specific associations with habitat types and trap depths were investigated using indicator species analysis (Dufrêne and Legendre 1997) using the “duleg” function from the labdsv package for R (Roberts 2007). Species with a probability lower than 0.05 determined using MonteCarlo simulation (999 permutations) were considered significant indicators.

5.3 Results

5.3.1 *Taxa*

A total of 1767 adult individuals belonging to 102 species of the Carabidae (n=442, 16 spp), Staphylinidae (n=1082, 41 spp) or Aranea (n=243, 45 spp) were identified and subjected to analysis (Appendix 5-A). Comparison of rarefaction estimates revealed that spiders had the highest species richness when standardized for the number of individuals sampled. The rarefaction curves reached an asymptote for ground and rove beetles but the accumulation rate for spider species remained high at the maximum sample size (Fig. 5.1).

5.3.2 *Habitat*

The assemblages of ground dwelling arthropods from the three habitat types are quite distinctive with respect to species composition (Fig. 5.2), and these differences were significant when assessed using a permutational MANOVA ($p<0.001$; Table 5.1). Furthermore, the habitat groups that are classified as the same ecosite (low bush cranberry Aw and low bush cranberry Sw) are closer in ordination space than either is to the tree bog ecosite.

Overall, consistently fewer individuals and species were collected at both depths (analysis of depth effects below) in black spruce stands than in aspen and white spruce stands (Figs. 5.3 and 5.4). Separate analyses for ground and rove beetles showed the same pattern as did the overall assemblages but no differences were found among habitats for either the number of individuals or species of spiders (Figs. 5.3 and 5.4). On average, ground beetles were more abundant in white spruce forests while rove beetles were more abundant in aspen forest (Fig. 5.3) but this pattern is less apparent in the data about species richness (Fig. 5.4). The fewest individuals and species were collected in black spruce stands, but rarefaction shows that the tree bogs have the highest species richness, when adjusted for sample size (Fig. 5.5), presumably because this habitat was more poorly sampled by pitfall traps.

Of the 103 species identified, 20 (twelve rove beetles, five ground beetles, and three spiders) had significant indicator value for of one of the three habitats sampled (Table 5.2). Twelve indicator species were associated with aspen forest, six with white spruce forest, and two with black spruce forest. Species from all three taxa were indicators of aspen stands but spiders were the only indicators of black spruce stands. The twelve species indicating the aspen dominated ecosite phase included nine rove beetles, two ground beetles and one spider. Three rove beetles and three ground beetles were significant indicators of the white spruce dominated ecosite phase.

5.3.3 ***Trap Depth***

There was no statistically significant overall effect of trap depth, suggesting that all species sampled were largely epigaeic. NMDS ordination (Fig. 5.2) did not achieve clear separation of the arthropod assemblages collected in surface and deep traps, even when compared within habitat. Furthermore, trap depth did not significantly affect assemblage composition in the perMANOVA analysis.

The overall number of individuals captured was not consistently affected by the depth at which the trap was installed. However, the interaction of habitat and depth did significantly affect trap captures (ANOVA all taxa, p=0.02). The surface traps in aspen understory collected more individuals than did deep traps, but this pattern is reversed in white spruce habitat (Fig. 5.3). Staphylinid beetles were captured more frequently in surface traps of the aspen stands and spiders were the only taxa consistently collected in higher number in the surface traps of all habitats (Fig. 5.3). Across all habitats, surface traps also collected more species than deep traps (rarefaction curves are not presented here, but they gave the same result) but when looking at the taxa separately, this pattern is significant only for spiders (Fig. 5.4).

No species were significant indicators of the depth at which pitfall traps were installed. However, 11 species were indicators of a certain trap depth within specific habitat. Three beetle species, two carabids and one staphylinid, significantly indicated deep traps (Table 5.3). These species are *Agonum retractum* (Carabidae) in aspen forest, and *Pterostichus brevicornis* (Carabidae) and *Quedius velox* (Staphylinidae) in white spruce forest. Because these three species are each strong indicators of the habitats in which the effect was significant, it appears that each is characterized by significant subsurface activity in the indicated habitat. As listed in Table 5.3, one carabid species indicates surface traps in white spruce forest, five staphylinid species in aspen forest, three spider species in black spruce forest and one spider species in aspen forest.

5.4 Discussion

5.4.1 *Habitat*

Pitfall catches of the dominant taxa of litter dwelling arthropods varied among forested habitats in parallel to the ecosite classification system as applied to the Lower Foothills Ecoregion (Fig. 5.2, Table 5.1). The arthropod community further reflected the hierarchical nature of the classification system by grouping the habitats (ecosite phases) belonging to the same ecosite closer than to the habitat belonging to a different ecosite. The moisture-nutrient gradient used to define the different ecological classes (ecosites) in Beckingham et al. (1996) and the further refinement into ecosite phases based on canopy cover thus provide a reasonable surrogate for describing the ground dwelling arthropod assemblages.

Use of the Canadian Forest Ecosystem Classification (CFEC) as habitat-based surrogate for arthropod associations may be advantageous because this system is becoming a standard for forested land classification in Canada and is becoming widely used in land management (Natural Resources Canada 2006). The close association observed between arthropod assemblages and the CFEC supports an important step toward developing strategy to facilitate widespread, efficient and effective biomonitoring (Langor and Spence 2006, Spence et al. 2008). Our results reinforce the idea that such biodiversity ‘surrogates’ can provide a framework for a coarse filter approach to conservation in forested land management.

Interestingly, combination of data about the three litter dwelling taxa also gives a more accurate representation of the ecosite classification system than does data for each separate taxon (Table 5.1). Buddle et al. (2006) also found that analysis of ground beetles, rove beetles and spiders together yielded a more accurate picture of the habitat features than did each taxon analyzed separately. This phenomenon may arise from the fact that each species has its own particular habitat requirement and consequently as more species are included in the analysis, a greater range of ecological niches is considered, leading to better correspondence with the habitat features. Based on these and other related findings (e.g., Buddle 2006), we conclude that a wider range of taxa will give a more robust representation of biodiversity as is appropriate for monitoring programs, especially when sampling effort is limited because of extraneous factors.

The low individual and species abundance of arthropods in the black spruce lowland forest (tree bog ecosite phase; k1) when compared to that in the low bush cranberry aspen (e2) and white spruce (e4) ecosite phases was also noted for ground beetles by Langor et al. (2006) in corresponding ecosite phases of the Upper Foothills natural subregion. Other studies about habitat associations of arthropods in the boreal forest have also noted fewer individuals and species of Carabidae in black spruce forests compared to deciduous forest (Niemelä et al. 1992, Pearce et al. 2003). Niemela (1993) suggest that coniferous boreal forest is a less suitable environment for ground beetles. The acidity, high water table, absence of mineral soils and low decomposition rate in black spruce dominated peatlands (Vitt 1994) further increase the adversity of these sites for ground dwelling beetles. In their review of insect biodiversity in boreal peat bogs, Spitzer and Danks (2008) also mention that bog arthropod fauna are generally composed of species performing well in adverse environments such as arctic, subarctic or alpine.

Altough fewer individuals and species were collected in the tree bog compared to other ecosite phases, it does not mean that this ecosite phase is of lower importance for biodiversity. When correcting species richness for the sample size using rarefaction, in fact, this forest habitat type has the most diverse fauna (Fig. 5.5, see also Langor et al. 2006). Even if this ecosite is not directly targeted for forest harvest in western Canada, it is indirectly affected by harvesting through water table variation that influences biodiversity. Black spruce bogs are also pressured by mineral exploration, management of beaver dams and oil sands extraction in Alberta. Because biodiversity is a landscape feature, it is important to monitor biodiversity in ecosites that are not directly affected by particular disturbances of interest, such as forest harvesting. In our study, this pattern of lower abundance and species richness in bogs held for ground and rove beetles but not for spiders.

5.4.2 *Spiders*

We collected as many species and individuals of spiders in the black spruce dominated site as in the upland sites dominated by either aspen or white spruce (Fig. 5.3 and 5.4). Many ground dwelling beetles rely on the presence of soil for hibernation, oviposition, and larval and pupal development (Thiele 1977) and, during these more immobile stages (Loveï and Sunderland 1996) will be subject to frequent flooding and freezing of the high water table in the tree bog. In contrast, spiders of the common forest-dwelling family Lycosidae (wolf spiders) carry their eggs and can therefore avoid effects of frequent water table rises. Young spiders are active and also capable of ballooning (Decae 1987), behavioural traits which may reduce mortality related to flooding. Wolf spiders clearly dominated the black spruce lowland forest community (over 51% of the spider individuals) in this study, while they accounted for a smaller percentage of individuals captured in aspen (13.6%) and white spruce (2%) stands. Both Uetz (1976) and Pearce et al. (2004) also remark that wolf spiders frequently dominate in areas subject to flooding. Lycosid spiders, thus, use a niche that other litter dwelling arthropods caught in pitfall traps less readily occupy, and numbers of species and individuals captured were as high in the tree bog black spruce dominated ecosite phase as in either of the two upland ecosite phases.

Only two spider species (*Pardosa uintana* and *Gnaphosa microps*) were significant indicators of the bog ecosite dominated by black spruce (Table 5.2). *P.uintana* has been previously recorded in spruce-fir forests, sphagnum bogs, lichen mats, and alpine tundra (Dondale and Redner 1990, Pearce et al. 2004, Work et al. 2004). Buddle et al. (2000, 2006) found *P.uintana* in recently burned deciduous stands but suggested that the species re-colonized the stand from a nearby patch of wet coniferous forest. *G.microps*' habitat is described as characteristic of willow thickets, under stones, in moss, meadows, and moors (Platnick and Dondale 1992) and previous authors have noted its affinities for wet environments with thick moss/lichen layer, peatlands, and arctic-alpine tundra (Aitchison-Bennel 1994, Koponen 1994). Another lycosid, *P. hyperborea* (Appendix 1), although uncommon, was collected only from the tree bog in our study and has been associated with coniferous forest, peatlands, bog and tundra environment (Nordstrom and Buckle 2002, Aitchison-Bennel 1994, Dondale and Redner 1990). Koponen (1994) noted that *G.microps* and *P.hyperborea* are northern species found mainly in bogs in more southern localities, a phenomena also characterizing other species inhabiting peat bogs (Spitzer and Danks 2006). Koponen (1987) suggests that these open bog habitats may offer more favorable microclimate on sunny days or that prey availability is more suitable for particular species. Trees in the bog ecosite are smaller and sparser than in the low bush cranberry ecosite and this allows more light to reach the ground and more opportunity for the wolf spiders to regulate temperatures experienced by their eggs.

Pardosa mackenziana, significantly indicated the low bush cranberry aspen dominated ecosite (Table 5.2). This species is among the commonest spiders of the boreal forest (Pearce et al. 2004, Work et al. 2004) and may be found in many different habitats such as salt marches, beaches and deciduous forest (Lowrie 1973, Dondale and Redner 1990, Buddle et al. 2000, Nordstrom and Buckle 2002). *P.mackenziana* could be considered as generalist but both in our study and the study by Work et al. (2004) conducted at the same site in north-western Alberta, this species is most common in deciduous forest, as compared to coniferous forest and bogs. Buddle (2000), who worked on the life history of *P.mackenziana* in central Alberta, noted that this species likes warmer microclimates where the female can bask their egg sacs in the sun (see also Buddle et al. 2000). Our conifer-dominated sites were darker than our deciduous stands which may explain why we collected a highest abundance of this species in the deciduous forest. However, factors other than temperature are involved as *P.mackenziana* is not common in the more open tree bog habitats.

Allomenga dentisetis, *Bathyphantes pallidus*, *Diplocentria bidentata*, and *Cybaeopsis euopla* were also collected in high abundance in the low bush cranberry aspen dominated ecosite relatively to the other habitats (Appendix 5-A). Among these, only *C. euopla* is recognized as being associated with deciduous stands (Aitchison-Benell and Dondale 1990). Published accounts about the other species do not directly associate them with deciduous forest (Ivie 1969, Millidge 1984, Aitchison-Benell and Dondale 1990); however, *A.dentisetis* and *B.pallidus* represented a major component of the catches in other studies conducted in deciduous forest (Koponen 1987, Buddle and Draney 2004, Work et al. 2004). In contrast, Koponen (1994) and Aitchison-Bennel

(1994) reported these two species from bogs in Québec and Manitoba. This discrepancy amongst studies about the ecology of *A.dentisetis* and *B.pallidus* may be related to the fact that peatland invertebrate fauna generally reflect the arthropod assemblages of the surrounding forest (Marshall and Finnamore 1994) and species habitat preference must be assessed on a landscape basis including multiple available habitats.

5.4.3 *Ground beetles*

Three ground beetle species were significant indicators of the low bush cranberry ecosite dominated by white spruce (Table 5.2): *Pterostichus brevicornis*, *Stereocerus haematopus* and *Calathus advena*. *P. brevicornis* and *S. haematopus* are characteristic of the northern boreal forest (Lindroth 1963, vol 4), and have been suggested as indicators of sustainable forest management (Pearse and Venier 2006). *C. advena* has affinity for shady closed forest (Lindroth 1963, vol 4). In other work at EMEND (Work et al. 2004, 2010, Jacobs et al. 2008) *S. haematopus* and *C. advena* were most often collected in sites dominated by white spruce and the highest abundances of *Agonum retractum* and *Platynus decentis* were found in deciduous forest. These latter two species were significant indicators of the low bush cranberry ecosite dominated by aspen in our study. Langor et al. (2006) also report similar associations in the upper foothills ecoregion, with *P. brevicornis* being indicative of conifer mesic ecosites and *A .retractum* and *P. decentis* indicative of mesic deciduous ecosites. Other carabid species, including *Trechus chalybeus, Pterostichus adstrictus, Calathus ingratus* and *Patrobus foveocollis,* are frequently collected in low bush cranberry ecosite, regardless of the canopy type (ecophase), but these generalist species are almost absent from the bog sites (Appendix 5-

A). This seems to be a common pattern in mixed forest (Lindroth 1961 &1963, Niemela et al. 1992, and Pearse and Venier 2006).

No ground beetles were significant indicators of the black spruce forest. *S. haematopus*, *Carabus chamissonis* and *P. punctatissimus* were, however, caught in relatively high abundance in the bog ecosite in comparison to other carabid species (Appendix 5-A). Larochelle and Larivière (2003) note that these species occur often in lowland coniferous forest and that *S. haematopus* has a special affinity for spruce-bogs, and Paquin (2008) lists *S. haematopus* as a strong indicator of black spruce bogs in eastern Canada. Although these three species are not necessarily more abundant in bogs than elsewhere, they are the only ground beetles that are reasonably common in the black spruce dominated bog ecosites.

5.4.4 *Rove beetles*

Three (*Lypoglossa angularis*, *Quedius velox* and *Tachinus frigidus*) of the twelve significant rove beetle indicators species were indicators of the white spruce dominated habitat (Table 5.2). In a study conducted in upland coniferous forest of western Alberta (Pohl et al. 2007), *T. frigidus* was the most common species collected and both *T. frigidus* and *Q. velox* were classified as specialists of mature coniferous forest. *L. angularis* has been collected in many different types of litter (Hoebeke 1992) but was most common in coniferous forest in our study.

The nine other rove beetle species with indicator status were most strongly associated with aspen dominated habitat, a pattern not surprising given that more specimens and species of rove beetles were caught in this latter habitat (Fig. 5.3 and 5.4).

The overall strong association of rove beetles with aspen stands may be related to the high decomposition rate relative to coniferous dominated stands. The amount of leaf litter input in deciduous stands is greater than litter input from coniferous trees and the deciduous matter decomposes faster than coniferous matter (Polyakova and Billor 2007). Thus fungal populations are likely higher, attracting more staphylinid species that are strongly associated with fungus and decomposing matter (Klimazewski 2000). *Tachinus fummipennis* was the strongest indicator of aspen dominated forest (Table 5.2) and it is common in other deciduous forests (Klimaszewski et al. 2008). In our study, *A.quadrata* also significantly indicated aspen dominated forest and was caught there in overwhelming numbers compared to white and black spruce dominated habitats.

For some rove beetles, old forest may be more important than canopy type. For example, *Acidota quadrata* has been classified as an indicator of mature stands in other studies of both deciduous (Buddle et al. 2006) and coniferous (Pohl et al. 2007) forests. In fact, *Quedius labradorensis, Ischnosoma splendidum*, *Dynothenarus pleuralis*, *Tachinus elongatus, Quedius rusticus* and *Quedius impar*, all of which are significant indicator species of aspen dominated forest in our study (Table 5.2), were all collected by Pohl et al. (2007) in coniferous forest. Many of these species were also collected in the coniferous habitats of our study (Appendix 5-A) but the catches were always higher in deciduous dominated forest. Pohl et al. (2007) found that *I. splendidum* is indicative of young, regenerating coniferous stands, perhaps reflecting that harvested coniferous sites tend to regenerate with aspen and deciduous shrubs.

None of the rove beetles species were identified by indicator species analysis as significant indicators of black spruce forest, because most also occurred elsewhere.

However, among staphylinids, *Eucnecosum brunnescens*, *A. quadrata*, and *Quedius brunnipennis* were collected in relatively high abundance in the black spruce bog (Appendix 5-A). *E. brunescens* is known to occur in moist leaf litter and can be found in any type of cool moist habitat (Campbell 1984). Many paleoenvironmental studies of insect fossils in peat stratigraphy have included *E. brunnescens* (Short and Elias 1987, Miller and Morgan 1991, Nelson and Carter 1987, Cong et al. 1996 and Lavoie et al. 1997) and it is often one of the abundant species. *A. quadrata* is also one of the most ubiquitous species found in quaternary peat deposit (Elias 1992) and is known to be a boreal species common in alpine tundra environment (Campbell 1982). *Q. brunnipennis* was common in 'fire skips' of the coniferous boreal forest which were most commonly wetter areas less susceptible to fire (Gandhi et al. 2004). Thus, our results combined with evidence from the literature, show that these three species of rove beetle frequently use bogs as habitat, and underscore the importance of the tree bog ecosite as a landscape component supporting biodiversity.

5.4.5 *Trap depth*

The depth at which the lip of the pitfall trap is placed in the forest floor had no discernable effect on the overall composition of the boreal arthropod assemblage that we studied (Fig. 5.2, Table 5.1). A trap sunken positioned at the top of the mineral soil layer catched the same species as a trap set flush with the surface. These results suggest that pitfall trap data are robust for general comparisons of arthropod composition among different sites in the mixedwood boreal forest and that variation in installation does not influence the overall composition of the catch in a way that affected the outcomes of our multivariate analyses.

Nonetheless, trap lip depth did significantly affect the number of species and abundance of arthropods collected (Fig. 5.3 and 5.4), with generally more species caught in surface traps than in deep traps. A likely hypothesis to explain this difference is that many surface active individuals escaped, perhaps during the initial fall into deep traps (e.g., Morril et al. 1990, Topping 1993). Given the 15 to 25 cm of organic soil above the trap lip of deep traps, there are more opportunities for arthropods to catch themselves and climb out of a trap than when it immediately encounters the plastic side wall of a surface trap. This is especially true for spiders which are able to use web anchors. In fact, the spiders are the only group having a constant higher number of species and individuals in surface traps (Figs. 5.3 and 5.4).

Although spiders were indicators for surface traps only, two ground beetle species (*A. retractum* and *P. brevicornis*) and one rove beetle species (*Q. velox*) were indicative of deep traps (Table 5.3). Interestingly, Spence and Niemela (1994) report that *A. retractum* was more commonly recovered from aspen litter samples than from pitfall trapping in aspen dominated stands. Based on this result, Larochelle and Larivière (2003) wrote that *A.retractum* is found in areas with thick leaf litter and that both *A.retractum* and *P.brevicornis* are sheltering during the day in the leaf litter, moss and humus portion of the forest soil. The results of this study lead us to suggest that these two species do not only rest in the humus and leaf litter but also moves actively beneath the soil surface. Our results suggest that *Q. velox* also exhibit the same behavior in the white spruce dominated ecosite phase (Table 5.3). In fact, in this ecosite phase, most of the ground beetle species were more abundant in deep traps (Appendix 5-A) and with the addition of the overwhelming abundance of the rove beetle *Q. velox* in deep traps, overall abundance of arthropods in deep traps was higher than in the surface traps (Fig. 5.3). In the aspen dominated ecosite phase, however, the surface traps collected more arthropods than the deep traps (Fig. 5.3). This latter result is mainly driven by the exceptional abundance of rove beetles in the surface traps of the aspen dominated ecosite phase but spiders also contribute to the pattern.

5.5 Conclusion

We demonstrate that ecosite classification system used for the Lower Foothills Natural Subregion (Beckingham et al. 1996) provides a reasonable surrogate measure for the ground-dwelling forest arthropod assemblages in NW Alberta. The congruence of our results with those of Langor et al. (2006) for corresponding ecosites of the Upper Foothills Natural Subregion suggest that the CEFC system (Natural resources Canada 2006) may be used in a coarse filter biodiversity conservation strategy. Furthermore, we suggest that ecosite classification provides a scientifically credible template for large scale biodiversity monitoring programs. Surface dwelling arthropods are present and generally abundant in any terrestrial habitat and, furthermore, much accumulated evidence suggests that these assemblages are sensitive to cover changes because individual species respond to fine-grain habitat variation. However, despite these advantages for sensitive biomonitoring, the challenge of accurately surveying and identifying every arthropod species so that the above advantages may be realized is frequently daunting and requires resources beyond what are available. Thus, landscapes must be managed in coarser manner. Our study suggests the approach of maintaining the full naturally occurring range of ecosites, ecophases and successional stages. Arthropod assemblages, as characterized here, can then be periodically assessed in representative ecosites and ecosite phases to ensure that associations between arthropods and their habitats remain as close as possible to the state observed in unaffected ‘control’ sites as landscapes change under human influence (Spence et al. 2008). Consistent departures from expectations would provide cause for concern, and the identity of missing species would suggest alterations of management regimes in relation to understanding of the habitat requirements of these species.

We also found that use of multiple indicator taxa in biodiversity studies provides a more robust picture of the whole forest environment. For example, our analysis shows that number of species and abundance of ground dwelling beetles are drastically lower in black spruce dominated bogs but that spiders do not differ much from upland ecosites and constitute an important part of the ground dwelling fauna in black spruce bog ecosites. The main species inhabiting peat bogs have northern distribution and are adapted to climatic and edaphic factors prevalent in arctic, subarctic and alpine environments. Black spruce dominated lowlands support a distinctive and rich arthropod community and should therefore not be ignored when planning biodiversity monitoring in managed forested landscapes.

Our study suggests that pitfall trapping is an effective method for evaluation of ground dwelling arthropod assemblages in mixedwood boreal forest. Differentiation of arthropod assemblages across habitats can be reliably assessed with pitfall traps set at the surface. Careful attention to consistency in setting these traps is required, however, because our results suggest that some species (e.g., *A. retractum, P. brevicornis* and *Q. velox*) are disproportionately active in or beneath the litter layer. Traps carefully set with the lip flush with the surface of the forest floor should maximize the catches and give the most reliable information to characterize the assemblages. This is especially true for spiders where installation irregularities resulting in a lower trap may significantly lower both number of species and abundance of spiders collected.

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Table 5.1: F and p values of the permutational MANOVA calculated for habitat, depth and the interaction

	All taxa		Araneae		Carabidae		Staphylinidae	
	F	p	F	p	F	p	F	p
Habitat	5.656	0.001*	0.889	0.594	1.238	0.212	1.219	0.242
Depth	1.082	0.318	0.747	0.729	0.808	0.631	0.687	0.684
Habitat& Depth	0.684	0.377	0.758	0.701	0.784	0.610	0.669	0.629

Table 5.2: Taxa having a significant affinity for certain habitat according to indicator species analysis

Species	Habitat	Indicator value (%)	*p*
Aranaea			
Pardosa uintana	Black spruce (k1)	100	0.001
Gnaphosa microps	Black spruce (k1)	94.4	0.001
Pardosa mackenziana	Aspen (e2)	66.7	0.016
Carabidae			
Pterostichus brevicornis	White spruce (e4)	77.6	0.001
Pterostichus haematopus	White spruce (e4)	74.2	0.001
Agonum retractum	Aspen (e2)	72.3	0.006
Calathus advena	White spruce (e4)	65.8	0.012
Platynus decentis	Aspen (e2)	47.4	0.046
Staphylinidae			
Tachinus fumipennis	Aspen (e2)	100	0.003
Quedius labradorensis	Aspen (e2)	88.3	0.002
Ischnosoma splendidum	Aspen (e2)	86.5	0.002
Lypoglossa angularis	White spruce (e4)	83.3	0.002
Dynothenarus pleuralis	Aspen (e2)	80.8	0.001
Tachinus elongatus	Aspen (e2)	79.6	0.011
Quedius velox	White spruce (e4)	78.8	0.001
Acidota quadrata	Aspen (e2)	76	0.022
Lypoglossa franclemonti	Aspen (e2)	71	0.027
Quedius rusticus	Aspen (e2)	68.1	0.011
Quedius impar	Aspen (e2)	66.1	0.004
Tachinus frigidus	White spruce (e4)	60.7	0.008

Table 5.3: Taxa having a significant affinity for certain trap depth according to indicator species analysis

Species	Habitat	Trap depth	Indicator value (%)	*p*
Aranaea				
Gnaphosa microps	Black spruce (k1)	Surface	76.4	0.009
Allomengea dentisetis	Aspen (e2)	Surface	63.3	0.036
Sciastes truncatus	Black spruce (k1)	Surface	62.4	0.046
Pardosa uintana	Black spruce (k1)	Surface	59	0.018
Carabidae				
Pterostichus brevicornis	White spruce (e4)	Deep	64.3	0.023
Agonum retractum	Aspen (e2)	Deep	54.2	0.04
Pterostichus haematopus	White spruce (e4)	Surface	45	0.025
Staphylinidae				
Tachinus elongatus	Aspen (e2)	Surface	77.5	0.04
Tachinus fumipennis	Aspen (e2)	Surface	75	0.035
Quedius velox	White spruce (e4)	Deep	60.1	0.019
Dynothenarus pleuralis	Aspen (e2)	Surface	53.1	0.02
Ischnosoma splendidum	Aspen (e2)	Surface	52.5	0.031

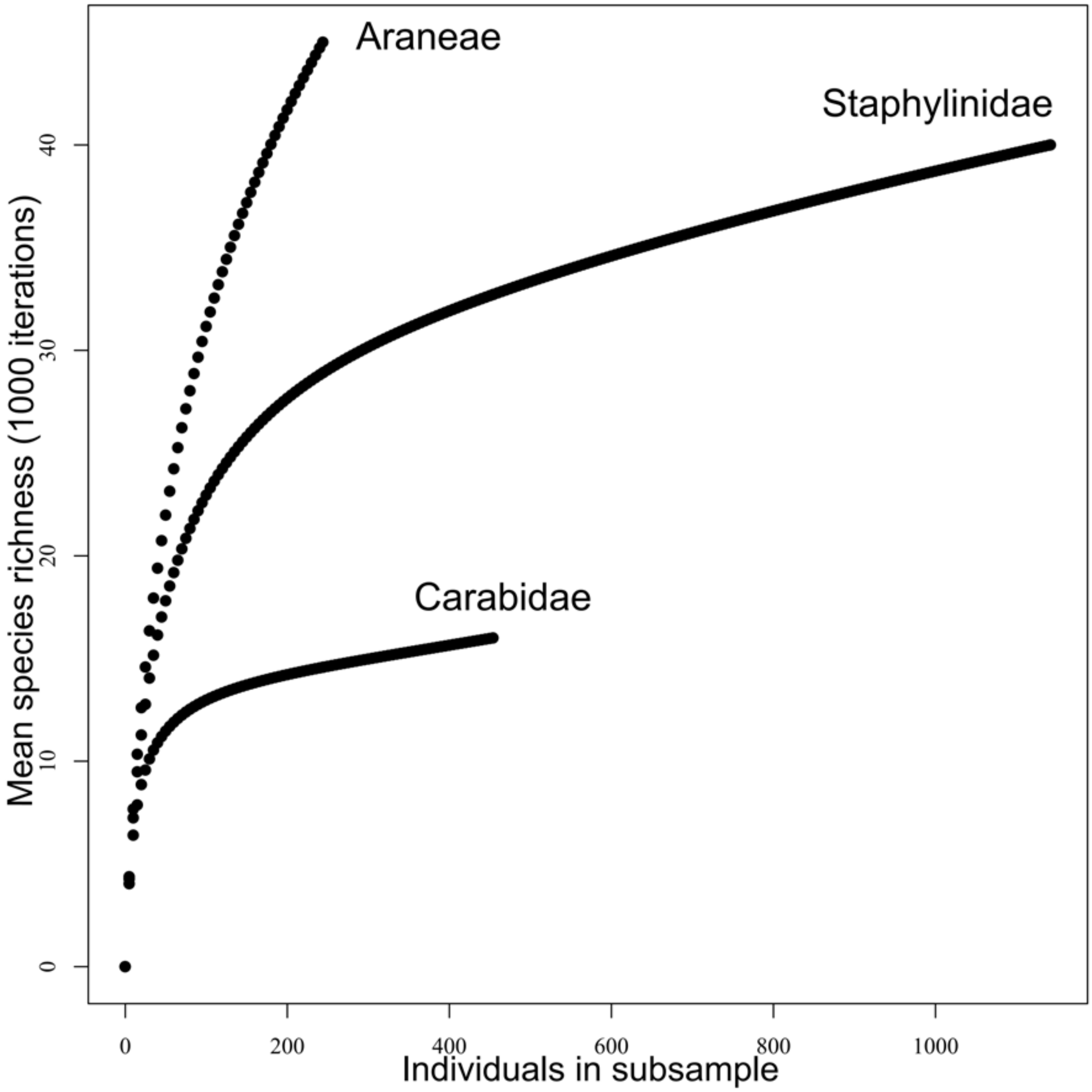


Figure 5.1: Individual based rarefaction for three arthropod taxa sampled by pitfall traps in the boreal mixedwood forest.

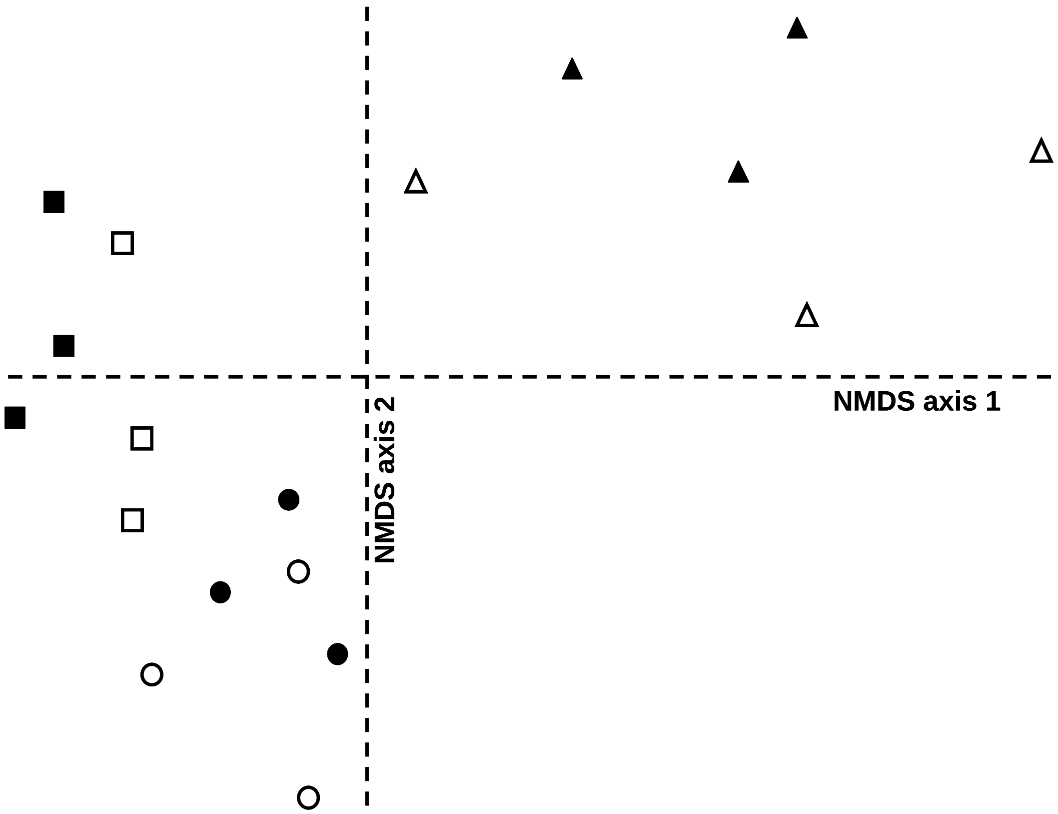


Figure 5.2: Non Metric Multidimentional Scaling Ordination of 18 sites sampled for forest dwelling arthropods in three habitats of the boreal mixedwood forest. Squares: low bush cranberry aspen dominated, circles: low bush cranberry white spruce dominated, triangles: treed bog black spruce dominated, empty symbols: deep traps, filled symbols: surface traps.

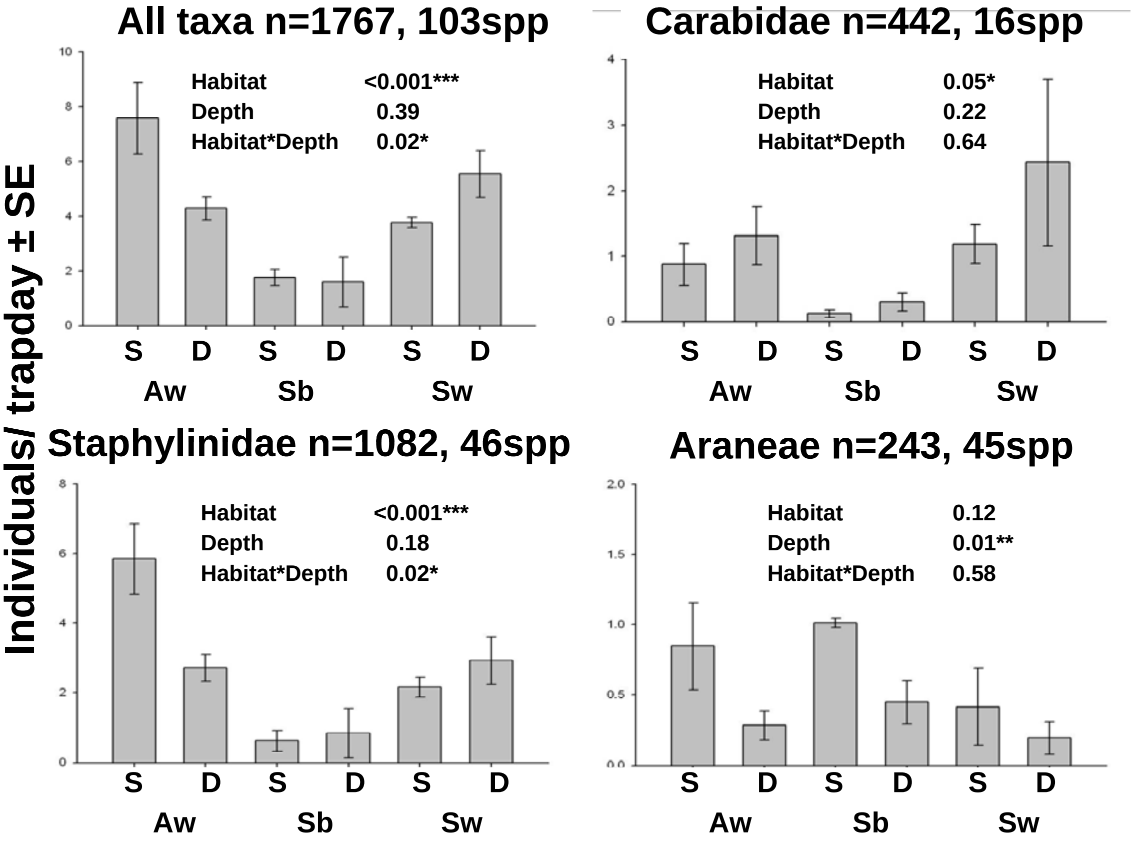
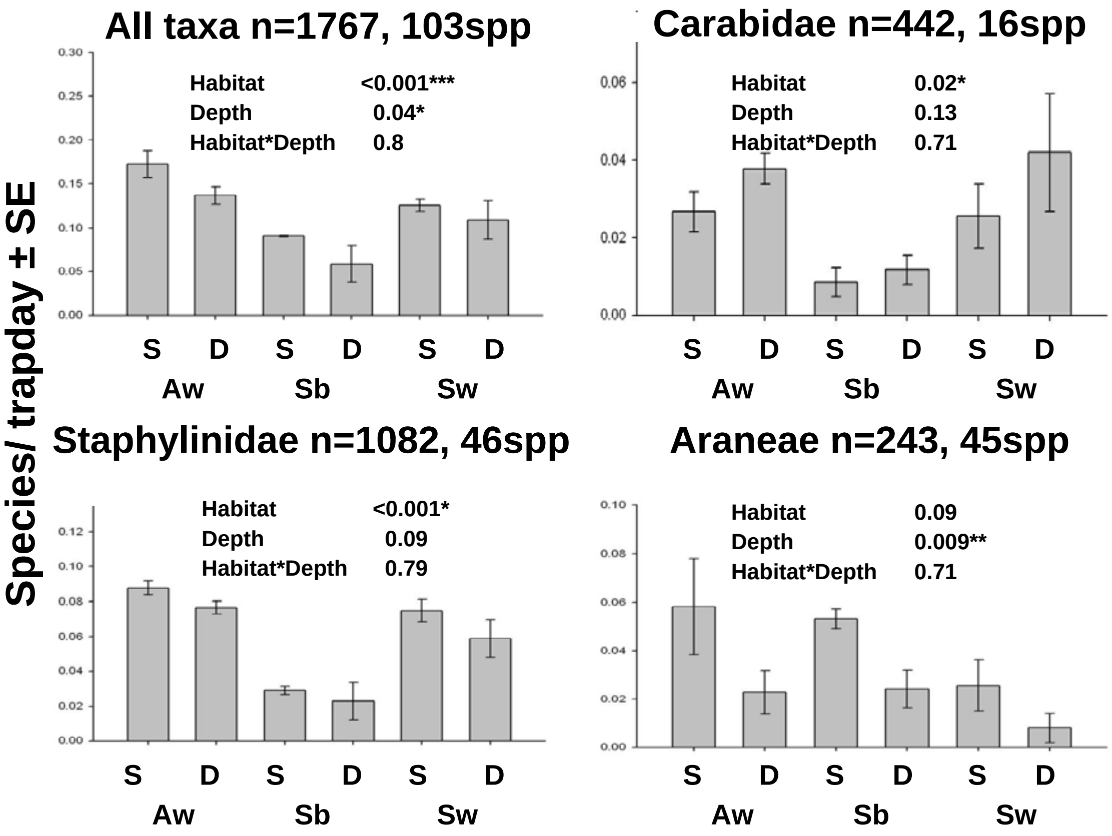


Figure 5.3: Average number of individuals caught per trapping day amongst habitats and trap depth. P values for habitat, trap depth, and the interaction after permutational ANOVA are given. S: surface trap, D: deep trap, Aw: low bush cranberry aspen dominated, Sb: treed bog black spruce dominated, Sw: low bush cranberry white spruce dominated.



All taxa n=1767, 103spp

Carabidae n=442, 16spp

Staphylinidae n=1082, 46spp

Araneae n=243, 45spp

Figure 5.4: Average number of species caught per trapping day amongst habitats and trap depth. P values for habitat, trap depth, and the interaction after permutational ANOVA are given. S: surface trap, D: deep trap, Aw: low bush cranberry aspen dominated, Sb: treed bog black spruce dominated, Sw: low bush cranberry white spruce dominated.

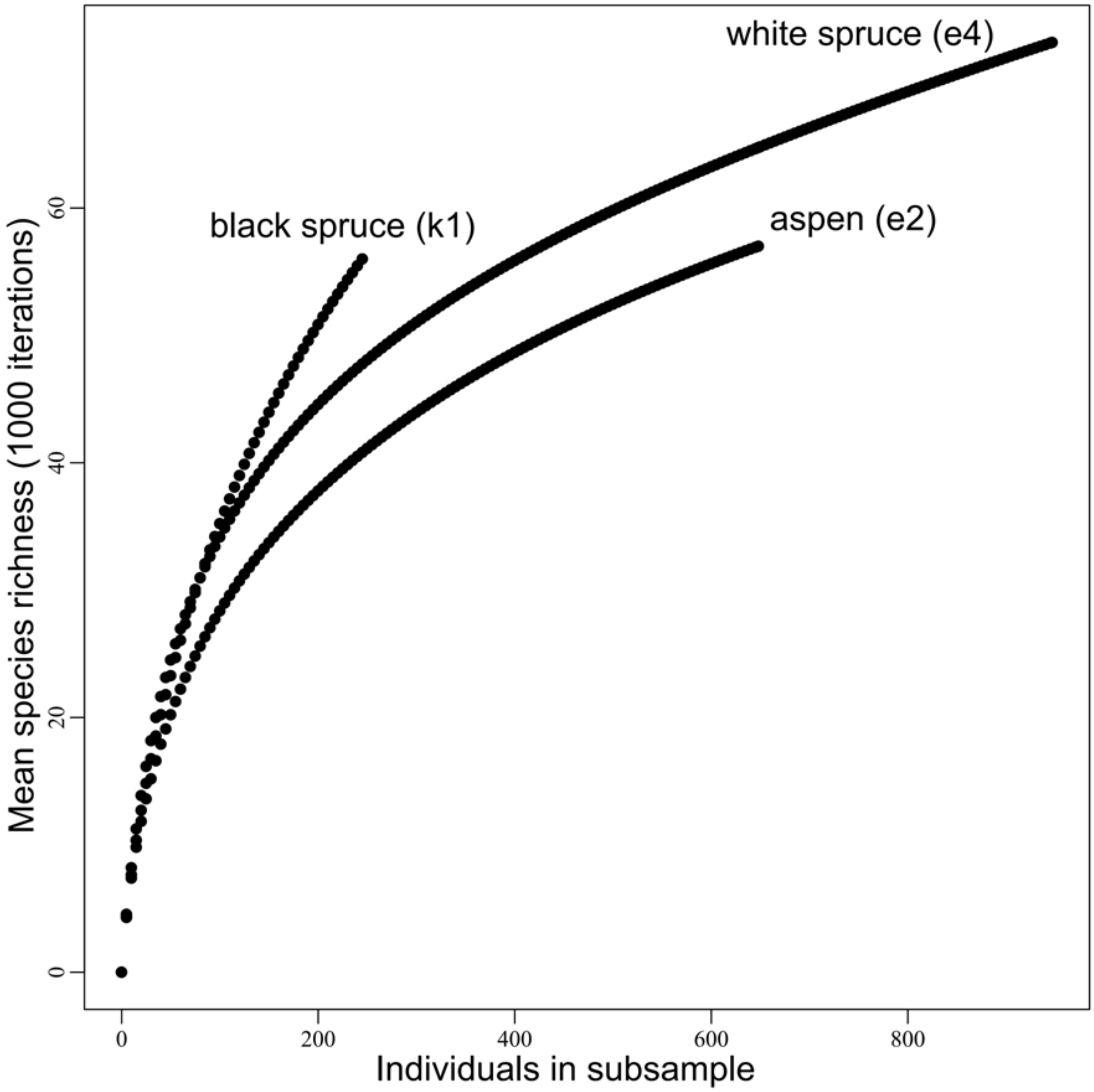


Figure 5.5: Individual based rarefaction for the three habitats studied. Black spruce: treed bog black spruce dominated, white spruce: low bush cranberry white spruce dominated, aspen: low bush cranberry aspen dominated. The codes correspond to the ecophase according to Beckingham et al. (1996).

Appendix 5-A: Number of individuals for each arthropod species collected in three habitats of the boreal mixedwood forest. De: deciduous dominated, Sb: black spruce dominated, Sw: white spruce dominated, 0: deep trap, 1: surface trap, carab: carabidae, staph: staphylinidae, Unknown unknown: Aleocarinae

taxa	Family	Genus	Species	De0	De1	Sb0	Sb1	Sw0	Sw1	Sum
carab	Carabidae	***Calathus***	***advena***	0	1	0	0	31	37	69
carab	Carabidae	***Trechus***	***chalybeus***	22	20	0	1	3	20	66
carab	Carabidae	***Pterostichus***	***adstrictus***	13	11	1	0	10	28	63
carab	Carabidae	***Pterostichus***	***haematopus***	1	4	3	7	26	17	58
carab	Carabidae	***Agonum***	***retractum***	10	30	0	0	2	8	50
carab	Carabidae	***Calathus***	***ingratus***	14	15	0	2	1	13	45
carab	Carabidae	***Patrobus***	***foveocollis***	3	13	0	0	3	12	31
carab	Carabidae	***Carabus***	***chamissonis***	4	3	0	7	0	4	18
carab	Carabidae	***Pterostichus***	***punctatissimus***	0	0	5	4	1	6	16
carab	Carabidae	***Pterostichus***	***brevicornis***	0	0	0	1	4	8	13
carab	Carabidae	***Platynus***	***decentis***	2	7	0	0	0	3	12
carab	Carabidae	***Pterostichus***	***pensylvanicus***	4	1	0	0	0	0	5
carab	Carabidae	***Trechus***	***apicalis***	0	4	0	1	0	0	5
carab	Carabidae	***Calosoma***	***frigidum***	1	0	0	0	0	0	1
carab	Carabidae	***Notiophilus***	***borealis***	0	0	1	0	0	0	1
carab	Carabidae	***Synuchus***	***impunctatus***	0	1	0	0	0	0	1
staph	Staphylinidae	**Unknown**	**unknown**	98	64	2	4	29	18	215
staph	Staphylinidae	***Tachinus***	***frigidus***	36	37	3	2	43	58	179
staph	Staphylinidae	***Acidota***	***quadrata***	109	28	2	15	14	6	174
staph	Staphylinidae	***Quedius***	***velox***	11	15	1	4	28	84	143
staph	Staphylinidae	***Ischnosoma***	***splendidum***	41	26	1	1	4	4	77
staph	Staphylinidae	***Quedius***	***rusticus***	32	10	0	1	4	14	61
staph	Staphylinidae	***Tachinus***	***elongatus***	46	9	0	0	1	1	57
staph	Staphylinidae	***Eucnecosum***	***brunnescens***	14	4	19	14	1	1	53
staph	Staphylinidae	***Quedius***	***brunnipennis***	10	4	4	10	9	11	48
staph	Staphylinidae	***Lypoglossa***	***franclemonti***	25	9	2	0	2	2	40
staph	Staphylinidae	***Mycetoporus***	***americanus***	17	7	2	0	10	2	38
staph	Staphylinidae	***Dynothenarus***	***pleuralis***	21	11	0	1	2	3	38

staph	Staphylinidae	***Lordithon***	***fungicola***	**23**	**1**	**1**	**0**	**2**	**0**	**27**
staph	Staphylinidae	***Tachinus***	***fumipennis***	**18**	**6**	**0**	**0**	**0**	**0**	**24**
staph	Staphylinidae	***Micropeplus***	***laticollis***	**9**	**3**	**0**	**0**	**5**	**4**	**21**
staph	Staphylinidae	***Pseudopsis***	***sagitta***	**11**	**7**	**0**	**0**	**0**	**0**	**18**
staph	Staphylinidae	***Quedius***	***labradorensis***	**8**	**8**	**0**	**0**	**2**	**0**	**18**
staph	Staphylinidae	***Ischnosoma***	***fimbriatum***	**2**	**4**	**4**	**2**	**3**	**1**	**16**
staph	Staphylinidae	***Quedius***	***impar***	**5**	**6**	**0**	**2**	**1**	**1**	**15**
staph	Staphylinidae	***Gabrius***	***brevipennis***	**4**	**5**	**0**	**0**	**1**	**2**	**12**
staph	Staphylinidae	***Lathrobium***	***washingtoni***	**3**	**5**	**0**	**1**	**0**	**3**	**12**
staph	Staphylinidae	***Bolitobius***	***horni***	**5**	**5**	**0**	**0**	**0**	**0**	**10**
staph	Staphylinidae	***Scaphium***	***castanipes***	**3**	**1**	**0**	**0**	**2**	**4**	**10**
staph	Staphylinidae	***Lypoglossa***	***angularis***	**0**	**0**	**0**	**0**	**4**	**5**	**9**
staph	Staphylinidae	***Stenus***	***austini***	**3**	**3**	**2**	**0**	**1**	**0**	**9**
staph	Staphylinidae	***Quedius***	***frigidus***	**1**	**0**	**4**	**0**	**2**	**1**	**8**
staph	Staphylinidae	***Mycetoporus***	***smetanai***	**0**	**1**	**0**	**0**	**1**	**2**	**4**
staph	Staphylinidae	***Quedius***	***caseyi***	**0**	**0**	**0**	**0**	**1**	**2**	**3**
staph	Staphylinidae	***Gabrius***	***picipennis***	**1**	**1**	**0**	**0**	**0**	**0**	**2**
staph	Staphylinidae	***Tachinus***	***borealis***	**0**	**0**	**2**	**0**	**0**	**0**	**2**
staph	Staphylinidae	***Tachinus***	***quebecensis***	**0**	**1**	**0**	**0**	**0**	**1**	**2**
staph	Staphylinidae	***Tachyporus***	***borealis***	**1**	**0**	**0**	**1**	**0**	**0**	**2**
staph	Staphylinidae	***Bisnius***	***tereus***	**0**	**0**	**0**	**0**	**0**	**1**	**1**
staph	Staphylinidae	***Lathrobium***	***fauveli***	**1**	**0**	**0**	**0**	**0**	**0**	**1**
staph	Staphylinidae	***Megarthrus***	***sinuaticollis***	**0**	**0**	**0**	**0**	**1**	**0**	**1**
staph	Staphylinidae	***Olophrum***	***rotundicolle***	**0**	**1**	**0**	**0**	**0**	**0**	**1**
staph	Staphylinidae	***Quedius***	***brevipennis***	**0**	**1**	**0**	**0**	**0**	**0**	**1**
staph	Staphylinidae	***Quedius***	***fulvicollis***	**1**	**0**	**0**	**0**	**0**	**0**	**1**
staph	Staphylinidae	***Quedius***	***simulator***	**0**	**0**	**0**	**0**	**1**	**0**	**1**
staph	Staphylinidae	***Stenus***	***immarginatus***	**0**	**0**	**0**	**0**	**1**	**0**	**1**
spider	Lycosidae	***Pardosa***	***uintana***	**0**	**0**	**30**	**18**	**0**	**0**	**48**
spider	Linyphiidae	***Zornella***	***cultigera***	**3**	**1**	**0**	**1**	**11**	**9**	**25**
spider	Gnaphosidae	***Gnaphosa***	***microps***	**1**	**0**	**13**	**3**	**0**	**0**	**17**
spider	Linyphiidae	***Improphantes***	***complicatus***	**2**	**2**	**1**	**1**	**7**	**4**	**17**
spider	Linyphiidae	***Allomengea***	***dentisteis***	**9**	**2**	**3**	**0**	**1**	**0**	**15**

spider	Linyphiidae	***Bathyphantes***	***pallidus***	**8**	**5**	**0**	**0**	**0**	**0**	**13**
spider	Linyphiidae	***Diplocentria***	***bidentata***	**6**	**0**	**1**	**2**	**0**	**1**	**10**
spider	Lycosidae	***Pardosa***	***mackenziana***	**5**	**3**	**0**	**1**	**1**	**0**	**10**
spider	Amaurobiidae	***Cybaeopsis***	***euopla***	**5**	**0**	**0**	**0**	**1**	**0**	**6**
spider	Gnaphosidae	***Haplodrassus***	***hiemalis***	**2**	**1**	**2**	**1**	**0**	**0**	**6**
spider	Linyphiidae	***Walckenaeria***	***castanea***	**1**	**0**	**1**	**0**	**4**	**0**	**6**
spider	Lycosidae	***Pardosa***	***moesta***	**2**	**1**	**2**	**0**	**0**	**0**	**5**
spider	Linyphiidae	***Sciastes***	***truncatus***	**0**	**0**	**3**	**0**	**1**	**1**	**5**
spider	Thomisidae	***Xysticus***	***canadensis***	**1**	**0**	**2**	**1**	**1**	**0**	**5**
spider	Linyphiidae	***Hybauchenidium***	***gibbosum***	**2**	**1**	**0**	**0**	**1**	**0**	**4**
spider	Lycosidae	***Pardosa***	***hyperborea***	**0**	**0**	**2**	**2**	**0**	**0**	**4**
spider	Linyphiidae	***Agyneta***	***olivacea***	**2**	**0**	**1**	**0**	**0**	**0**	**3**
spider	Linyphiidae	***Lepthyphantes***	***alpinus***	**1**	**0**	**0**	**0**	**1**	**1**	**3**
spider	Linyphiidae	***Pocadicnemis***	***americana***	**0**	**0**	**2**	**0**	**1**	**0**	**3**
spider	Linyphiidae	***Walckenaeria***	***atrotibialis***	**2**	**0**	**1**	**0**	**0**	**0**	**3**
spider	Linyphiidae	***Walckenaeria***	***fallax***	**0**	**0**	**2**	**0**	**1**	**0**	**3**
spider	Thomisidae	***Xysticus***	***emertoni***	**2**	**0**	**1**	**0**	**0**	**0**	**3**
spider	Liocranidae	***Agroeca***	***ornata***	**0**	**0**	**1**	**0**	**1**	**0**	**2**
spider	Amaurobiidae	***Amaurbious***	***borealis***	**2**	**0**	**0**	**0**	**0**	**0**	**2**
spider	Gnaphosidae	***Gnaphosa***	***parvula***	**0**	**0**	**2**	**0**	**0**	**0**	**2**
spider	Linyphiidae	***Hilaria***	***herniosa***	**0**	**0**	**1**	**0**	**1**	**0**	**2**
spider	Linyphiidae	***Walckenaeria***	***arctica***	**0**	**1**	**1**	**0**	**0**	**0**	**2**
spider	Linyphiidae	***Walckenaeria***	***palustris***	**0**	**0**	**1**	**1**	**0**	**0**	**2**
spider	Linyphiidae	***Agyneta***	***allosubtilis***	**1**	**0**	**0**	**0**	**0**	**0**	**1**
spider	Linyphiidae	***Agyneta***	***unimaculata***	**1**	**0**	**0**	**0**	**0**	**0**	**1**
spider	Lycosidae	***Alopecosa***	***aculeata***	**0**	**0**	**1**	**0**	**0**	**0**	**1**
spider	Linyphiidae	***Diplocentria***	***rectangulata***	**1**	**0**	**0**	**0**	**0**	**0**	**1**
spider	Gnaphosidae	***Gnaphosa***	***borea***	**0**	**1**	**0**	**0**	**0**	**0**	**1**
spider	Gnaphosidae	***Gnaphosa***	***muscorum***	**0**	**0**	**1**	**0**	**0**	**0**	**1**
spider	Linyphiidae	***Helophora***	***insignis***	**0**	**0**	**0**	**0**	**1**	**0**	**1**
spider	Araneidae	***Hyposinga***	***rubens***	**1**	**0**	**0**	**0**	**0**	**0**	**1**
spider	Linyphiidae	***Oreonetides***	***rotundus***	**0**	**0**	**1**	**0**	**0**	**0**	**1**
spider	Linyphiidae	***Oreonetides***	***vaginatus***	**1**	**0**	**0**	**0**	**0**	**0**	**1**

spider	Lycosidae	***Pardosa***	***fuscula***	**0**	**0**	**1**	**0**	**0**	**0**	**1**
spider	Linyphiidae	***Pityohyphantes***	***subarcticus***	**0**	**1**	**0**	**0**	**0**	**0**	**1**
spider	Theridiidae	***Robertus***	***fuscus***	**1**	**0**	**0**	**0**	**0**	**0**	**1**
spider	Linyphiidae	***Scotynotilus***	***sacer***	**0**	**0**	**1**	**0**	**0**	**0**	**1**
spider	Linyphiidae	***Walckenaeria***	***directa***	**0**	**1**	**0**	**0**	**0**	**0**	**1**
spider	Linyphiidae	***Walckenaeria***	***lepida***	**1**	**0**	**0**	**0**	**0**	**0**	**1**
spider	Linyphiidae	***Walckenaeria***	***spiralis***	**0**	**0**	**1**	**0**	**0**	**0**	**1**

General Discussion

6.1 *Synthesis*

Evidence presented in this dissertation supports the thesis that invertebrate assemblages respond to the forest mosaic established by natural disturbance, and that these effects can be seen well beyond the early stages of succession. Furthermore, I show that landscape data available for planning natural resource exploitation partly reflects these processes inherent in development of local biodiversity patterns. In the following, I summarize the key findings and conclusions of each of the four main data chapters and discuss the implications for ecological management.

Data presented in the second chapter corroborate the hypothesis that ground-beetle assemblages of old forest that has repeatedly escaped fire differ drastically from and are more diverse than those found in the surrounding matrix of pyrogenic stands. Furthermore, I show that the general directional pathway of boreal mixedwood forest succession presented by Bergeron (2000) is also reflected in the ground-beetle fauna. Therefore, natural resource exploitation activities, especially those associated with forestry, must maintain an appropriate mix of all successional stages, even the most advanced, in order to maintain native biodiversity of these landscapes (Bergeron et al. 1999). This hypothesis has been well accepted as reasonable for some years (e.g., Spence 2001, Burton et al. 2003) but I have tested this hypothesis here using biodiversity and fire history data. Because old-growth forests host a distinct and rich biodiversity, and this feature is often the result of fire breaks locally lengthening the fire cycle (Cyr et al. 2005 and 2007), their detection and preservation is essential for management plans that ensure conservation of biodiversity. Because the beetle assemblages associated with forest of different fire histories are also characteristic of different mixes of tree species, I suggest that canopy tree composition can serve in locating different successional stages hosting specific ground beetle assemblages on the landscape.

The third chapter confirms that patterns of association between ground-beetles and tree species are strong enough to support useful characterization of the beetle community using tree species mixture. Landscape patterns detected using the percentage volume of tree species are clearly reflected in the beetle assemblages. This confirms that the arthropod assemblages associated with the cover type gradient, as studied by Work et al. (2004) and Jacobs et al. (2008), does in fact represent a general sucessional trend, embracing both the overstory and other biotic elements in boreal mixedwood forests. Furthermore, beetle species are associated with tree species of the same rank order of abundance, suggesting that conservation of less abundant trees will concomitantly foster conservation of less abundant beetle species. This close relationship supports application of a more fine-tuned ‘coarse filter’ approach for landscape conservation. Results of my dissertation suggest that forest management striving to maintain all species of trees in something that approximates a post-fire mixture, should also maintain ground beetle populations of native species.

In the fourth chapter, tree data presently used in forested land management are found to be only weakly correlated with the ground-beetle fauna in comparison to tree data from field surveys. Confusion between tree species in data derived from aerial photography lead to discrepancy between the biodiversity surrogacy models built based on either remotely sensed or field data. Furthermore, the depiction and estimation of the volume of the less abundant tree species is curently too inaccurate in aerial survey data to realistically include it in useful biodiversity surrogacy models. One of the problems in using forest inventory data as base maps in managing the forest for biodiversity arises from the process of averaging forest attributes over a defined area (polygon) on a map. Such maps tend to homogenize stand characteristic and thus, the fine tuning of species mixture or the presence of old legacy trees that are crucial for biodiversity are not accurately represented. The combined use of many geo-referenced landscape attributes to generate ecosystem classification maps improves the predictive power of forest characterizations for use in biodiversity surrogacy models. This is especially true for depiction of compositional habitat features associated with ground-beetle species characteristic of old forest. For forest industries harvesting the boreal forest, knowledge of the land under management is crucial in order to develop operational strategies aimed to minimize the impact on biodiversity, and for this purpose ecosystem classification maps provide the best representation of biodiversity on the landscape.

The fifth chapter reveals that ecosystem classification is an appropriate surrogacy framework not only for ground beetles, but also rove beetles and ground dwelling spiders. In fact, combining data about all three taxa yields a much more accurate representation of the forest habitat than using any of these taxa. In biodiversity surveys, these three taxa may be simultaneously sampled using pitfall traps, thus providing data for a reasonably precise characterization of the local biodiversity depending on ground-level habitats that are always present, regardless of disturbance. Furthermore, the shortcomings of pitfall trapping (e.g., Spence & Niemelä 1994) seem to be constant between the forest types studied here, supporting the use of this technique for landscape scale assessment of forest invertebrate diversity in the northwestern boreal zone of

Canada. However, my study showed that consistent and proper installation of traps is required because catches of some taxa are drastically influenced by placement of the pitfall trap.

6.2 *Implications for ecosystem based forest management*

Overall, my dissertation demonstrates that fire history influences the landscape distribution of ground beetle assemblages even in the latter stages of forest succession. Together with Paquin (2008), it underscores the conclusion that biodiversity of North American old growth boreal forest is highly diverse and differs dramatically from that of earlier successional stages. Because local conditions in fire history result in development of old forest patches, forest management inspired by natural disturbance should consider the local characteristic of forest stands to strategically leave canopy tree structure where old forest is more likely to develop. I found here that old forest in north western Alberta develops in association with wet sites likely because of longer fire return intervals. Thus, I suggest that special caution must be taken in the design of harvest blocks in wet forest and that a higher percentage of canopy tree retention should be left in these areas. Drainage of swamps and peatlands for the purpose of forest harvesting has the potential to put further pressure on the existence of late succession forest on the landscape (Hörnberg et al. 1998) as does exploration and exploitation for fossil energy that does not even consider the forest destroyed. These industries should at least know the accurate location of forest with high biodiversity value and try to avoid them or mitigate their impact as much as possible.

Fire history influences composition of trees within a stand (Bergeron 2000), and this in turn is closely related to the biodiversity inhabiting the forest. Unfortunately, present data about widespread forest composition in Canada as derived from aerial photography can be only weakly associated with biodiversity. Improvement in the detection and estimation of tree species is required especially for less common species in order to effectively apply biodiversity surrogacy model involved in the coarse filter approach to landscape conservation. Ecosystem classification maps generated through use of many geo-referenced landscape attributes apparently improve models for biodiversity surrogacy and have proven efficient here at depicting old growth forest habitat as used by epigaeic arthropods.

6.3 *Future research*

I concluded here that time since fire does influence the biodiversity of mixedwood boreal forest. However, the mecanisms by which ground beetle species are ecologically linked to tree species are still largely unknown and much research is needed in order to unveil the processes underlying the patterns observed in this thesis. Furthermore, fire is not the only disturbance influencing the structure and composition of a forest. Other natural phenomena also influence the biodiversity inhabiting these forests. Therefore, the study of other disturbances such as insect outbreaks, flooding or even logging together with efforts to characterize associated stand structure and composition may better reflect historical effects on biodiversity and support a conservation approach that is inspired by the whole range of natural disturbances. Because natural disturbance of a site may be recorded in tree radial growth, it is possible that ring width chronology of a site could be used to model its biodiversity. I suggest that sites with similar disturbance patterns will have similar biodiversity. Because the annual variation in tree ring width and invertebrate reproductive success are potentially influenced by the same environmental conditions, it is possible that tree ring variation may correlate with invertebrate population fluctuations. Defining and understanding such relationships would not only enable a reconstruction of the past conditions influencing the biodiversity of a stand, but also allow prediction of biodiversity under different scenarios involving changes in natural disturbances regime as driven by climate. This, in turn, would provide useful tools to manage forest ecosystems in the face of changing drivers, rather than blindly emulating patterns established in the past.

6.4 *Data management*

The data collected in support of this thesis is deposited in the EMEND database accessible at http://www.emend.rr.ualberta.ca.

6.5 *Literature cited*

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