

EFFECT OF DISTURBANCE TYPE (FIRE AND HARVESTING)
ON THE ECOLOGICAL DIVERSITY OF CARABID BEETLES
(COLEOPTERA: CARABIDAE) IN BLACK SPRUCE (*PICEA MARIANA* (Mill.) BSP.)
FORESTS OF EASTERN MANITOBA

BY

Lisa N. Capar

A Thesis
Submitted to the Faculty of Graduate Studies
In Partial Fulfillment of the Requirements for the Degree of

MASTER OF SCIENCE

Department of Entomology
University of Manitoba
Winnipeg, Manitoba
R3T 2H2

© Lisa N. Capar, November 2003

THE UNIVERSITY OF MANITOBA

FACULTY OF GRADUATE STUDIES

COPYRIGHT PERMISSION

**Effect of Disturbance Type (Fire and Harvesting)
on the Ecological Diversity of Carabid Beetles
(Coleoptera: Carabidae) in Black Spruce (*Picea Mariana* (Mill.) BSP.)
Forests of Eastern Manitoba**

BY

Lisa N. Capar

A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of

Manitoba in partial fulfillment of the requirement of the degree

Of

MASTER OF SCIENCE

Lisa N. Capar © 2004

Permission has been granted to the Library of the University of Manitoba to lend or sell copies of this thesis/practicum, to the National Library of Canada to microfilm this thesis and to lend or sell copies of the film, and to University Microfilms Inc. to publish an abstract of this thesis/practicum.

This reproduction or copy of this thesis has been made available by authority of the copyright owner solely for the purpose of private study and research, and may only be reproduced and copied as permitted by copyright laws or with express written authorization from the copyright owner.

Acknowledgments

I most of all thank the students in the laboratory for their help and support throughout this study. I thank the members on my thesis committee, Dr. Neil Holliday for all his guidance especially with the statistical analysis, Dr. Richard Staniforth for plant identifications and advice, and my supervisor Dr. Richard Westwood for giving me the opportunity to work on this project and his valuable feedback.

I thank Jon Warkentin, Catherine Ivory, Sheri Streinein, and Eva Walker for all their hard work in the field and for all the good times we had. For accommodations in the woods, I thank Bryan Stefaniuk and Tim Swanson. I am very grateful for the assistance and entertainment provided by the people of Bissett and the Van Gerwens of Beresford Lake. A special thank you to Dr. Yves Bousquet for verifying identifications of the more difficult carabid species and for use of his laboratory. I also thank Scott Longridge for supplying maps and site histories. I would also like to extend my thanks to my friends and family who offered their support during this project, especially to Natalie Shykoluk who helped me correct my grammar.

The funding for this project was provided by Manitoba Conservation Forestry Branch, Tembec Inc., and NSERC.

Capar, L. N., M.Sc., The University of Manitoba, 2003. Effect of Disturbance Type (Fire and Harvesting) on the Ecological Diversity of Carabid beetles (Coleoptera: Carabidae) in Black Spruce (*Picea mariana* (Mill.) BSP.) Forests of Eastern Manitoba.

Major Professor: A. R. Westwood

Burned and harvested black spruce (*Picea mariana* (Mill.) BSP.) dominated forest stands were compared over three age classes: sites burned or harvested in 1999 - 2000, sites burned or harvested in 1983, and sites burned in 1929 or harvested in 1957. Carabid beetles (ground beetles) were collected in pitfall traps from burned and harvested plots during 1999, 2000, 2001, and 2002. Carabid diversity was examined only from the years 2000 and 2002. There were no significant differences in number of beetles, numbers of species, log alpha diversity, evenness and beta diversity between the burned and harvested plots in the 1983 sites or the 1957 harvest and 1929 burned sites. There were differences in carabid diversity between burned and harvested sites in the most recently disturbed sites (harvested and burned 1999 and 2000 sites). Differences in diversity between recently disturbed plots were likely due to the higher numbers of generalist species (*Pterostichus adstrictus* Eschscholtz, *Synuchus impunctatus* (Say), *Platynus decentis* (Say)), and higher numbers of pyrophilous species in the burned sites (*Sericoda quadripunctatum* (DeGeer), and *Harpalus laticeps* LeConte). Carabid beetle species diversity differed between age classes. Carabid species were influenced by environmental variables such as canopy closure, percent cover of dead woody debris, and vegetation. Herbaceous vegetation, bryophytes and lichens had more influence on carabid assemblages than did the shrub or tree species. Temporal variation occurred in individual carabid species abundances throughout the collecting seasons.

Table of Contents

	Page
Chapter 1	
Introduction.....	1
Chapter 2	
Literature Review.....	4
2.1 Black Spruce in the Boreal Forest.....	4
2.2 Fire.....	5
2.2.1 Effect of Fire on Forest Soil.....	6
2.2.2 Fire Suppression and Fire Cycles.....	7
2.3 Harvesting.....	7
2.4 Harvesting and Fire Cycles.....	8
2.5 Bioindicators.....	9
2.6 Carabidae.....	12
2.6.1 Carabid Habitats.....	13
2.6.2 Sampling Methods for Carabids.....	14
2.7 Biodiversity.....	15
2.5.1 Measuring Biodiversity: Using Statistical Indices.....	17
2.8 Ordination.....	19
2.8.1 PCA.....	19
2.8.2 RDA.....	20
Chapter 3	
Methods and Materials.....	21
3.1 General Study Area Description.....	21
3.2 Experimental Design.....	21
3.3 Soil Characterization.....	22
3.4 Canopy Closure and Light.....	23
3.5 Temperature and Precipitation.....	23
3.6 Vegetation Sampling.....	24
3.7 Sampling of Carabids.....	24
3.8 Carabid Identification.....	25
3.9 Statistical Analysis.....	26
3.9.1 Means, Standard Errors, ANOVAs, and Contrasts.....	26
3.9.2 Carabid Beetle Data.....	27
3.10 Diversity Data.....	28
3.11.1 Vegetation.....	28
3.11.2 Carabids.....	28
3.11 Ordination.....	28

Chapter 4

Results.....	30
4.1 Visual Descriptions of Sites.....	30
4.1.1 New Sites.....	30
4.1.2 Intermediate Aged Sites.....	30
4.1.3 Old Sites.....	31
4.2 Environmental Site Variables.....	32
4.2.1 Vegetation.....	32
4.2.2 Canopy Cover and Light.....	32
4.2.3 Percent Cover of Downed Woody Debris.....	33
4.2.4 Soil Type and pH.....	33
4.2.5 Climatic Data.....	33
4.3 Carabid Beetles.....	34
4.3.1 Number of Individuals, Number of Species, and Most Common Species.....	34
4.3.2 Seasonal Trends in Selected Species.....	36
4.3.3 Carabid Beetle Diversity.....	36
4.4 Ordination Analysis.....	37
4.4.1 PCA.....	37
4.4.2 RDA.....	39

Chapter 5

Discussion.....	72
5.1 Disturbance Type and Age Class Effects on Environmental Variables.....	72
5.2 Disturbance Type and Age Class Effects on Carabid Beetles Species Composition.....	75
5.3 Habitat Characteristics and Seasonal Effects on Carabid Species Assemblages.....	79
5.4 Disturbance Type and Age Class Effects on Diversity of Carabid Beetles.....	82

Chapter 6

Synthesis.....	84
References.....	86
Appendices.....	96

List of Tables

	Page
Table 1. Location, average age of trees, and years sampled for burned (B) and harvested (H) plots.....	40
Table 2. Composition of trees of two size classes: between 1m and 3 m, and above 3 m.....	41
Table 3. The length of the sampling season in 1999, 2000, 2001, and 2002 and adjusted data for 2000.....	42
Table 4. Effect of age class, disturbance type, and interactions between age class and disturbance type on herbaceous vegetation collected in 2000 (mean $\pm$ SE).....	43
Table 5. Effect of age class, disturbance type, and interactions between age class and disturbance type for shrubs collected in 2000 (Mean $\pm$ SE).....	44
Table 6. Effect of age class, disturbance type, and interactions of age class and disturbance type on environmental variables (Mean $\pm$ SE).....	45
Table 7. Soil types based on Soil Classification Working Group (1998).....	46
Table 8. Effect of age class, disturbance type, and interaction between age class and disturbance type on carabid beetles collected in 2000 (Mean $\pm$ SE).....	47
Table 9. Effect of age class, disturbance type, and interaction between age class and disturbance type on carabid beetles collected in 2002 (Mean $\pm$ SE).....	48
Table 10. A comparison between mean catches of <i>Pterostichus adstrictus</i> and <i>Pterostichus pensylvanicus</i> for 2000 and 2002. (Mean $\pm$ SE).....	49
Table 11. A comparison between mean catches of <i>Synuchus impunctatus</i> , <i>Platynus decentis</i> and <i>Agonum gratiosum</i> for 2000 and 2002. (Mean $\pm$ SE).....	50

List of Figures

	<u>Page</u>
Figure 1. Location of sites. For longitude and latitude see Table 1.....	51
Figure 2. Pattern of pitfall traps within a plot. Each letter corresponds to a pitfall trap. Distance between each trap was 20 m.....	52
Figure 3. Canopy closure. A) Percent shade measured with a light meter. B) Percent canopy closure with a densiometer.....	53
Figure 4. Mean number of pyrophilous carabid species A) <i>Sericoda quadripunctatum</i> and B) <i>Harpalus laticeps</i> caught per sampling year with standard error bars.....	54
Figure 5. Percent of shared carabid species between burned and harvested plots for each age class for the collecting seasons in 2000 and 2002.....	55
Figure 6. Seasonal changes in carabid beetle numbers for selected species in 2000 from a total of 17 plots. Note: the Y-axis changes with species.....	56
Figure 7. Seasonal changes in carabid beetle numbers for selected species in 2002 from a total of 12 plots. Note: the Y-axis changes with species.....	57
Figure 8. 2000 vegetation data: PCA ordination diagram with plots (O) and vegetation species (arrows).....	58
Figure 9. Tree species in all plots: PCA ordination diagram with plots (O) and tree species (arrows).	59
Figure 10. 2000 carabid data: PCA ordination diagram with plots (O) and carabid species (arrows).....	60
Figure 11. 2000 carabid data without common species: PCA ordination diagram with plots (O) and carabid species (arrows).....	61
Figure 12. 2002 carabid data: PCA ordination diagram with plots (O) and carabid species (arrows).....	62
Figure 13. 2002 carabid data with common species removed: PCA ordination diagram with plots (O) and carabid species (arrows).....	63

Figure 14. Carabid data of young plots: PCA ordination diagram with plots (O) and carabid species (arrows). Numbers indicate collecting year: 1 = 1999, 2 = 2000, 3 = 2001.....	64
Figure 15. Carabid data of intermediate plots: PCA ordination diagram with plots (O) and carabid species (arrows). Numbers indicate collecting year: 1 = 2000 and 2 = 2002.....	65
Figure 16. Carabid data of old plots: PCA ordination diagram with plots (O) and carabid species (arrows). Numbers indicate collecting year: 1 = 2000 and 2 = 2002.....	66
Figure 17. 2000 carabid and age class/disturbance type (environmental data): RDA ordination diagram with plots (O), carabid species (arrows) and environmental data (▲).....	67
Figure 18. 2002 carabid and age class/disturbance type (environmental data): RDA ordination diagram with plots (O), carabid species (arrows) and environmental data (▲).....	68
Figure 19. 2000 vegetation and age class/disturbance type (environmental data): RDA ordination diagram with plots (O), vegetation species (arrows) and environmental data (▲).....	69
Figure 20. 2000 carabid and age class/disturbance type (environmental data): RDA triplot ordination diagram with plots (O), carabid species (solid arrows), environmental (boxes).....	70
Figure 21. 2002 carabid and age class/disturbance type (environmental data): RDA triplot ordination diagram with plots (O), carabid species (solid arrows), environmental (boxes).....	71

List of Appendices

Appendix 1. Climate data for A) 2000 and B) 2002. Daily maximum temperatures on the first Y-axis is represented by lines and total daily precipitation on the second Y-axis is represented by bars.....	96
Appendix 2. Species list with authorities and percent cover of herbaceous species sampled in 2000. Mean number of percent cover were calculated from 20 1 m X 1 m quadrats.....	97
Appendix 3. Species list with authorities and percent cover of shrubs species sampled in 2000. Mean number of percent cover were calculated from 15 2 m X 2 m quadrats	99
Appendix 4. Species list of carabid beetles collected in 1999. Total catches for each plot.....	100
Appendix 5. Species list of carabid beetles collected in 2000 with authorities. Total catches for each plot.....	101
Appendix 6. Species list of carabid beetles collected in 2001. Total catches for each plot.....	102
Appendix 7. Species list of carabid beetles collected in 2002. Total catches for each plot.....	103

Chapter 1 - Introduction

Disturbance, especially fire, is a crucial part of boreal forest succession, returning the forest to return to an early successional stage. In the boreal forest, fire had been the main disturbance type on the landscape until advances in mechanical harvesting methods allowed for large scale harvesting. At the same time as these advances in harvesting, there has been an increase in fire suppression by active firefighting (Smith *et al.* 2000). Large-scale harvests are becoming the main disturbance type on the landscape, causing fire-initiated succession to become a threatened process (Kimmins 1997, Niemela 1999).

With harvesting now becoming a significant disturbance, forest health must be quantified to determine whether harvesting has the same impact on the forest as fires. Forest health can be assessed using bioindicators. Bioindicators are a group of organisms (that can be from various taxonomic levels) used to represent the diversity patterns of all other organisms in an ecosystem (National Research Council 2000). Choosing the most suitable indicator is based on a combination of the following three criteria: how representative the indicator is of the ecosystem, ease of identification of the indicator, and the time and cost of sampling (Anderson 1999).

Carabid beetles (Coleoptera: Carabidae) ecophysiological adaptations (Thiele 1977) and their ability to cope with disturbances in forests make them ideal bioindicators of forest health (Rainio and Niemela 2003). Carabid fauna in several parts of the world, has been investigated in forested systems, including Poland (Fedorenko 1999), Finland (Niemela *et al.* 1994b), the United Kingdom (Jukes *et al.* 2001), and Canada (Holliday 1991, Niemela *et al.* 1993).

Ecological diversity is the variation and distribution of groups of organisms in an ecosystem over a geographical unit (Noss 1990). Diversity is an ecological concept and diversity indices are a mathematical approach to representing this concept diversity indices have been used to indicate the health of forests. Samples of species abundance are used to calculate various diversity indices at the stand and landscape level (Southwood 1978, Magurran 1988). Indicators are a group of organisms (e.g., at family level) which represent the diversity of all organisms in an ecosystem. Diversity index values may have no units, but are comparable to each other (e.g. comparison between different age classes within disturbance types in a black spruce forest stand). In addition to the calculation of diversity indices, species composition should also be examined by using ordination techniques. Changes in diversity indices may alert forest managers to possible differences between ecosystems in time and/or space. Differences in diversity can be applied where forestry practices, such as harvesting, could be causing effects different than those caused by natural disturbances, such as fire at different ages.

Currently, it is not known whether fire and harvesting produce the same effect on black spruce stands in eastern Manitoba, nor is it known whether carabid diversity and species composition are different between burned and harvested stands.

The objectives of this study are as follows:

- 1) To determine if carabid beetle diversity and therefore forest health differ between disturbance types (burns and harvests) and/or age classes of black spruce forests in Manitoba.

- 2) To investigate the relationship between environmental variables and carabid beetle assemblages in different disturbance types and age classes of black spruce.

Chapter 2 - Literature Review

2.1 - Black Spruce in the Boreal Forest

The boreal forest (or taiga) lies in the northern portions of North America, Europe, and Asia, ringing the Arctic Circle. This forest is approximately 20 million square kilometers in area, and extends from approximately 45° to 65° North latitude. Common tree genera found in the boreal forest include spruce, pine, aspen, and birch. However, coniferous trees, especially black spruce (*Picea mariana* (Mill.) B. S. P.) dominate the Nearctic boreal forest landscape (Begin and Filion 1999).

Black spruce is a cold-tolerant species, able to grow in areas near the northern tree limit with frost-free periods of 60 days or less. These cold-tolerant characteristics reflect the phenotypic plasticity of black spruce (Safford *et al.* 1990, Pereg and Payette 1998). The roots of black spruce do not require substantial soil depth and often only penetrate the soil to depths of approximately 20 cm. This shallow root system allows the tree to grow on permafrost or in other harsh soil conditions (Krause and Fournier 1997).

Black spruce usually grows in cool, poorly drained nutrient-poor bogs and swamps. In more nutrient-rich plots, black spruce is often out-competed by other tree species. Although black spruce can be found growing in a number of different soils such as deep humus, clays, loams, sands, and coarse till (as well as on boulder pavements and shallow soil over bedrock), it is usually found growing in wet organic soils (Safford *et al.* 1990). Black spruce forests accumulate large amounts (in contrast to drier deciduous forests) of organic matter of black spruce the rate of decomposition is often slower than accumulation in the bogs and wetter areas of forests (Vance and Chapin 2001).

A continuous ground cover of feather mosses (*Hylocomium* spp., *Pleurozium* spp., and *Ptilium* spp.) and peat mosses (*Sphagnum* spp.) is characteristic of black spruce forests, except in some northern sites, lichens (*Cladonia* spp.) grow in mats in place of the mosses (Bisbee *et al.* 2001). Mosses influence soil temperature regimes, nutrient availability, and hydrology. Peat mosses maintain the low temperature of the soil, lower the pH and increase soil moisture to a greater degree than do feather mosses (Bisbee *et al.* 2001); these temperature and moisture characteristics further decrease the rate of organic matter decomposition in black spruce stands.

2.2 - Fire

Forest fires have been a part of the ecosystem succession in the boreal forest of Canada since the Miocene (30 M years B. P.) or early Pliocene (12 M years B. P.), when modern forest assemblages evolved (Weber and Taylor 1992). The ecological effects of fire in the boreal forest vary depending on many factors, including vegetation type, soil moisture content, current climatic conditions, time of year, quality and/or quantity of fuel, and the severity and intensity of fire (Wierzchowski *et al.* 2002). Changes in these factors cause fires to burn more intensely in some areas and not others, leading to a patchy landscape (Kimmins 1997).

Many different ecosystems rely on fire to maintain their successional development (Johnson and Matchett 2001); however, the timing of fire cycles differs depending on the geographical region and ecosystem type. For example, some grasslands in Manitoba require fire to maintain grassland species and to withstand encroachment by aspen (Shay *et al.* 2001). In prairie systems of Missouri, fires may occur on an annual

basis (Kucera and Ehrenreich 1962), whereas the porcupine grass of the Great Victoria Desert has a fire return interval of 20 years (Haydon *et al.* 2000). Boreal conifers in the Northwest Territories have a fire return cycle of approximately 110 years (Johnson and Rowe 1975). In North America, the average fire cycles of black spruce (78 years) and white spruce (*Picea glauca* (Moench) Voss) (96 years) are much longer than that of jack pine (*Pinus banksiana* Lamb.) (39 years) (Larsen 1997).

Black spruce is often a post-fire pioneer tree species on peatlands and upland sites. As long as there is a seed source available, black spruce can quickly re-establish after fire (Safford *et al.* 1990). When a fire has occurred, the cones of the black spruce in surrounding unburned areas often have enough seed to adequately reseed the burned area. Fire accelerates seed fall in both unburned trees and burned trees (Safford *et al.* 1990), and removal of the surface organic layer of the soil by fire provides a suitable seedbed.

2.2.1 - Effect of Fire on Forest Soil

Ground fires cause the organic layer to become mineralized and also initiates the redistribution of carbon in forest systems (Choromanska and DeLuca 2002). In the absence of fire, it may take microbes years to mineralize the same amount of organic matter that a fire would mineralize in minutes. In forest systems where peat moss mats accumulate over the soil, paludification (the gradual conversion of upland to wetlands) results whereby nutrients are withheld in the soil. Fire releases nutrients, thereby making them available for plant growth (Little *et al.* 2002).

Depending on factors such as moisture and soil type, a fire may burn only the top of the duff layers, or a fire may burn the entire organic layer down to rock or mineral soil

(Kimmins 1997). This loss of organic matter can change the vegetation due to losses in the seedbank, as well as changes in pH and in moisture levels. There may also be secondary effects due to fire, such as increases in light from gaps in the canopy which can in turn alter the vegetation composition, and cause in changes in soil composition.

2.2.2 - Fire Suppression and Fire Cycles

It has been suggested that global warming may increase fire frequency in the boreal forest (Johnson *et al.* 1999), but decrease the number of large fires (Bergeron *et al.* 2001). However, it may be difficult to measure changes in fire cycles of the boreal forest since anthropogenic influences are constantly changing and have affected the original fire cycles (Nagy and Warner 1999).

Wherever commercial harvesting takes place across Canada, fires are being suppressed (Smith *et al.* 2000). Since fires are a natural part of boreal forest succession, suppression may cause changes in natural forest succession, leading to an increase of late successional tree species, such as white spruce. There are divergent opinions on the impact of fire suppression on managed forests in terms of whether fire management may lead to changes in natural fire return intervals (Ward and Tithecott 1993, Ward and Mawdsley 2000, Miyanishi and Johnson 2001).

2.3 - Harvesting

Coniferous and deciduous tree species have been harvested from the boreal forests of Canada for hundreds of years (Kimmins 1997). Since the 1950s, advances in harvesting machinery have accelerated forest harvesting. The demand for forest products

has increased with increasing human population growth. Black spruce is an important species for the pulpwood industry in Canada and to a lesser degree is used for lumber (Safford *et al.* 1990). Clearcuts (the removal of all trees in a large area) provide large quantities of wood fiber in a short amount of time and in an economical manner.

However, the ecological impacts of large-scale clearcut harvesting are now the subject of considerable scientific investigation in regards to their ecological impact (Keenan and Kimmins 1993, Niemela 1997, Niemela 1999, Roy *et al.* 2000).

2.4 - Harvesting and Fire Cycles

In general, it is assumed that the boreal forests in North America have relatively short fire cycles. This assumption is often used to justify current forest management principals and practices (i.e., harvesting); however, since a fire cycle is extremely variable in time and space, it is difficult to determine how management practices affect their cycles (Bergeron *et al.* 2001). It is commonly considered that forest harvesting should be based on the specific fire cycle of a particular forest region (Kimmins 1997). In most regions of Canada, little is know about boreal forest fire cycles and their relationship to harvest schedules and forest rotation planning.

After a fire, black spruce usually regenerate as an even aged stand. On the other hand, after harvesting, regenerating stands maybe composed of uneven ages of trees (Perry and Bousquet 2001). In black spruce-dominated wetlands during a harvest, the water table rises more than in burned wetlands and disrupts the natural regeneration of seedlings. It may take up to three years before the water drops to normal levels and black spruce regeneration improves (Roy *et al.* 2000). After a harvest, soil may become

compacted and the ground is often covered by slash (woody material left-over from harvesting). Whereas a fire changes the soil in different ways, with less intense fires not dramatically changing the soil and more intense fires completely removing the soil structure (Ahlgren and Ahlgren 1960). There can be residual woody debris after a fire, although this woody debris is often charred and occurs in smaller amounts than in a harvest (Ahlgren and Ahlgren 1960).

2.5 - Bioindicators

It may be easier to observe patterns in biodiversity by directing studies of ecosystem health assessments towards one representative subset of organisms in an ecosystem (National Research Council 2000). The use of bioindicators may save both time and money when compared to an intensive study which takes into account all taxa.

Controversy exists regarding the criteria to be used in the selection of indicator taxa (Rainio and Niemela 2003). One arrangement recommends use of rare or endangered species, however these species are not always indicative of the environment (Pearson 1995). Alternatively taxa may be chosen exclusively on the basis of familiarity and/or the researchers' personal interests rather than the organisms' proven performance as an indicator (Anderson 1999).

It is best to use species-rich faunal groups such as insects (Humphrey *et al.* 1999), spiders (Buddle and Hammond 2003), fungi (Elmholt 1996), and lichens (Nimis and Martellos 2001) in the measurement of biodiversity within a forest. Many small habitats may go unnoticed in a seemingly uniform landscape and may be excluded if one does not use sensitive organisms to measure biodiversity (Spence 2001).

It is unreasonable to expect that one indicator species can represent the diversity of all other taxa in an ecosystem. This is especially true if verification of the relationship between indicators and “entities” of which they are hypothetically indicative of has yet to be tested (Lindenmayer 1999). The choice of indicator taxa should be based on the type of ecological measurement from the system under study. By choosing taxa based on appropriate criteria, we can avoid the use of inappropriate species as indicators which could lead to erroneous conclusions regarding the health of the area being monitored (Noss 1990, Lindenmayer 1999).

Pearson (1995) suggested a grading system that would evaluate which taxa could be used as indicators and also recommended the following seven criteria be employed when choosing an indicator: 1) the organism must be taxonomically well-known and stable, 2) the biology and life history must be known, as well as the organism’s interactions with other organisms, 3) populations must be easily surveyed and manipulated, 4) the organism should occur over a broad geographical range at higher taxonomic levels (e.g., order, family, tribe, genus), 5) there should be some habitat specialization at the species level making them more sensitive to habitat change, 6) evidence that the indicator taxon shows parallel patterns of biodiversity in the ecosystem as other taxa, and 7) the indicator should have economic importance. Noss (1990) and Anderson (1999) have suggested similar criteria in the selection of indicator taxa. Ordination techniques can be used to verify whether an indicator species or group will appropriately represent environmental conditions and other organisms in the ecosystem (Kremen 1992).

Insects make good bioindicators because they have short life spans, high rates of population increase, short generation times, and high habitat specificity (Rosenberg *et al.* 1986, Brown 1997). However, in certain groups of insects identification might be time-consuming and require the skills of a specialist. Oliver and Beattie (1993) compared the use of species identification to recognizable taxonomic units based on visual differences. Their results showed that recognizable taxonomic units could be separated by non-specialists with less time and cost than species identification. Although there are time and cost benefits of using recognizable taxonomic units, much information could be lost, such as the ability to examine an individual's species' habitat. Currently most studies use indicators identified to the species level. The use of computerized interactive keys has been suggested (Behan-Pelletier and Newton 1999) to facilitate identification by non-specialists and to decrease identification time.

Phytophagous insects may be useful indicators since they are influenced by factors such as light, humidity, nutrient availability, and specific plant growth cycles (Brown 1997); also, phytophagous insects have a direct reliance on plants. However, predators may be more representative as an indicator group because of their reliance on invertebrates (including phytophagous insects) at lower trophic levels, as well as their sensitivity to the physical environment (Sousa 1984). Carabid beetles are reliable bioindicators since their species distributions are determined by habitat type (Dufrene *et al.* 1990, Rainio and Niemela 2003) and many are predaceous. Carabids are often distributed over a range of terrestrial habitats, are fairly easy to identify (Maelfait and Desender 1990), and have been used successfully as indicators of ecosystem health in

many studies (Holliday 1991, Niemela *et al.* 1993, Niemela *et al.* 1994a, Niemela *et al.* 1994b, Humphrey *et al.* 1999, Pearce *et al.* 2003).

2.6 - Carabidae

Carabids belong to the suborder Adephaga and are considered the most primitive forms among the order Coleoptera (Villani *et al.* 1999). Taxonomy of the Canadian Carabidae is well known and remains relatively stable (Lindroth 1961, 1963, 1966, 1968, 1969). There are also checklists of the Canadian carabids fauna available (Bousquet 1991, Paquin and Duperre 2001).

Carabids may breed one or more times a year depending on the climate and the species (Den Boer and Den Boer-Daanje 1990). Eggs are laid singly in moist soils in preformed cells (Basedow 1994) or may be laid in other substrates in the forest, such as under bark or in rotting wood (Goulet 1974). Carabid larvae may be predators, mainly eating other insects, or herbivores, eating plants or seeds (Thiele 1977, Hengeveld 1980). North American adult carabids (depending on the species and location) typically live for one to two years (Thiele 1977, Milne and Milne 1995).

Carabids possess a body plan that is not dramatically modified for different habitats (Evans 1994), and their morphological characters show a great deal of uniformity throughout the family (Thiele 1977).

The general shape of carabids is conducive to quick movement through and on top of the soil (Evans 1994). The segmentation of the tarsi (5-5-5) in the carabids is representative of a primitive condition in the Coleoptera (Villani *et al.* 1999). Their long and thin legs allow for quick, large strides; ideal for sudden movements and fast running.

The eyes and antennae are situated laterally, which is most advantageous during penetration of crevices in soil or rock. The antennae are filiform, a shape which is easy to clean and well adapted for moving through the soil.

The presence of wings in carabids is considered to be a primitive feature. There is great variability in wing size and shape and ability to fly within this family (Lindroth 1961, 1963, 1966, 1968, 1969, Thiele 1977, Holliday 1991). Wing development differs between species level and even within a species. Their flight ability is related to the ratio between wing length and body length. Even in possession of large wings, wings may not allow flight if the ratio is inadequate (Thiele 1977). Flight is a significant factor which determines the speed at which the beetles are able to disperse and colonize new areas.

2.7.1 – Carabid Habitats

It has been difficult to observe carabids in a natural setting (Loreau 1990), because they occur in the soil, under stones, in moss and rotting wood, and under bark. Carabids are generally observed running on top of, or digging into soil (Thiele 1977). A majority have an unmetallic dark coloration, a camouflage against the soil, however some are metallic and brightly coloured. Their colouring may be related to ground temperature (Terrell-Nield 1990).

Some carabids are generalists occupying many habitats, while some are specialists exclusive to a single habitat. For many species there are no morphological features that suggest different ecological distribution, thus differences in habitat selection may be physiologically or behaviorally dependent (Thiele 1977).

Studies on the effects of environmental factors on carabids (Thiele 1977, Grum 1994, Neve 1994, Nyilas 1994), found that factors such as time of day, temperature, humidity, and salinity of the soil determine habitat preferences and the number of species present in different ecosystems.

2.7.2 - Sampling Methods for Carabids

Many sampling methods have included litter sampling (Spence and Niemela 1994), quadrat counts (Greenslade 1964), and pitfall trapping because most carabid activity is restricted to ground level,. Litter sampling involves taking samples of litter and organic material from the ground and placing it into a floatation chamber so that any beetles float to the surface of the water (Spence and Niemela 1994). Quadrat counts involve counting individuals occurring in a quadrat (Greenslade 1964).

Pitfall traps vary in size and shape, but for the purpose of this thesis pitfall traps consists of a circular containers placed in the ground such that the rim is level with the ground surface. A board is suspended over the top of the trap to prevent flooding from rainfall. Unsuspecting carabids moving on the surface of the ground will, fall into the trap and are unable to climb the smooth sides. Pitfall traps may contain fluids, such as salt water, which kill the beetles, or traps can be left dry to capture live beetles. The first published use of pitfall traps was to capture cave dwelling insects Barber (1931). Pitfall traps are now the most commonly used method of capture for carabid beetles for quantitative studies (Niemela *et al.* 1994a, Beaudry *et al.* 1997, Spence *et al.* 1997, Abildsnes 2000). The pitfall method is an inexpensive and labour efficient way to collect carabids for statistical analysis.

Experiments have determined if differences between trap types are detectable by diurnal carabids by changing the colour of the container or by baiting the traps. The results showed no differences in carabid densities in traps of different colours or with bait (Greenslade 1964).

Circular pitfall traps are most often used because they seem to provide higher catches of beetles than square pitfalls (Spence and Niemela 1994). Debate still exists regarding the use of pitfalls in quantitative assessments. Greenslade (1964) believed pitfalling could not be used for quantitative assessment of carabids in all habitats. Maelfait and Desender (1990) argue that it is possible to use pitfalling for carabids in most habitats, but that results should be interpreted with care to account for phenological differences (Baars 1979). Adis (1979) discussed several problems associated with using pitfall traps and stressed the importance of standardizing pitfall traps such that they are always the same size and colour.

2.8 - Biodiversity

Biodiversity is difficult to define, but from a community ecologist's point of view it has been termed the variety and distribution of species or vegetation types over a geographical unit (Noss 1990). Biodiversity represents the overall heterogeneity in nature and higher biodiversity allows for an ecosystem to become increasingly resilient (Niemela 1999). Understanding biodiversity allows us to describe environmental problems holistically instead of examining individual situations on a species-by-species and stress-by-stress basis (Noss 1990). Environmental issues, such as disturbances by logging, could soon be monitored by calculating forest biodiversity on a periodic basis.

Biodiversity is not simply the total number of species of an area; but it represents a range of indices that take into account measures of species richness and species abundance. Since there is no index suitable for all situations, choosing the best index must be based on criteria to be emphasized (Anderson 1999). A number of indices have been devised, some of which have been described as more useful than others (Magurran 1988).

Local or stand-level diversity is also known as alpha diversity. Measured at the community scale, stand level diversity describes species richness and species evenness (Hill 1973) within the environment. Species richness is characterized as the number of species found in a community (Kimmins 1997). Species evenness can be defined as the degree to which species abundances are equal within a community (Magurran 1988), or, to the frequencies of different species within a system (Kimmins 1997).

Landscape diversity or beta diversity is the degree of change in species between communities. Beta diversity measures the difference in species composition between local assemblages and/or regional assemblages. As beta diversity increases for a given level of regional species richness, the individual localities differ more distinctly from each other (Southwood 1978, Koleff *et al.* 2003). Beta diversity is useful in that it shows the level of partitioning of habitats by species. Habitats of different study systems can be compared using beta diversity, and when combined with alpha diversity, may provide a good measure of the overall species diversity within an area (Wilson and Shmida 1984). Variation in species richness, species evenness, and/or community structure is usually a result of soil characteristics and landforms causing differences in soil moisture and fertility, and the succession and disturbance history of an area (Kimmins 1997). Thus,

diversity indices also reflect the influence of the physical environment on plant and animal populations.

2.7.1 - Measuring Biodiversity: Using Statistical Indices

There are several different measures of alpha diversity (Pielou 1975). Two of the most common measures currently used are the Shannon-Wiener index and the log series alpha index.

The Shannon-Wiener index, also known as the Shannon index of diversity (Margalef 1958, Magurran 1988), assumes the following: an infinite population of individuals, random sampling of all species, that all species are represented within the sample, and all species are randomly sampled and represented in the sample (Pielou 1975). This index has been criticized in the past due to its sensitivity to rare species and to sample size (Magurran 1988). This index tends to be used most when describing the diversity of vegetation.

The log series alpha index was developed by Fisher *et al.* (1943) and mathematically describes the relationship between species richness and species evenness. This index is little affected by common or rare species and is independent of sample size (Magurran 1988). Fisher *et al.* (1943) and Kempton and Taylor (1974) have found log series alpha to be the most efficient diversity index for insect species and populations. One disadvantage of using log series alpha is that it is a less powerful way to discriminate when species richness and number of individuals are constant (Magurran 1988).

Measurements of beta diversity are independent of alpha diversity, such that a landscape with high measures of alpha diversity can have high or low measures of beta

diversity at the community level (Kimmins 1997). Two of the most widely used beta diversity are the Jaccard's index (Goodall 1973) and Sorenson's quantitative index (Bray and Curtis 1957). These beta diversity indices have values that can vary from one, with both sets of species identical (i.e., both sets of species identical), to zero, with no species in common (i.e., no species in common) (Thomas 2001).

Jaccard's and Sorenson's indices each have the advantage of being easy to use, although species abundance is not included in the calculation. This leads to equal weighting of common and rare species (Magurran 1988). The Jaccard's index is qualitative, and relates the presence and absence of species in two samples. On the other hand, Sorenson's index can be either quantitative, considering the relative abundance of individual species between two samples or qualitative, examining only presence absence data (Magurran 1988). The correct use of the above indices depends on the situation and the types of organisms being recorded.

These diversity calculations produce numbers without units that usually decrease with increasing diversity. Currently, there is no universal standard to compare against; a biodiversity index value should be compared to others of the same index, either over time or space.

Even though diversity indices relate to the number of a species, they do not distinguish between the specific species that are present or absent from an ecosystem. Therefore, if forest management workers were to rely on diversity indices alone, they could unknowingly cause the extinction of a species. Other techniques such as ordination should be combined with diversity indices to produce a more accurate representation of ecosystem health and biodiversity.

2.8 – Ordination Analysis

Ordination is a method used to represent multivariate data in lower dimensional space, while at the same time attempting to maximize the amount of trended variation (Pielou 1984, Kenkel *et al.* 2002). Ordination allows large biological data sets to be displayed in a scattergrams that suggest trends, which would otherwise be difficult to spot, in the data. When displayed in an ordination diagram, the distances between points are related to their similarity, with like data grouped closer together. Ordination can be used to illustrate similarity between plots based their species or environmental variables. And can be used to determine plot associations (Ter Braak and Smilauer 2002).

Axes in the ordination diagram are arranged orthogonally in order to explain the maximum variation in the data. Each axis has an eigenvalue that denotes the linear variance described by that particular axis (Kenkel *et al.* 2002). Axes are ranked in order of their eigenvalues: axis one has the greatest eigenvalue and therefore explains the greatest amount of variance, and as the axes increase from one, they explain less and less of the amount of variance. An ordination diagram usually only represents the variation in the first two axes, and if the eigenvalues are quite large then trends have been revealed in the data.

2.8.1 - PCA

PCA (Principal Component Analysis) is an ordination analysis that describes the relationship between two quantitative variables, such as species abundance within several

plots (Colunga-Garcia et al. 1997). PCA requires data attributes to be linear in order to properly maximize the variance. PCA can be used to separate plots based species present, therefore, grouping plots together that have a similar species composition. In this study, groupings of plots and species of vegetation and carabid beetles could reveal patterns in age class and disturbance types based on species data.

2.8.2 - RDA

RDA (Redundancy Analysis) is a multiple regression analysis which employs environmental data to constrain the species data (Ter Braak and Smilauer 2002). In other words, RDA is a constrained form of PCA, so data must also have linear attributes. RDA attempts to maximize predictions of two sets of variables: biotic data and abiotic data (Kenkel *et al.* 2002). RDA is a relatively new method of analysis and it seems to prove useful in finding patterns of species with respect to environmental data. In this study, RDA might reveal patterns in relatedness of plots and species based on environmental variables in different age classes and disturbance types of black spruce.

Chapter 3 - Methods and Materials

3.1 - General Study Area Description

The area selected for this study was located within the Subhumid Transitional Low Boreal ecozone (Zoladeski et al. 1998) of the boreal forest region east of Lake Winnipeg, Manitoba near the Manitoba-Ontario provincial boundary. Black spruce is the dominant tree species in this ecozone. The forest stands sampled were situated between 50°33' and 50°56' North latitudes, and 095°11' and 096°15' West longitudes. The majority of stands were located on open Crown land; the easternmost stands were located in Nopiming Provincial Park (Figure 1).

3.2 - Experimental Design and Site Selection

Two types of forest stands were used in the study: stands that had been either burned by fire or clearcut harvested. Neither planting techniques nor harvest machinery used were considered when selecting the stands used in this study. Black spruce dominated all stands before either burns or harvests took place; several stands regenerated to become dominated by black spruce (Table 2).

The stands sampled in this study were established between 1998 and 2001 using harvesting records and fire maps supplied by Pine Falls Paper Company - Tembec Inc. For each stand type, the following three age classes were assigned: "old", "intermediate", and "young". "Old" stands had either burned in 1929 or had been harvested in 1957,

“intermediate” stands had either burned or had been harvested in 1983, and “young” stands had either burned in 1999 or had been harvested in 1999 or 2000 (Table 1).

Two sites were established for each stand type; within each site there were two plots. However, a second plot in one of the burned in 1929 could not be established due to the limited area available that had remained undisturbed since 1929. In total there were 23 plots located within 12 sites. Plots were 100 X 100 m and were located at least 50 m away from each other and from other bordering areas of discontinuity (e.g. roads and bodies of water).

Plots were assigned abbreviations corresponding to their disturbance type and approximate age of disturbance (Table 1). There is two numbers which follow the year: the first number refers to the site number and the second refers to the plot number. For example, B29 1P2 is the second plot located in site one of a stand that had burned in 1929. H57 2P1 represents plot one located in site two of a stand that had been harvested in 1957.

A grid was placed over each plot and the northernmost edge was numbered from one to ten, at 10 m intervals. The westernmost edge was numbered in the same fashion. Where the north and west numbers were positive (excluding zero and 10), 16 intersecting locations were referred to as “points” and labeled from A to P, respectively (Figure 2).

3.3 - Soil Characterization

A soil pit 10 X 10 X 10 cm was dug near the center of each plot. A soil sample was collected from the base of the pit the soil type and pH were determined. Soil types

were identified using The Canadian System of Soil Classification (Soil Classification Working Group 1998). Analysis of pH followed methods of Scott (2001).

3.4 - Canopy Closure and Light Meter Readings

At every second point in the plot a canopy closure measurement was recorded at a distance of 1 m from the ground using a Model C densiometer (Lemmon 1956). The area of mirrored squares not occupied by foliage was recorded and a mean percent cover was calculated for each plot. A single reading consisted of four measurements taken at each compass point (N, S, E, and W). The four compass point measurements were averaged to give a single densiometer reading per point.

A single light reading was recorded at each of the points (Figure 2) using a Gossen Tri-Lux foot-candle light meter. The light readings were taken only when there was no cloud cover. One light reading was taken at a distance of 1 m from the ground at an open area nearest to the plot (e.g., a body of water or a road). Each of the light meter readings within the plot was divided by the open area reading to give a percentage of light. This percentage was then subtracted from 100 to give a value of percent shade per point. The percent shade values were then averaged to give a mean percent shade value per plot.

3.5 – Temperature and Precipitation

Maximum daily temperatures and precipitation were obtained from the Manitoba Conservation Fire Program's Knob Hill South weather station located in a central

position in the study area (Figure 1). Daily maximum temperatures and precipitation are presented graphically in Appendix 1.

3.6 - Vegetation Sampling

Vegetation sampling took place in July of 2000 and followed methods similar to Johnston and Elliott (1996). Percent cover of two separate vegetation layers, herbaceous vegetation and shrubs, was determined for plots established by the year 2000 (Table 1). Herbaceous vegetation was sampled using 20 randomly placed 1 X 1 m quadrats per plot. Any plant below 1 m in height was considered part of the herbaceous category, including lichens, bryophytes, and percent cover of woody debris. Percent cover of downed woody debris was also included in the vegetation quadrats. Shrubs consisted of woody plants between 1 m and 3 m tall, and were sampled using 15 randomly placed 2 X 2 m quadrats per plot.

Numbers of individual trees for each tree species were recorded in 2001 from five 10 X 10 m quadrats per plot and are represented as percent composition (Table 2). For the purpose of this study, a "tree" consisted of any woody plant over 3 m. Tree core samples were taken from four to six trees within each size class to confirm the age of each plot (Table 1). Plant authorities are given in Appendix 2 and 3.

3.7 - Sampling of Carabids Beetles

Carabid sampling took place over a five-year period between 1998 and 2002. This thesis focuses on results gathered from the 2000 and 2002 collecting years. These two years were most comparable in terms of carabid collection dates, disturbance types,

and age classes. Since the start and the end of the carabid collecting season differed between 2000 and 2002, only the overlapping sampling periods were used in the analysis. This was accomplished by removing samples from the 2000 collecting season that dated to either before May 31 or June 14 (depending on collection dates) and after September 6 (Table 3). B83 3P2 was also removed from the 2000 data since this plot was not sampled consistently throughout the season.

Pitfall traps were used in this study to collect carabids. These traps consisted of two plastic 450 ml cups nested together, with the rim placed at ground level. The cup was filled approximately 4 cm from the bottom of the cup with salt water. Salt water acted as both a killing agent and a preservative. Cups were sheltered by suspended 30 X 30 cm plywood squares to prevent flooding and interference by animals. In each plot, 16 pitfall traps were placed, one on each of the points (Figure 2). Traps were emptied every two weeks and their contents were placed into vials containing 70% ethanol solution pending identification.

3.8 - Carabid Identification

Adult carabid identification was based primarily on keys by Lindroth (1961, 1963, 1966, 1968, and 1969) and Bousquet (1986). Carabids were identified to the species level except where identification could not be confirmed below the level of genus. It is extremely difficult to identify female individuals of *Agonum trigeminum*, *Agonum fidele*, and *Agonum mutatum* past the level of genus. Therefore, male and female *A. trigeminum*, *A. fidele*, and *A. mutatum* were combined into the species complex *tfm* for the purposes of this thesis (where *tfm* refers to the first letters of the three species

respectively). Other *Agonum* species, not including the *tfn* species complex, that were not identifiable to the species level from the year 2000 were labeled *Agonum spp.*

Carabid authorities are given in Appendix 5, and if beetle species did not occur in 2000 the authority is given in appropriate Appendix.

3.9 - Statistical Analysis

3.9.1 – Means, Standard Errors, ANOVAs, and Contrasts

The mean and standard error was calculated for each disturbance type and age class combination. Mean numbers and standard errors were calculated based on the mean of all plots for each treatment type (both disturbance types in each age class) for each collecting season. Mean and standard errors values were calculated using SYSTAT (Wilkinson 1998).

Analysis of variance were performed to determine if there was statistically significant effect of age class, disturbance type, and the interaction of disturbance type with age class for each of the dependant variables. Dependant variables included vegetation, environmental variables, and carabid beetles. Analysis were performed using the ANOVA option in SYSTAT. Tukey's Post Hoc tests were performed on those results showing a statistical difference between age classes to determine which age class or classes were statistically different from each other.

In addition, contrasts were used to determine if there were significant differences between disturbance types at the level of each age class. This test was performed on all

experimental variables including vegetation, environmental variables, and carabid beetle data.

3.9.2 - Carabid Beetle Data

Analysis of the carabid beetle data from the year 2000 was performed using the date-adjusted data, this included mean and standard error calculations, beetle species averages, and ANOVAs. No adjustments were made for the 2002 data.

Mean carabid catch data (number of individuals and number of species) for each plot were log-transformed to satisfy assumptions of normality and heterogeneity of variance for analysis with the ANOVA test.

Means and standard errors were calculated for the top five occurring carabids species (*Pterostichus adstrictus*, *Pterostichus pensylvanicus*, *Platynus decentis*, *Agonum gratiosum*, and *Synuchus impunctatus*) in 2000 (using adjusted data) and 2002. Contrasts and ANOVAs were calculated to compare the mean of each species between age classes and disturbance types, and disturbance types within age classes.

Percent shared species between burns and harvests within an age class for a given year were calculated for 2000 and 2002. For example: burned plots containing one or more of a particular species in which that same species was also present in harvested plots of the same age class were considered a shared species.

3.10 - Diversity Data

3.10.1 - Vegetation

Shannon diversity indices (Margalef 1958, Magurran 1988) were calculated for shrub and herbaceous strata (including bryophytes and lichens) using the software program Bio-DAP (Thomas 2000). These were calculated from percent species cover averaged for the quadrats in each plot.

3.10.2 - Carabids

Species evenness was calculated for each plot by obtaining the slope of the log abundance-rank regression using SYSTAT. Evenness values were the absolute value of the slope. The closer the result was to zero, the more equally species were represented in the sample. ANOVA tests were then performed separately on evenness data for 2000 and 2002.

The alpha diversities (log series alpha and Berger Parker index) were calculated from the sums of individuals and species in each plot for the collecting season. Calculations were done using the software program Bio-DAP (Thomas 2000) which is based on Magurran (1988). Differences in alpha diversity indices between disturbance types and age classes were analyzed by ANOVAs.

3.11 - Ordination

DCA (Detrended Correspondence Analysis) were performed on species data, and if the length of the gradient on the first axis was less than or equal to four then PCA (Principal Component Analysis) was performed (Ter Braak and Smilauer 2002), this was

found to be the case for all analysis. Data was arranged in Excel with plots as columns and individual carabid species as rows. Data was copied into CANOCO (Ter Braak and Smilauer 2002) where PCA was performed on the sums per plot. Species data were log-transformed using options in CANOCO. Beetle species data for 2000 and 2002, vegetation species for 2000, tree species, and environmental variables were analyzed using PCA. Unadjusted data was used in all ordinations on beetle data for the year 2000. Further analyses were performed on beetle species using PCA by removing beetle species which were most common for 2000 and 2002.

RDA (Redundancy Analysis) was performed on beetle species data (sums per plot) with disturbance type and age classes added as environmental variables for both 2000 and 2002 using CANOCO (Ter Braak and Smilauer 2002). In all cases beetle species were plotted in environmental space. Beetle species selected for use in RDAs had to satisfy the criterion that they were caught more than four times in 2000, and more than once in 2002.

Using the same disturbance type and age class environmental variables, RDA was performed on percent cover means per plot of vegetation species for the year 2000. Vegetation species (herbaceous, bryophytes, and lichens) that occurred as more than 50% cover total sum over all plots were included in the analysis.

RDA was performed on carabid species data and environmental data (pH, percent cover of woody debris, and canopy closure) for 2000 and 2002.

Chapter 4 - Results

4.1 - Visual Descriptions of Sites

4.1.1 - Young Sites

Cinders were present in all young burned plots (B99 1P1, B99 1P2, B99 2P1, and B99 2P2). In all burned plots, ash-covered snags remained standing or lay on the ground. Fire had left many large areas of rock exposed in the two B99 1P plots. Both B99 2P plots were located in a lower and wetter area and therefore experienced a larger rise in the water table and less exposed rock than B99 1P plots.

Young clearcut plots had been harvested either in the winter of 1999 (H99 1P1 and H99 1P2) or the winter of 2000 (H99 2P1 and H99 2P2). Young harvested plots also experienced an initial rise in the water table after a disturbance much like the young burned plots. Soon after the disturbance, graminoids became the main herbaceous plants and caused a decrease in the water table. Both harvested and burned plots experienced an initial increase in the water table followed by the presence of dominate graminoid species. Harvested plots had a ground cover consisting mostly of slash, and therefore they had smaller areas of rock exposed than young burns.

4.1.2 - Intermediate Age Sites

The ground cover of intermediate burned plots (B83 2P1, B83 2P2, B83 3P1, and B83 3P2) consisted of mostly brown coniferous leaf litter, rocks (approximately 40 cm to over 6 m in diameter), and many wind-blown black spruce snags (with no bark

remaining) left from the fire. Large rock areas were present and covered with lichen. Wet-grassy areas with a few small ephemeral streams were also present in intermediate burn plots.

Harvested intermediate plots (H83 1P1, H83 1P2, H83 2P1, and H83 2P2) were similar to the burned 1983 sites in having similar sized rocks covered with lichen. The burned and harvested plots differed in that the harvested plots had a lower coniferous leaf litter, and fewer snags. Chainsaws and skidders had been used to harvest plots in 1983. Two of the plots (H83 1P1 and H83 1P2) had been planted with black spruce after harvesting.

4.1.3 - Old Sites

The ground was covered with mosses and wind-thrown trees in the old burned plots (B29 1P1, B29 1P2, and B29 2P2). The number of wind-thrown trees dramatically increased after two wind storms in mid-summer of 2002. Large lichen covered rock areas were present in some plots. Older burn plots were notably easy to navigate through, as lower branches of black spruce trees had self-pruned.

The old harvested plots (H57 1P1, H57 1P2, H57 2P1, and H57 2P2) were similar to the B29s in having a ground cover of mosses, and some lichen-covered

4.2 - Environmental Site Variables

4.2.1 - Vegetation

Herbaceous and shrub species data that had been collected from 2000, along with authorities, is in shown Appendices 2 and 3. The number of species, and Shannon's Diversity index of herbaceous plants showed no difference between age class or disturbance type, and no interaction between age and disturbance (Table 4).

The number of species of shrubs was greater in old harvested plots than in old burned plots (Table 5). Intermediate plots had a greater number of shrub species compared to older plots, but did not differ from younger plots. Similarly, intermediate plots had higher Shannon's diversity values than older plots, but were not significantly different from younger plots (Table 5).

4.2.2 - Canopy Cover and Light

Percent canopy closure and percent shade, measured with the densiometer and light meter respectively, showed similar trends of increasing with site age (Figure 3). Canopy closure as well as percent shade were significantly different between age classes and disturbance types (Table 6). Burned plots had greater canopy closure and percent shade than harvested plots; this difference was also observed by contrasts (with the exception of percent shade in old plots). There were no interactions between site age and disturbance type.

4.2.3 - Percent Cover of Downed Woody Debris

Percent cover of downed woody debris was significantly different between sites of various ages and disturbance types. Younger plots had higher percent cover values than the old or intermediate plots (Table 6). In addition, harvested plots had higher percent cover values for woody debris than burned plots. The interaction effect was significant where the percent cover of woody debris increased with both a decrease in site age and date of harvest.

4.2.4 - Soil Type and pH

Soil type varied between plots. Most were organic soils, with the exception of Chernozems in some plots (Table 7). The water table was high in most areas, resulting in wet acidic soils and an understory of sphagnum moss.

Age classes showed a difference in soil pH where older plots had a lower pH than young plots (Table 6). Soil pH did not differ between disturbance types and showed no interaction.

4.2.5 - Climatic Data

In general, the summer of 2000 was cooler and wetter than 2002 (Appendix 1).

4.3 - Carabid Beetles

4.3.1 - Number of Individuals, Number of Species, and Most Common Species

The total number of carabid beetles collected was 1052 in 1999 (Appendix 4), 1347 (854 used in analysis when adjusted for the length of the collecting season) in 2000 (Appendix 5), 796 in 2001 (Appendix 6), and 786 in 2002 (Appendix 7). All carabid scientific names and authorities are listed in Appendix 5, except where a species does not occur in 2000 then species information is located in other appendices.

The number of beetles in 2000 was different between age classes (Table 8), since younger plots had more individuals than either intermediate or old age classes. Burned plots had more individuals than harvested plots within old and young plots contrasts. Overall disturbance types did not show differences between the numbers of individuals. In 2002, number of beetles did not differ between age classes or disturbance types (Table 9). However, there was an interaction effect of age class and disturbance type where the number of individuals appeared to be greatest in old and intermediate burn plots. All contrasts of 2002 data comparing disturbance types between each age class the burned plots had higher numbers of individuals.

In 2000, the total number of species was found to be different among age classes (Table 8). Young sites had a higher number of beetle species than intermediate or old plots. Both old and young burned plots had a greater number of species than harvested plots of the same age. In 2002, there was no significant difference in the number of species between age classes or disturbance types (Table 9).

The most common beetle in 2000 was *Platynus decentis*, whereas *Pterostichus adstrictus* was the most common species in 2002. The five most frequently occurring species in 2000 and 2002 were: *P. adstrictus*, *Pterostichus pensylvanicus*, *Synuchus impunctatus*, *P. decentis*, and *Agonum gratiosum*. Mean numbers of *P. adstrictus* were highest in old and young plots in 2000, and for old plots in 2002 (Table 10). Burned plots had higher numbers of *P. adstrictus* than harvested plots. In the 2002 data, there was an interaction between age class and disturbance type, where old burned plots had more *P. adstrictus* than intermediate or young harvest plots. Young burned plots had more individuals of *P. adstrictus* than young harvested plots for both 2000 and 2002.

Intermediate plots had higher number of *P. pensylvanicus* than old or young plots (Table 10). *Synuchus impunctatus* was caught more frequently in burned plots than harvested plots in 2000 (Table 11). In 2002 *S. impunctatus* was caught more frequently in intermediate plots than old or young plots. *Platynus decentis* showed no differences between age classes or disturbance types (Table 11). In 2002, *A. gratiosum* was more numerous in burned intermediate plots (Table 11).

Pterostichus punctatissimus was found almost exclusively in old plots in 2000 and 2002 (Appendix 5 and 7). Pyrophilous species, *Sericoda quadripunctatum*, was exclusively caught in young burn plots (Appendix 5 and 7). *Harpalus laticeps* also tended to found in young burns (Appendix 5 and 7). The numbers of *S. quadripunctatum* caught was highest during 1999 and 2000 compared to 2001 and 2002 (Figure 4), whereas *H. laticeps* was most numerous in 2000 (Figure 4).

The number of species of the genera to *Harpalus* and *Amara* tended to be higher in burned plots. During 2000, 58 individuals of *Agonum metallescens* were found exclusively in H99 1P1 (Appendix 5).

The percent of shared species was greatest in intermediate sites in 2002 and lowest in young sites in both 2000 and 2002 (Figure 5).

4.3.2 - Seasonal Trends in Selected Species

Five of the most frequently occurring carabid species (*P. decentis*, *A. gratiosum*, *P. adstrictus*, *P. pensylvanicus*, and *S. impunctatus*) showed consistent seasonal patterns of catches (Figures 6 and 7). The highest numbers of *P. decentis* occurred during the spring of 2000 and 2002, although in 2000 there was a second peak from the end of July to mid-August. The highest numbers of *A. gratiosum* were found in mid-July for both 2000 and 2002. The highest numbers of *P. adstrictus* and *P. pensylvanicus* were observed early in the summer, and numbers of individuals then decreased throughout the season in both 2000 and 2002. *Synuchus impunctatus* was most numerous from the middle to the end of the summer. In 2000, *S. quadripunctatum* numbers were highest at the beginning of the summer and then decreased until none were present during mid-August and September.

Syntomus americanus was present 1999, 2000 and 2001, but was absent in 2002.

4.3.3 - Carabid Beetle Diversity

Log-Series Alpha, species evenness and the Berger Parker Index did not significantly differ between age classes and disturbance type, and there was no significant

interaction between age class with disturbance type in 2000 and 2002 (Table 8 and 9), with the exception of Berger Parker index values being different between burns and harvests of young plots in 2002.

4.4 - Ordination Analysis

4.4.1 - PCA

The relationship of plant species and plots was analyzed with PCA. The first two axes accounted for 48.1% of the variation (Figure 8). The PCA of vegetation showed that plots did not strongly group by age or disturbance type. However, old plots grouped closely due to the abundance of mosses (*Pleurozium scheberi*, *Dicranum* spp., *Ptilium crista-castrensis*) and *Trientalis borealis*, *Maianthemum canadense*, and *Cornus canadensis*. Young burns were grouped away from other plots primarily due to the dominance of grasses, sedges, *Epilobium angustifolium*, and *Rubus idaeus*.

Tree species were analyzed with PCA (Figure 9). The first two axes accounted for 95.8% of the variation. The presence or absence of black spruce in plots was separated by the first axis.

PCA of carabid species data for 2000 explained 55.5% of the variance in the first two axes (Figure 10). Plots tended to group according to age class. The older plots clustered together, except one of the old harvest plots was located towards the center of the ordination. Intermediate plots clustered very closely. Younger plots were clustered together, with the exception of one harvested plot (H99 1P2) being located closer to the older plots.

When the most common species were removed from the 2000 carabid species data, 48.7% of the variance was explained in the first two axes (Figure 11). Plots generally grouped closely with the exception of young burned and harvested plots that were found grouped away from each other as well as all other plots.

The first two axes in the PCA of carabid species data for 2002 accounted for 70.1% of the variation (Figure 12). The PCA showed the same general pattern of groupings of the three age classes as in the 2000 diagram. The older plots were grouped together, with one of the intermediate harvest plots pulled somewhat closer to the newly disturbed plots. Burn and harvest intermediate plots were grouped together with one of the burn plots closer to the newly disturbed plots. Newly disturbed plots were closely grouped together.

A PCA of carabid species data for 2002 with the most common species removed had the first two axes account for 68.0% of the variation (Figure 13). Plots grouped together by age class in the same manner as in Figure 12, when the common species were present.

Plots were also analyzed by PCA for the collecting years for each age class. In the young age class PCA included the sampling years 1999, 2000 and 2001. The first two axes accounted for 68.3% of the variation (Figure 14). Generally harvested plots were grouped away from burned plots regardless of year sampled. The PCA for the intermediate plots included sampling years 2000 and 2002. The first two axes accounted for 60.5% of the variation (Figure 15). Intermediate plots were separated by disturbance type by the second axis, however harvested plots were more closely grouped together than burned plots. The PCA for old plots included the sampling years 2000 and 2002.

The first two axes accounted for 67.3% of the variation (Figure 16). Old plots were generally separated by sampling year on the second axis.

4.4.2 - RDA

RDA was used to examine the relationship between beetle species and environmental data. The environmental data was coded for disturbance type (burn or harvest) and age class (old, intermediate, and young) for both 2000 and 2002 data. These RDAs were more influenced by age classes than disturbance type (Figure 17 & 18). In the RDA, the first two axes accounted for 43.6% of the variance in the species data in 2000 and 54.7% in 2002.

Disturbance type and age class code variables were used in a RDA as environmental variables with plant species. Burned plots and harvested plots separated on the second axis and age classes separated on the first axis. The first two axes accounted for 31.8% of the variance in vegetation species data (Figure 19).

Environmental variables pH, percent cover of dead woody debris, and canopy closure were analyzed using RDA with beetle species data 2000 and 2002. The first and second axes accounted for 28.1% of the variance in the species data in 2000 (Figure 20). Most beetle species were clustered in more open areas with less debris/litter depth. The first and second axes in 2002, accounted for 53.3% of the variance in the species data (Figure 21).

Table 1. Information about plot labels, location in degrees and minutes, age of trees (mean $\pm$ SE).

Plots	Year of Fire or Harvest	Age	Burn or Harvest	Location		Ave. Age of trees (years)
				Latitude	Longitude	
B29 1P1	1929	Old	Burn	50°41.06'	095°19.49'	64 $\pm$ 5.8
B29 1P2	1929	Old	Burn	50°40.94'	095°20.15'	58 $\pm$ 1.7
B29 2P2	1929	Old	Burn	50°41.15'	095°20.35'	56 $\pm$ 1.4
H57 1P1	1957	Old	Harvest	50°46.98'	096°12.52'	35 $\pm$ 1.2
H57 1P2	1957	Old	Harvest	50°36.78'	096°12.66'	66 $\pm$ 7.1
H57 2P1 ^T	1957	Old	Harvest	50°40.77'	095°56.96'	40 $\pm$ 1.7
H57 2P2 ^T	1957	Old	Harvest	50°40.85'	095°57.03'	32 $\pm$ 2.3
B83 2P1	1983	Intermediate	Burn	50°50.49'	095°17.86'	16 $\pm$ 0.8
B83 2P2	1983	Intermediate	Burn	50°46.15'	095°18.08'	43 $\pm$ 15.2
B83 3P1	1983	Intermediate	Burn	50°33.18'	095°27.41'	16 $\pm$ 0.7
B83 3P2	1983	Intermediate	Burn	50°34.35'	095°25.76'	16 $\pm$ 0.8
H83 1P1	1983	Intermediate	Harvest	50°36.78'	096°07.25'	21 $\pm$ 1.6
H83 1P2	1983	Intermediate	Harvest	50°36.70'	096°07.37'	19 $\pm$ 1.3
H83 2P1	1983	Intermediate	Harvest	50°47.46'	096°12.74'	30 $\pm$ 3.2
H83 2P2	1983	Intermediate	Harvest	50°47.57'	096°12.81'	23 $\pm$ 2.7
B99 1P1	1999	Young	Burn	50°56.25'	096°12.77'	0
B99 1P2	1999	Young	Burn	50°56.29'	096°12.64'	0
B99 2P1 ^T	1999	Young	Burn	50°54.72'	096°15.53'	0
B99 2P2 ^T	1999	Young	Burn	50°54.87'	096°15.63'	0
H99 1P1	1999	Young	Harvest	50°48.12'	095°12.05'	0
H99 1P2	1999	Young	Harvest	50°48.18'	095°11.27'	0
H99 2P1 ^T	2000	Young	Harvest	50°54.78'	096°14.90'	0
H99 2P2 ^T	2000	Young	Harvest	50°54.73'	096°15.00'	0

^TThese plots were established in 2001, the rest were established in 1998/1999.

Table 2. Composition of trees of two size classes: between 1m and 3m, and above 3m. Scientific names and authorities listed below[†].

		B29 1P1	B29 1P2	B29 2P2	H57 1P1	H57 1P2	H57 2P1	H57 2P2	H83 1P1	H83 1P2	H83 2P1	H83 2P2	B83 2P1	B83 2P2	B83 3P1	B83 3P2
Trees Over 3m [†]	Black Spruce	14.8	47.8	87.5	99.0	99.0	76.8	91.1	70.0	19.4	20.0	28.4	0	0.8	0.8	0
	White Spruce	0	0	0	0	0	0	0	0	3.9	0	0	0	0	0	1.0
	Jack Pine	85.2	31.0	12.5	0	0	0	0.9	0	0	40.0	4.9	85.8	98.4	59.7	97.2
	Tamarack	0	3.5	0	0	1.0	23.2	8.0	3.3	0	21.4	11.8	0	0	0	0
	Alder	0	13.3	0	0	0	0	0	0	0	0	0	0	0	1.7	0
	Paper Birch	0	0	0	0.5	0	0	0	0	0	5.7	20.6	0	0	5.9	0
	Trembling Aspen	0	0	0	0.5	0	0	0	6.7	73.6	12.9	33.3	13.8	0.8	31.1	0.8
	Willow	0	0	0	0	0	0	0	20.0	3.1	0	1.0	0.4	0	0.8	1.0
	Other	0	4.4	0	0	0	0	0	0	0	0	0	0	0	0	0
Trees Under 3m [*]	Black Spruce	6.0	0	4.0	12.2	41.0	/	/	16.0	18.0	10.0	8.0	19.0	49.0	38.0	13.0
	White Spruce	0	0	0	0	0	/	/	0	0	0	0	0	0	0	0
	Jack Pine	0	0	0	0	0	/	/	0	0	0	5.0	0	16.0	4.0	2.0
	Tamarack	0	0	0	0	2.0	/	/	0	0	4.0	9.0	0	1.0	0	0
	Alder	0	25.0	0	8.4	0	/	/	0	0	22.4	23.4	6.0	14.0	0	0
	Paper Birch	0	0	0	0	0	/	/	0	0	35.0	15.0	0	0	0	0
	Trembling Aspen	1.0	0.6	3.0	0.2	0	/	/	18.0	4.0	3.0	3.2	0	0	4.0	4.0
	Willow	0	4.0	0	0.2	0.2	/	/	53.0	85.0	0	0	0	65.0	2.2	83.0
	Other	0	0	0	0.4	0	/	/	0	0	0	0	0	0	0	0

[†]Trees over 3m are percent count per 10m X 10m quadrat per plot.

^{*}Trees under 3m and over 1m are percent cover as an average of 15 2m X 2m quadrats per plot.

[†]Black Spruce (*Picea mariana* (Mill) B.S.P.), White Spruce (*Picea glauca* (Moench) Voss), Jack Pine (*Pinus banksiana* Lamb.), Tamarack (*Larix laricina* (Du Roi) K. Koch), Alder (*Alnus* spp.), Paper Birch (*Betula papyrifera* Marsh.), Trembling Aspen (*Populus tremuloides* Michx.), Willow (*Salix* spp.)

Table 3. The length of the sampling season in 1999, 2000, 2001, and 2002 and adjusted data for 2000.

SITE	PLOT	1999 SAMPLING	2000 SAMPLING	2000 ADJUSTED	2001 SAMPLING	2002 SAMPLING
Burn 1929	1p1	May 27 - Aug 31	May 31 - Sept 06	May 31 - Sept 06		Jun 1 - Aug 31
	1p2	May 27 - Aug 31	May 31 - Sept 06	May 31 - Sept 06		Jun 1 - Aug 31
	2p2	Jun 23 - Aug 31	May 31 - Sept 06	May 31 - Sept 06	Jun 06 - Aug 09	
Harvest 1957	1p1	Jun 17 - Aug 24	May 25 - Sept 12	Jun 14 - Sept 06	May 30 - Aug 13	
	1p2	Jun 28 - Aug 11	May 25 - Sept 12	Jun 14 - Sept 06	May 30 - Aug 13	
	2p1				Jul 13 - Aug 29	Jun 1 - Aug 31
	2p2				Jul 13 - Aug 29	Jun 1 - Aug 31
Burn 1983	2p1	May 26 - Aug 30	Jun 01 - Sept 06	Jun 01 - Sept 06		Jun 1 - Aug 31
	2p2	May 26 - Aug 30	Jun 01 - Sept 11	Jun 14 - Sept 06		Jun 1 - Aug 31
	3p1	May 26 - Aug 31	May 31 - Sept 06	May 31 - Sept 06		
	3p2	May 25 - Aug 31	May 31 - Jul 24	removed		
Harvest 1983	1p1	Jun 03 - Aug 23	May 25 - Sept 12	Jun 14 - Sept 06	May 29 - Aug 21	
	1p2	Jun 03 - Aug 23	May 25 - Sept 12	Jun 14 - Sept 06	May 29 - Aug 21	
	2p1	Jun 01 - Aug 24	May 25 - Sept 12	Jun 14 - Sept 06	May 30 - Aug 14	Jun 1 - Aug 31
	2p2	Jun 01 - Aug 11	May 25 - Sept 12	Jun 14 - Sept 06	May 30 - Aug 14	Jun 1 - Aug 31
Burn 1999	1p1	Jul 26 - Aug 25	May 24 - Sept 12	Jun 14 - Sept 06	Jun 04 - Aug 14	
	1p2	Jul 26 - Aug 25	May 24 - Sept 12	Jun 14 - Sept 06	Jun 04 - Aug 14	
	2p1				Jul 04 - Sept 04	Jun 1 - Aug 31
	2p2				Jul 04 - Sept 04	Jun 1 - Aug 31
Harvest 1999	1p1	Jun 02 - Aug 26	Jun 14 - Sept 12	Jun 14 - Sept 06	Jun 05 - Aug 23	
	1p2	Jun 02 - Aug 20	Jun 14 - Sept 17	Jun 14 - Sept 06	Jun 05 - Aug 23	
	2p1				Jul 04 - Sept 04	Jun 1 - Aug 31
	2p2				Jul 04 - Sept 04	Jun 1 - Aug 31

Table 4. Effect of age class, disturbance type, and interactions between age class and disturbance type on herbaceous vegetation sampled in 2000 (mean $\pm$ SE).

		Number of Species ¹	Shannon's Diversity Index
Old Plots	Burn	30 $\pm$ 5.36	1.89 $\pm$ 0.30
	Harvest	27 $\pm$ 11.50	1.67 $\pm$ 0.37
	<i>F</i> (df = 1,11), <i>P</i>	1.42, 0.259	0.27, 0.617
Intermediate Plots	Burn	28 $\pm$ 1.11	2.12 $\pm$ 0.21
	Harvest	34 $\pm$ 2.29	2.27 $\pm$ 0.18
	<i>F</i> (df = 1,11), <i>P</i>	3.59, 0.085	0.25, 0.629
Young Plots	Burn	38 $\pm$ 4.00	2.55 $\pm$ 0.20
	Harvest	25 $\pm$ 2.50	2.35 $\pm$ 0.16
	<i>F</i> (df = 1,11), <i>P</i>	0.24, 0.636	0.35, 0.565
Age Class	Old	29 $\pm$ 2.99	2.01 $\pm$ 0.24
	Intermediate	32 $\pm$ 2.96	2.18 $\pm$ 0.15
	Young	29 $\pm$ 3.67	2.23 $\pm$ 0.18
	<i>F</i> (df = 2, 11), <i>P</i>	0.34, 0.720	3.04, 0.089
Disturbance	Burn	31 $\pm$ 2.21	2.14 $\pm$ 0.15
	Harvest	30 $\pm$ 2.98	2.14 $\pm$ 0.15
	<i>F</i> (df = 1,11), <i>P</i>	0.96, 0.348	0.20, 0.667
Interaction Age Class*Disturbance		<i>F</i> (df = 2,11), <i>P</i>	2.55, 0.123
			0.41, 0.673

¹Mean calculated from a sum of 20 quadrats for each plot.

Table 5. Effect of age class, disturbance type, and interactions between age class and disturbance type for shrubs sampled in 2000 (Mean $\pm$ SE).

		Number of Species ¹	Shannon's Diversity Index
Old Plots	Burn	6 $\pm$ 0.0	1.15 $\pm$ 0.09
	Harvest	8 $\pm$ 2.5	0.79 $\pm$ 0.18
	<i>F</i> (df = 1,11), <i>P</i>	7.92, 0.017*	0.17, 0.686
Intermediate Plots	Burn	9 $\pm$ 0.85	1.49 $\pm$ 0.16
	Harvest	12 $\pm$ 0.85	1.71 $\pm$ 0.17
	<i>F</i> (df = 1,11), <i>P</i>	0.81, 0.388	0.90, 0.365
Young Plots	Burn	10 $\pm$ 0.05	1.670 $\pm$ 0.17
	Harvest	8 $\pm$ 0.00	1.290 $\pm$ 0.24
	<i>F</i> (df = 1,11), <i>P</i>	2.94, 0.115	0.01, 0.937
Age Class	Old	7 $\pm$ 0.87a	1.01 $\pm$ 0.12a
	Intermediate	10 $\pm$ 0.80b	1.60 $\pm$ 0.12b
	Young	9 $\pm$ 0.48ab	1.48 $\pm$ 0.16ab
	<i>F</i> (df = 2,11), <i>P</i>	6.65, 0.013*	7.30, 0.010*
Disturbance	Burn	8 $\pm$ 0.62	1.42 $\pm$ 0.10
	Harvest	10 $\pm$ 0.98	1.37 $\pm$ 0.17
	<i>F</i> (df = 1,11), <i>P</i>	1.39, 0.263	1.44, 0.255
Interaction	<i>F</i> (df = 2,11), <i>P</i>	2.43, 0.133	2.14, 0.164
Age Class * Disturbance			

¹Mean calculated from a sum of 20 quadrats for each plot.

* Indicates significance at $P < 0.05$, from ANOVA and contrasts.

Within a group, values followed by different letters differ significantly at $P < 0.05$, (Tukey's post hoc test).

Table 6. Effect of age class, disturbance type, and interactions of age class and disturbance type on environmental variables (Mean $\pm$ SE), $n = 4$ (except old burn $n = 3$).

		Densimeter (% Canopy Cover)	Light Meter (% Shade)	Downed Woody Debris (% Cover)	pH
Old Plots	Burn	74.13 $\pm$ 2.36	78.76 $\pm$ 5.84	2.35 $\pm$ 0.58	2.80 $\pm$ 0.15
	Harvest	65.81 $\pm$ 5.16	75.86 $\pm$ 5.40	3.22 $\pm$ 2.21	3.60 $\pm$ 0.51
	<i>F</i> (df = 1,17), <i>P</i>	5.00, 0.039*	0.33, 0.575	0.43, 0.522	0.01, 0.963
Intermediate Plots	Burn	48.03 $\pm$ 8.74	55.69 $\pm$ 10.85	7.03 $\pm$ 0.21	4.10 $\pm$ 0.31
	Harvest	46.47 $\pm$ 8.96	49.92 $\pm$ 5.6	2.09 $\pm$ 0.76	3.78 $\pm$ 0.40
	<i>F</i> (df = 1,17), <i>P</i>	8.83, 0.009*	7.82, 0.012*	0.01, 0.910	2.87, 0.109
Young Plots	Burn	28.76 $\pm$ 3.95	50.23 $\pm$ 6.53	5.65 $\pm$ 0.95	4.08 $\pm$ 0.085
	Harvest	4.47 $\pm$ 2.94	32.47 $\pm$ 2.46	32.47 $\pm$ 2.46	4.48 $\pm$ 0.53
	<i>F</i> (df = 1,17), <i>P</i>	50.70, 0.001*	30.50, 0.001*	191.87, 0.001*	2.69, 0.119
Age Class	Old	69.38 $\pm$ 3.35a	77.10 $\pm$ 3.68a	2.85 $\pm$ 1.21a	3.26 $\pm$ 0.32a
	Intermediate	47.25 $\pm$ 5.80b	52.81 $\pm$ 5.77a	4.56 $\pm$ 1.00a	3.94 $\pm$ 0.24ab
	Young	16.61 $\pm$ 5.13c	36.69 $\pm$ 6.29b	19.06 $\pm$ 5.21b	4.28 $\pm$ 0.26b
	<i>F</i> (df = 2,17), <i>P</i>	36.04, 0.001*	16.82, 0.001*	69.07, 0.001*	3.87, 0.041*
Disturbance	Burn	48.14 $\pm$ 6.51	60.00 $\pm$ 5.75	5.25 $\pm$ 0.69	3.74 $\pm$ 0.21
	Harvest	38.92 $\pm$ 8.37	49.64 $\pm$ 7.03	12.59 $\pm$ 4.36	3.95 $\pm$ 0.28
	<i>F</i> (df = 1,17), <i>P</i>	4.97, 0.040*	4.43, 0.050*	36.68, 0.001*	0.85, 0.369
Interaction Age Class*Disturbance	<i>F</i> (df = 2,17), <i>P</i>	1.83, 0.191	1.85, 0.187	63.40, 0.001*	1.08, 0.363

* Indicates significance at $P < 0.05$, from ANOVA and contrasts.

Within a group, values followed by different letters differ significantly at $P < 0.05$, (Tukey's post hoc test).

Table 7. Soil types based on Soil Classification Working Group (1998).

Site	Soil Type
B29 1P1	Dystric Brunisol
B29 1P2	Dystric Brunisol
B29 2P2	Humic Gleysol
H57 1P1	95% Organic Mesisol
H57 1P2	95% Organic Mesisol
H57 2P1	Mesisol
H57 2P2	Mesisol
B83 2P1	Luvic Gleysol
B83 2P2	Fibric Mesisol or Peaty Gleysol
B83 3P1	Dystric Brunisol
B83 3P2	Fibrisol
H83 1P1	(Heavy) Dark Gray Chernozem
H83 1P2	(Heavy) Dark Gray Chernozem
H83 2P1	Mesisol
H83 2P2	Fibric Mesisol
B99 1P1	Peaty Gleysol
B99 1P2	Dark Gray Chernozem
B99 2P1	Dark Gray Chernozem
B99 2P2	Peaty Gleysol
H99 1P1	Dark Gray Chernozem
H99 1P2	Peaty Gleysol
H99 2P1	Peaty Gleysol
H99 2P2	Peaty Gleysol

Table 8. Effect of age class, disturbance type, and interaction between age class and disturbance type for carabid beetles collected in 2000 (Mean $\pm$ SE). Means are calculated from plot averages of adjusted total catches from all traps in a plot in 2000.

		Number of Individuals	Number of Species	Log-Series Alpha	Berger-Parker Index	Evenness
Old Plots	Burn	41 $\pm$ 3.1	9 $\pm$ 2.2	3.49 $\pm$ 1.24	0.40 $\pm$ 0.10	0.47 $\pm$ 0.13
	Harvest	28 $\pm$ 15.5	6 $\pm$ 1.5	2.24 $\pm$ 0.14	0.56 $\pm$ 0.20	0.75 $\pm$ 0.35
	<i>F</i> (df = 1,10), <i>P</i>	12.78, 0.005*	12.85, 0.005*	1.80, 0.210	0.23, 0.645	2.44, 0.149
Intermediate Plots	Burn	24 $\pm$ 6.5	6 $\pm$ 2.0	2.90 $\pm$ 1.09	0.44 $\pm$ 0.16	0.52 $\pm$ 0.21
	Harvest	40 $\pm$ 3.24	9 $\pm$ 0.4	3.69 $\pm$ 0.37	0.44 $\pm$ 0.05	0.35 $\pm$ 0.02
	<i>F</i> (df = 1,10), <i>P</i>	0.01, 0.919	0.10, 0.763	0.18, 0.682	1.30, 0.280	0.35, 0.570
Young Plots	Burn	102 $\pm$ 26	21 $\pm$ 0.5	8.12 $\pm$ 1.24	0.28 $\pm$ 0.32	0.16 $\pm$ 0.03
	Harvest	85 $\pm$ 43	18 $\pm$ 6.5	6.12 $\pm$ 1.28	0.42 $\pm$ 0.10	0.21 $\pm$ 0.04
	<i>F</i> (df = 1,10), <i>P</i>	6.68, 0.027*	8.11, 0.017*	2.66, 0.134	0.34, 0.575	4.81, 0.053
Age Class	Old	36 $\pm$ 6.2a	7 $\pm$ 1.5a	2.89 $\pm$ 0.74	0.47 $\pm$ 0.09	0.58 $\pm$ 0.15
	Intermediate	33 $\pm$ 4.4a	8 $\pm$ 1.0a	3.35 $\pm$ 0.45	0.44 $\pm$ 0.07	0.42 $\pm$ 0.09
	Young	94 $\pm$ 21.1b	19 $\pm$ 2.8b	7.12 $\pm$ 0.98	0.35 $\pm$ 0.06	0.18 $\pm$ 0.02
	<i>F</i> (df = 2,10), <i>P</i>	7.80, 0.009*	9.16, 0.005*	1.13, 0.360	0.23, 0.799	3.19, 0.085
Disturbance	Burn	50 $\pm$ 12.9	11 $\pm$ 2.4	4.43 $\pm$ 1.00	0.37 $\pm$ 0.07	0.41 $\pm$ 0.10
	Harvest	48 $\pm$ 12.1	10 $\pm$ 2.1	3.94 $\pm$ 0.61	0.47 $\pm$ 0.05	0.42 $\pm$ 0.10
	<i>F</i> (df = 1,10), <i>P</i>	0.21, 0.659	0.11, 0.746	0.46, 0.510	3.07, 0.110	0.19, 0.673
Interaction	<i>F</i> (df = 2,10), <i>P</i>	2.58, 0.125	2.08, 0.175	2.59, 0.124	0.554, 0.591	1.16, 0.354
Age Class*Disturbance						

* Indicates significance at $P < 0.05$, from ANOVA and contrasts.

Within a group, values followed by different letters differ significantly at $P < 0.05$, (Tukey's post hoc test).
ANOVA on number of individuals and number of species was done using logged data.

Table 9. Effect of age class, disturbance type, and interaction between age class and disturbance type on carabid beetles collected in 2002 (Mean $\pm$ SE), $n = 2$. Means are calculated from plot averages of total catches from all traps in a plot in 2002.

		Number of Individuals	Number of Species	Log-Series Alpha	Berger-Parker Index	Evenness
Old Plots	Burn	121 $\pm$ 7.0	9 $\pm$ 1.5	2.12 $\pm$ 0.52	0.76 $\pm$ 0.11	0.65 $\pm$ 0.17
	Harvest	27 $\pm$ 4.5	7 $\pm$ 1.0	3.27 $\pm$ 1.08	0.41 $\pm$ 0.068	0.51 $\pm$ 0.16
	F (df = 1,6), P	48.22, 0.001*	0.24, 0.644	0.55, 0.486	1.90, 0.218	0.70, 0.434
Intermediate Plots	Burn	88 $\pm$ 73.5	8 $\pm$ 2.5	2.57 $\pm$ 0.21	0.36 $\pm$ 0.07	0.48 $\pm$ 0.04
	Harvest	78 $\pm$ 3.5	7 $\pm$ 1.0	1.86 $\pm$ 0.33	0.52 $\pm$ 0.12	0.61 $\pm$ 0.03
	F (df = 1,6), P	18.56, 0.005*	1.27, 0.303	0.65, 0.452	1.02, 0.353	0.19, 0.678
Young Plots	Burn	49 $\pm$ 9.5	9 $\pm$ 1.0	3.43 $\pm$ 0.92	0.64 $\pm$ 0.07	0.38 $\pm$ 0.11
	Harvest	21 $\pm$ 0.1	8 $\pm$ 0.5	4.20 $\pm$ 0.52	0.52 $\pm$ 0.05	0.31 $\pm$ 0.03
	F (df = 1,6), P	8.75, 0.025*	2.60, 0.158	1.46, 0.272	8.87, 0.025*	0.73, 0.427
Age Class	Old	74 $\pm$ 27.2	8 $\pm$ 0.8	2.69 $\pm$ 0.59	0.58 $\pm$ 0.11	0.58 $\pm$ 0.10
	Intermediate	83 $\pm$ 30.1	7 $\pm$ 1.1	2.22 $\pm$ 0.26	0.44 $\pm$ 0.07	0.54 $\pm$ 0.04
	Young	34.8 $\pm$ 8.8	8 $\pm$ 0.62	3.82 $\pm$ 0.48	0.58 $\pm$ 0.04	0.34 $\pm$ 0.05
	F (df = 2,6), P	1.74, 0.254	0.69, 0.540	2.97, 0.127	2.03, 0.213	2.63, 0.151
Disturbance	Burn	86 $\pm$ 23.3	8 $\pm$ 0.5	2.71 $\pm$ 0.40	0.60 $\pm$ 0.03	0.50 $\pm$ 0.07
	Harvest	42 $\pm$ 11.6	7 $\pm$ 0.4	3.11 $\pm$ 0.54	0.48 $\pm$ 0.04	0.48 $\pm$ 0.07
	F (df = 1,6), P	0.04, 0.858	3.47, 0.112	0.54, 0.491	2.27, 0.183	0.07, 0.804
Interaction Age Class*Disturbance	F (df = 2,6), P	37.7, 0.001*	0.32, 0.738	1.06, 0.404	4.75, 0.058	0.78, 0.502

* Indicates significance at $P < 0.05$, from ANOVA and contrasts.

ANOVA on number of individuals and number of species was done using logged data.

Table 10. A comparison between mean catches of *Pterostichus adstrictus* and *Pterostichus pensylvanicus* for 2000 and 2002. (Mean $\pm$ SE). Means are calculated from total catches from all traps in a plot in the 2000 and 2002 sampling seasons. Error degrees of freedom of the mean square denominator for 2000 are 11, and for 2002 is are 6.

		<i>Pterostichus adstrictus</i>		<i>Pterostichus pensylvanicus</i>	
		2000	2002	2000	2002
Old Plots	Burn	49 $\pm$ 3.4	93 $\pm$ 18.5	13 $\pm$ 5.0	5 $\pm$ 2.0
	Harvest	4 $\pm$ 2.5	6 $\pm$ 5.0	0 $\pm$ 0.0	3 $\pm$ 2.0
	F (df = 1), P	0.00, 0.984	0.35, 0.574	3.57, 0.086	0.29, 0.610
Intermediate Plots	Burn	1 $\pm$ 0.5	13 $\pm$ 12.5	10 $\pm$ 3.5	19 $\pm$ 14.0
	Harvest	1 $\pm$ 0.3	5 $\pm$ 4.5	19 $\pm$ 4.0	24 $\pm$ 7.0
	F (df = 1), P	3.97, 0.072	0.00, 1.000	0.09, 0.772	0.07, 0.797
Young Plots	Burn	54 $\pm$ 40.5	1 $\pm$ 0.0	5 $\pm$ 0.5	3 $\pm$ 2.5
	Harvest	19 $\pm$ 3.5	6 $\pm$ 5.0	3 $\pm$ 0.5	0 $\pm$ 0.0
	F (df = 1), P	7.83, 0.017*	41.21, 0.001*	4.24, 0.064	0.046, 0.837
Age Class	Old	31 $\pm$ 11.1a	50 $\pm$ 26.2a	8 $\pm$ 4.1	4 $\pm$ 1.3a
	Intermediate	1 $\pm$ 0.2b	9 $\pm$ 5.9b	14 $\pm$ 3.0	22 $\pm$ 6.6b
	Young	36 $\pm$ 19.4a	1 $\pm$ 0.4b	4 $\pm$ 0.6	2 $\pm$ 1.2a
	F (df = 2), P	6.53, 0.014*	14.85, 0.005*	3.89, 0.053	5.58, 0.043*
Disturbance	Burn	29 $\pm$ 11.1	36 $\pm$ 19.0	10 $\pm$ 2.3	9 $\pm$ 4.9
	Harvest	6 $\pm$ 2.9	4 $\pm$ 2.0	10 $\pm$ 3.8	9 $\pm$ 5.1
	F (df = 1), P	8.919, 0.012*	16.39, 0.007*	0.30 $\pm$ 0.593	0.00, 0.976
Interaction Age Class*Disturbance	F (df = 2), P	2.82, 0.103	12.58, 0.007*	3.95, 0.051	0.20, 0.821

* Indicates significance at $P < 0.05$, from ANOVA and contrasts.

Within a group, values followed by different letters differ significantly at $P < 0.05$, (Tukey's post hoc test).

Table 11. A comparison between mean catches of *Synuchus impunctatus*, *Platynus decentis* and *Agonum gratiosum* for 2000 and 2002. (Mean $\pm$ SE). Means are calculated from total catches from all traps in a plot in the 2000 and 2002 sampling seasons Error degrees of freedom of the mean square denominator for 2000 are 11, and for 2002 is are 6.

		<i>Synuchus impunctatus</i>		<i>Platynus decentis</i>		<i>Agonum gratiosum</i>	
		2000	2002	2000	2002	2000	2002
Old Plots	Burn	13 $\pm$ 5.0	8 $\pm$ 5.0	13 $\pm$ 5.0	6 $\pm$ 2.0	1 $\pm$ 0.3	1 $\pm$ 0.5
	Harvest	0 $\pm$ 0.0	5 $\pm$ 2.0	0 $\pm$ 0.0	6 $\pm$ 1.5	7 $\pm$ 6.5	6 $\pm$ 5.5
	<i>F</i> (df = 1), <i>P</i>	1.35, 0.269	1.36, 0.288	0.01, 0.947	3.41, 0.114	3.44, 0.090	0.09, 0.771
Intermediate Plots	Burn	10 $\pm$ 3.5	24 $\pm$ 23.5	10 $\pm$ 3.5	11 $\pm$ 10.0	9 $\pm$ 2.8	5 $\pm$ 5.0
	Harvest	19 $\pm$ 4.1	41 $\pm$ 7.5	19 $\pm$ 4.0	0 $\pm$ 0.0	20 $\pm$ 6.3	3 $\pm$ 1.0
	<i>F</i> (df = 1), <i>P</i>	3.08, 0.107	0.00, 1.000	1.71, 0.218	0.03, 0.866	0.26, 0.618	9.71, 0.021*
Young Plots	Burn	5 $\pm$ 0.5	0 $\pm$ 0.0	5 $\pm$ 0.5	2 $\pm$ 0.5	13 $\pm$ 6.5	31 $\pm$ 8.5
	Harvest	19 $\pm$ 3.5	0 $\pm$ 0.0	3 $\pm$ 0.5	1 $\pm$ 0.5	8 $\pm$ 7.0	11 $\pm$ 1.0
	<i>F</i> (df = 1), <i>P</i>	2.82, 0.121	0.42, 0.844	0.01, 0.931	0.008, 0.933	0.59, 0.457	0.578, 0.476
Age Class	Old	4 $\pm$ 3.0	7 $\pm$ 2.4	3 $\pm$ 1.5	6 $\pm$ 1.0	3 $\pm$ 2.6	3 $\pm$ 2.7a
	Intermediate	6 $\pm$ 1.4	32 $\pm$ 11.2	2 $\pm$ 1.2	6 $\pm$ 4.9	15 $\pm$ 3.9	4 $\pm$ 2.1a
	Young	8.0 $\pm$ 2.6	0 $\pm$ 0.0	15 $\pm$ 10.1	1 $\pm$ 0.5	11 $\pm$ 4.1	21 $\pm$ 6.9b
	<i>F</i> (df = 2), <i>P</i>	0.74, 0.501	5.38, 0.046*	2.45, 0.131	0.84, 0.476	2.29, 0.147	9.74, 0.013*
Disturbance	Burn	3 $\pm$ 0.8	11 $\pm$ 7.6	4 $\pm$ 1.8	6 $\pm$ 3.0	7 $\pm$ 2.3	12 $\pm$ 6.6
	Harvest	9 $\pm$ 2.0	15 $\pm$ 8.3	7 $\pm$ 5.4	2 $\pm$ 1.2	14 $\pm$ 4.2	6.5 $\pm$ 2.1
	<i>F</i> (df = 1), <i>P</i>	7.24, 0.021*	0.31, 0.599	0.59, 0.457	1.49, 0.269	0.97, 0.346	2.36, 0.175
Interaction Age Class*Disturbance	<i>F</i> (df = 2), <i>P</i>	0.36, 0.706	0.55, 0.605	0.71, 0.512	0.982, 0.428	1.11, 0.363	4.01, 0.078

Note: * Indicates significance at $P < 0.05$, from ANOVA and contrasts.

Within a group, values followed by different letters differ significantly at $P < 0.05$, (Tukey's post hoc test).

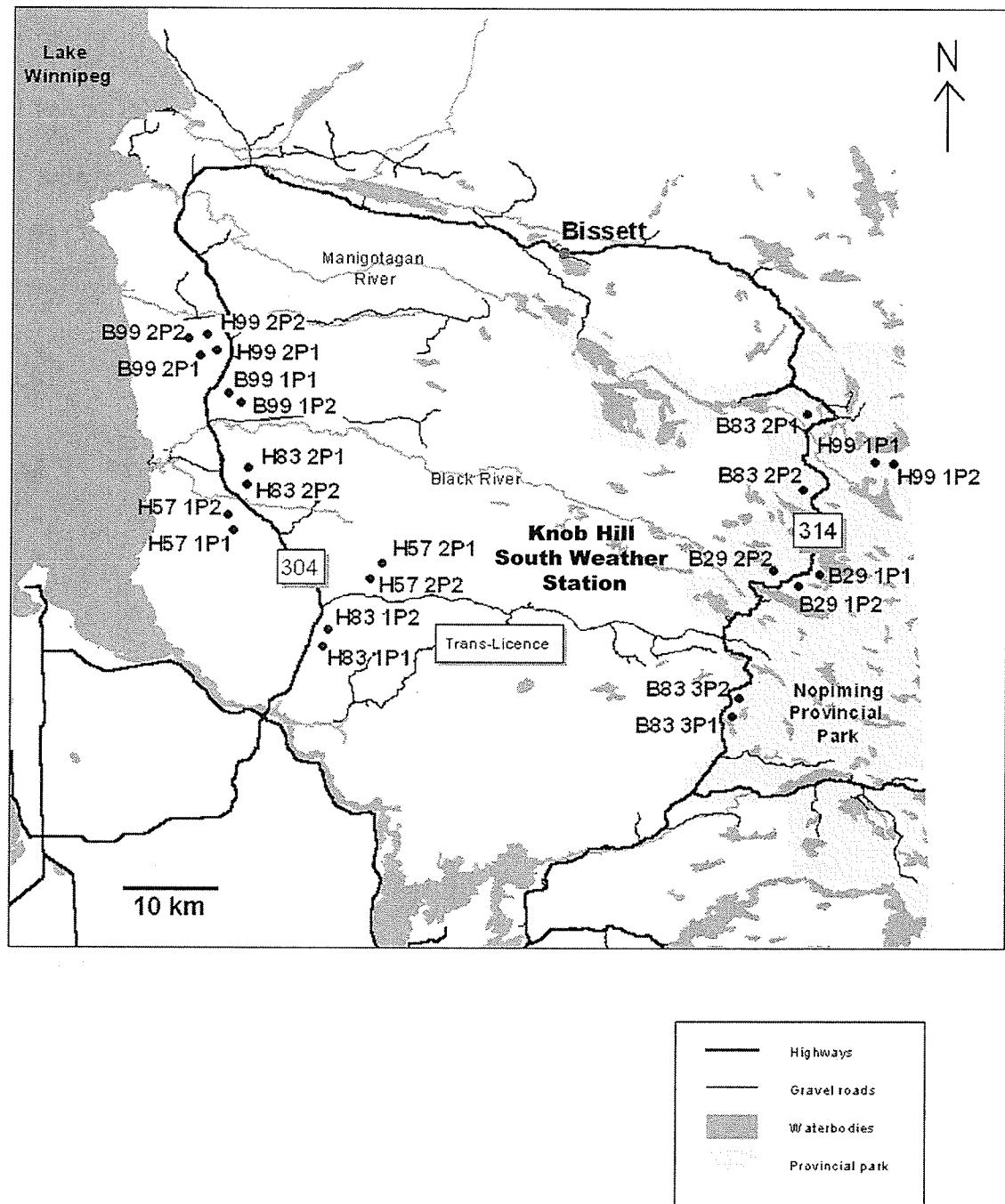


Figure 1. Location of plots. For longitude and latitude see Table 1.

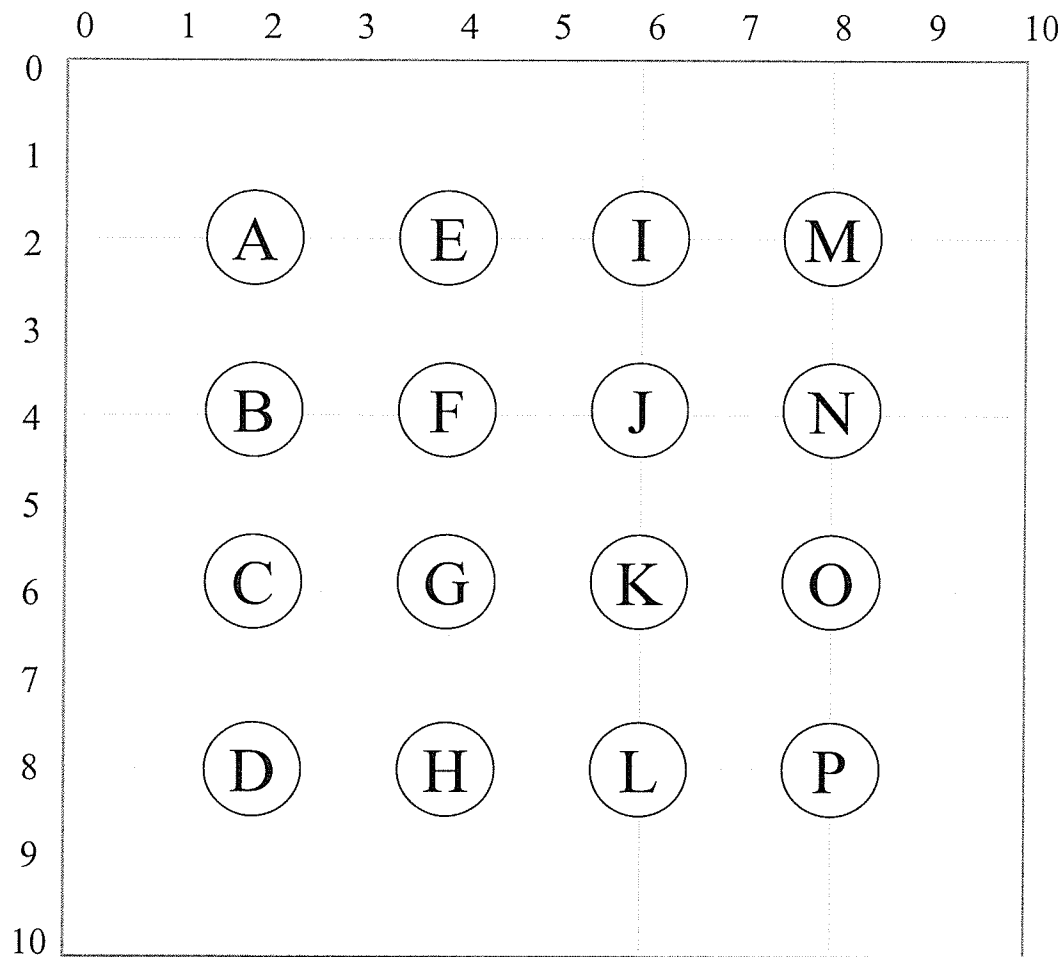


Figure 2. Pattern of pitfall traps within a plot. Each letter corresponds to a pitfall trap. Distance between each trap was 20m.

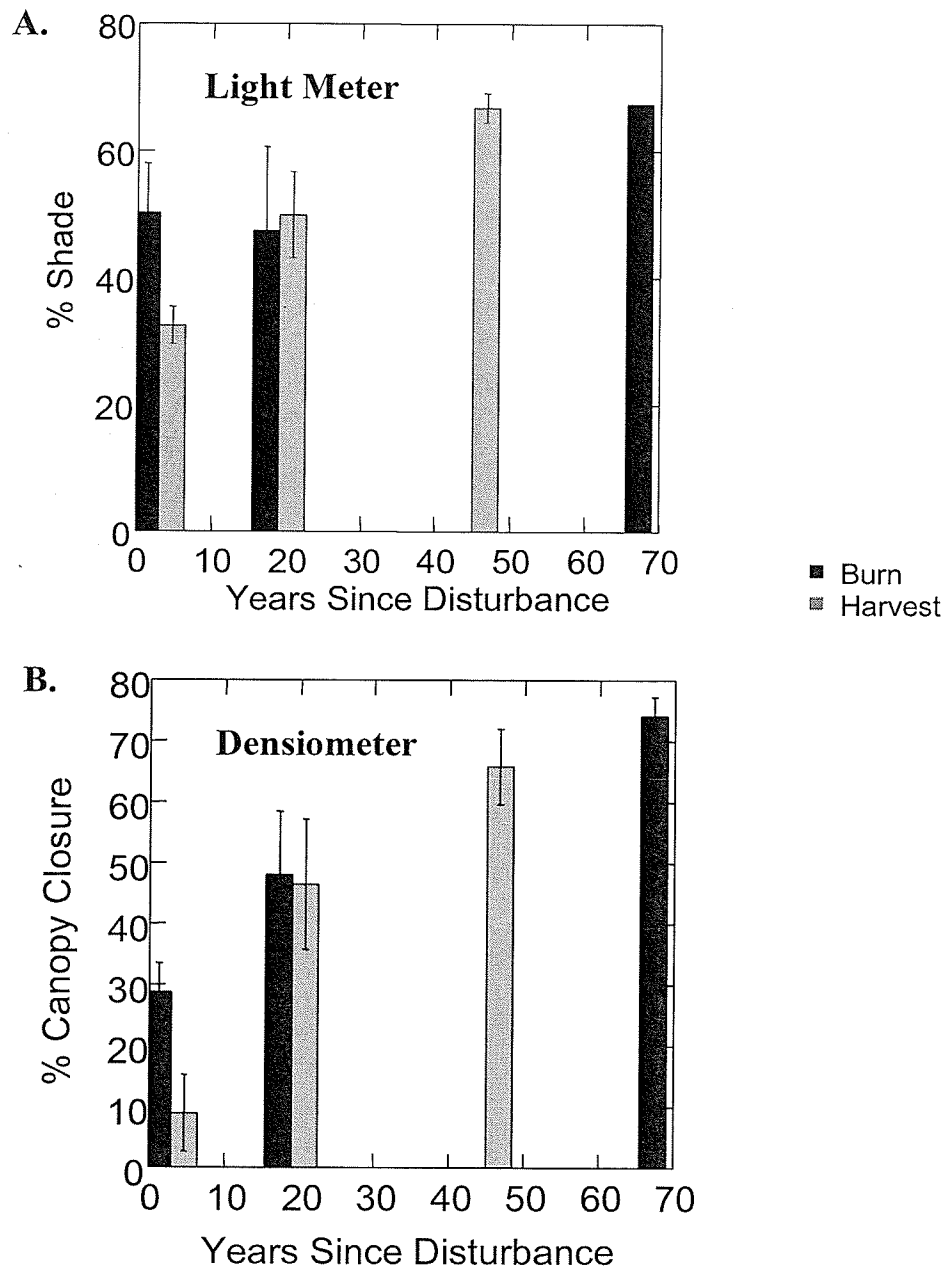


Figure 3. Canopy closure. **A)** Percent shade measured with a light meter.
B) Percent canopy closure with a densiometer.

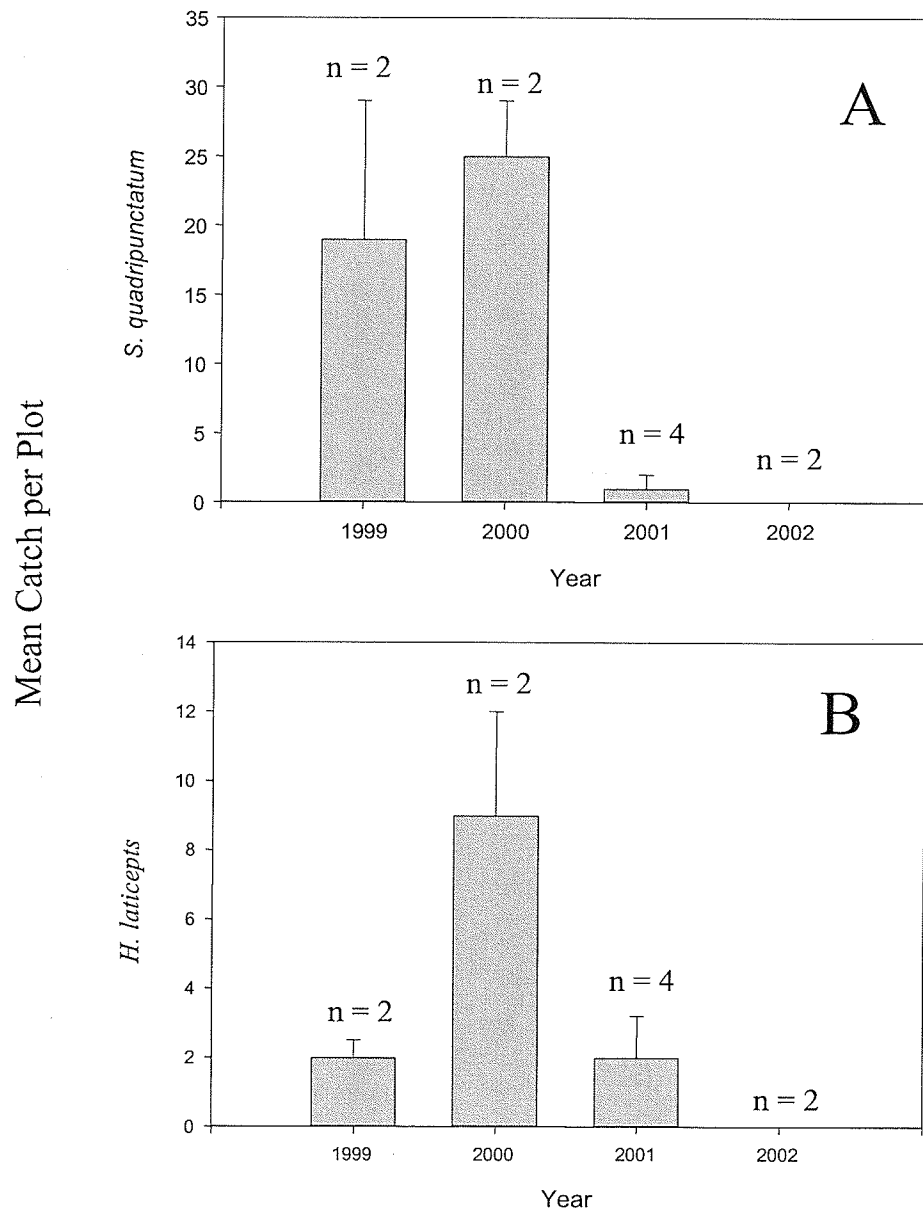


Figure 4. Mean number of pyrophilous carabid species A) *Sericoda quadripunctatum* and B) *Harpalus laticeps* caught per sampling year with standard error bars.

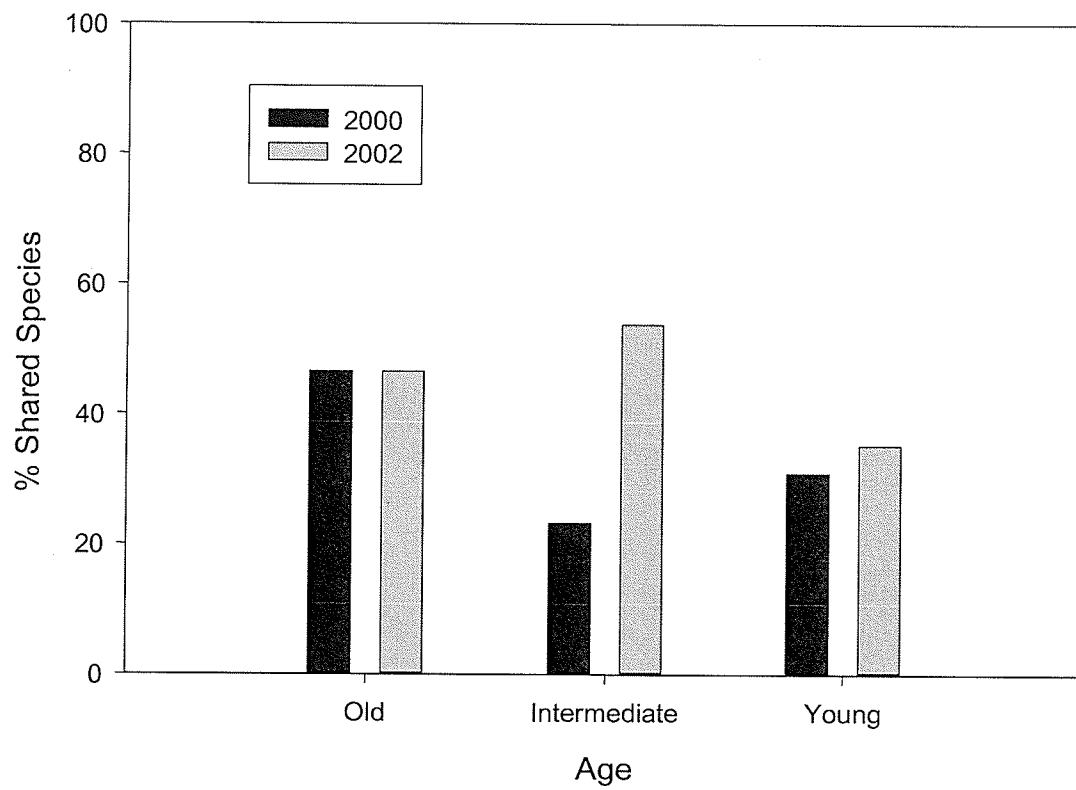


Figure 5 . Percent of shared species of carabids between burned and harvested plots for each age class for the collecting seasons in 2000 and 2002.

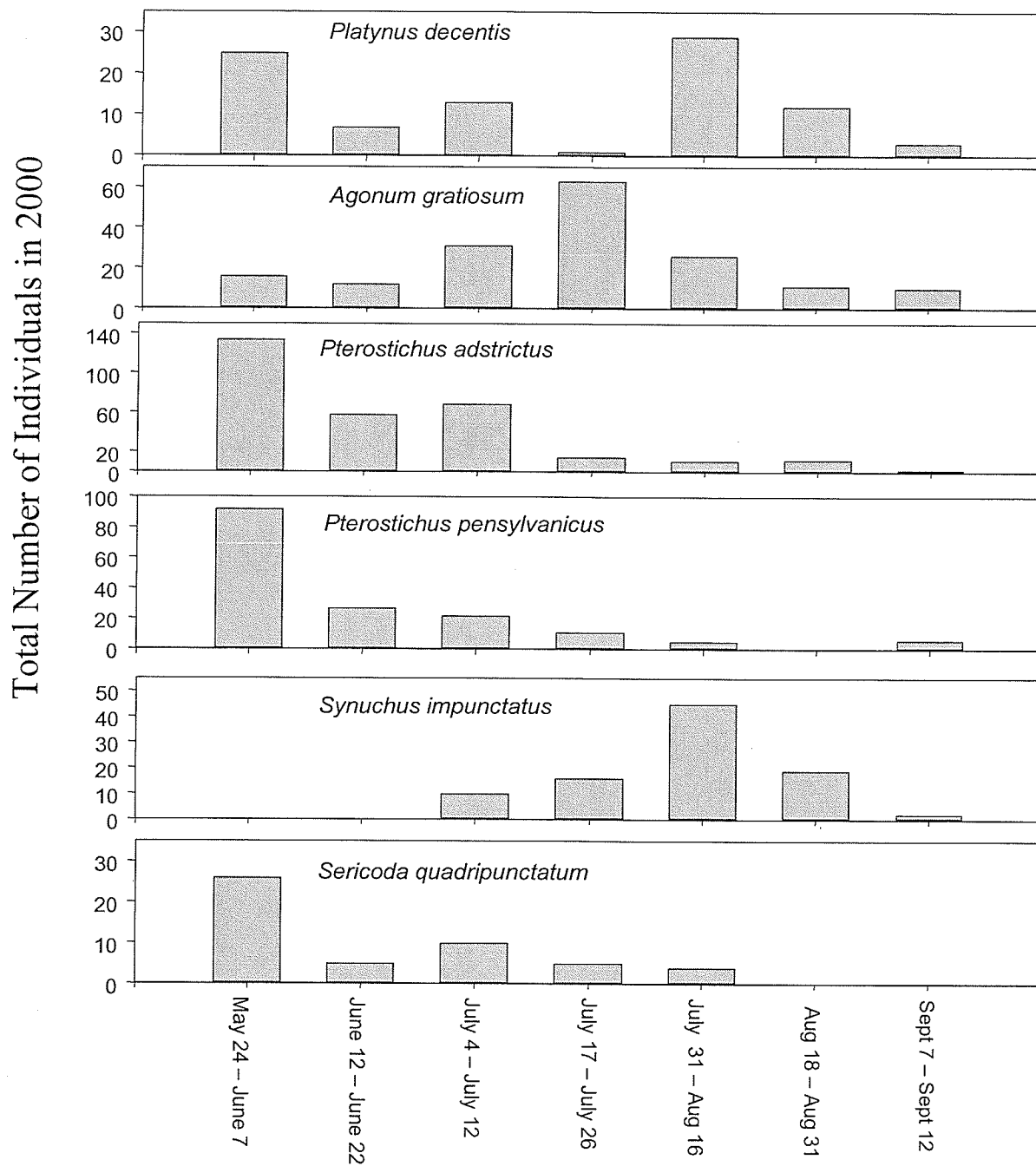


Figure 6. Seasonal changes in carabid beetle numbers for selected species in 2000 from a total of 17 plots.

Note: the Y-axis changes with species.

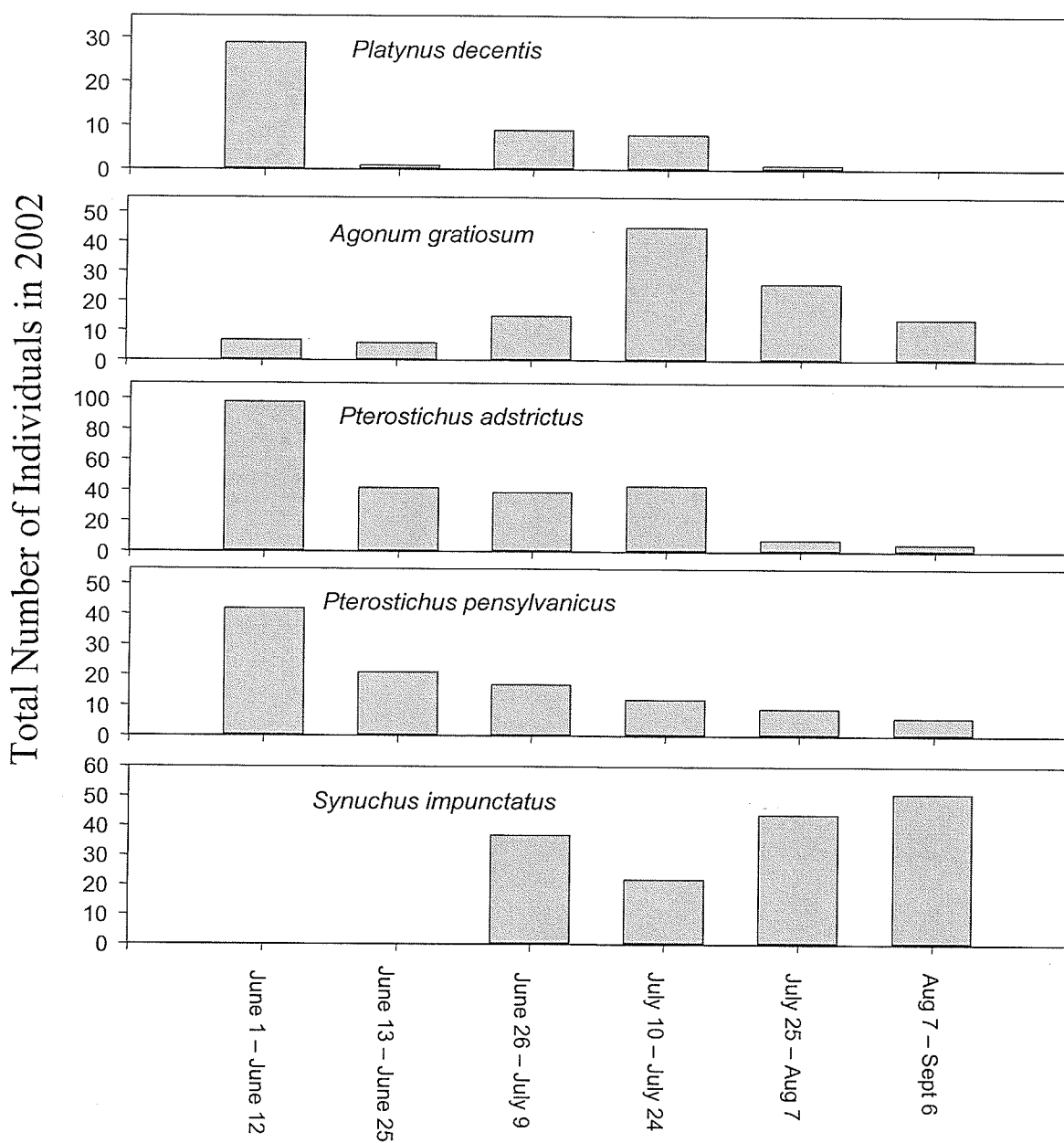


Figure 7. Seasonal changes in Carabid beetle numbers for selected species in 2002 from a total of 12 plots.

Note: the Y-axis changes with species.

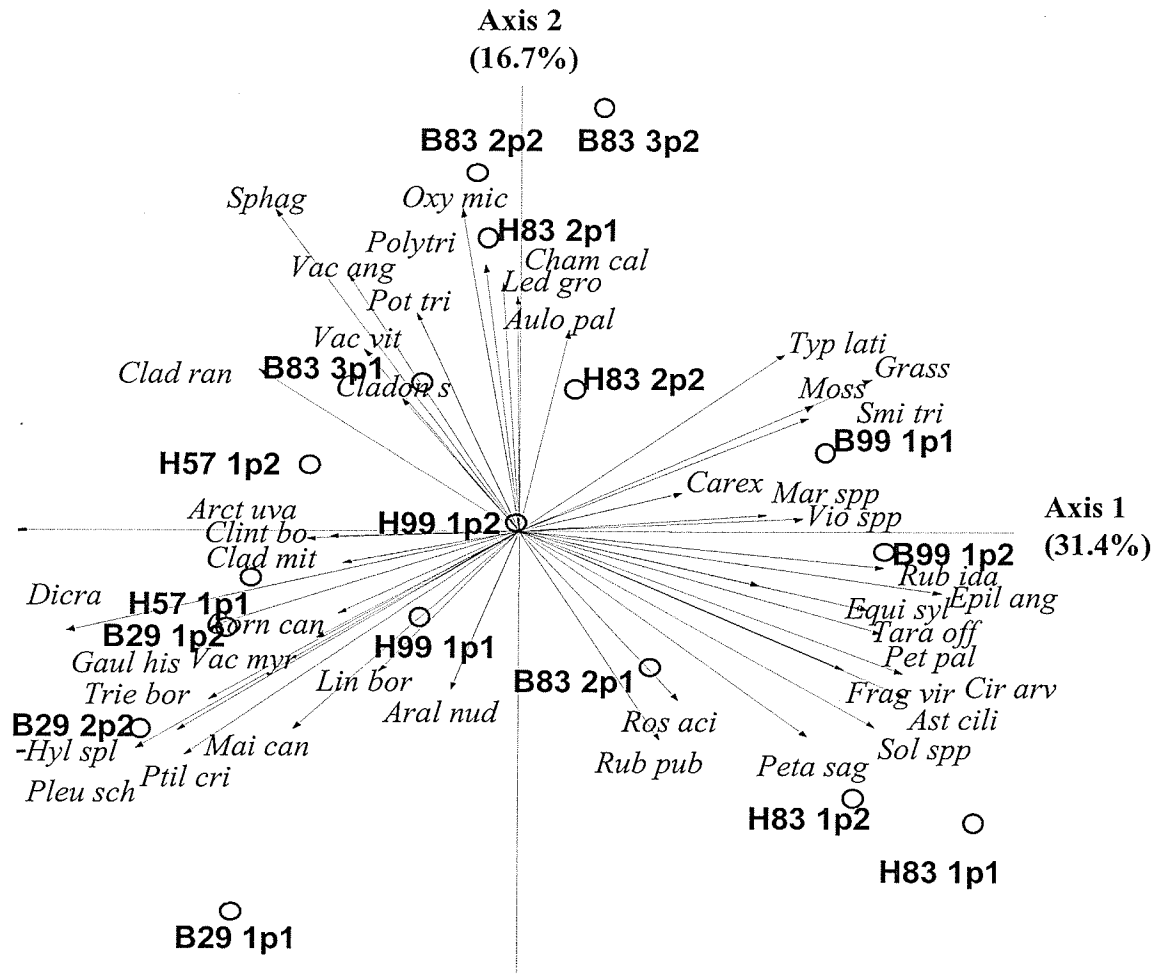


Figure 8. 2000 vegetation data: PCA ordination diagram with plots (O) and vegetation species (arrows). Vegetation species are: *Aral nud* = *Aralia nudicaulis*, *Arct uva* = *Arctostaphylos uva-ursi*, *Ast cilio* = *Aster ciliolatus*, *Aulo pal* = *Aulocomium palustre*, *Carex* = *Carex spp*, *Cham cal* = *Chamaedaphne calyculata*, *Cir arv* = *Cirsium arvense*, *Clad mit* = *Cladina mitis*, *Clad rang* = *Cladina rangiferina*, *Cladon spp* = *Cladonia spp*, *Clint bor* = *Clintonia borealis*, *Corn can* = *Cornus canadensis*, *Dicra* = *Dicranum spp*, *Epil ang* = *Epilobium angustifolium*, *Equi syl* = *Equisetum sylvaticum*, *Frag virg* = *Fragaria virginiana*, *Gaul hisp* = *Gaultheria hispidula*, *Grass* = *Grass spp*, *Hyl spl* = *Hylocomium splendens*, *Led gro* = *Ledum groenlandicum*, *Lin bor* = *Linnaea borealis*, *Lyc ann* = *Lycopodium annotinum*, *Mai can* = *Maianthemum canadense*, *Mar spp* = *Marchantia spp*, *Moss* = *Moss spp*, *Oxy mic* = *Oxycoccus microcarpus*, *Pet pal* = *Petasites palmatus*, *Peta sag* = *Petasites sagittatus*, *Pleu sch* = *Pleurozium scheberi*, *Polytri spp* = *Polytrichum spp*, *Pot tri* = *Potentilla tridentata*, *Ptil cris* = *Ptilium crista-castrensis*, *Ros aci* = *Rosa acicularis*, *Rub ida* = *Rubus idaeus*, *Rub pub* = *Rubus pubescens*, *Smi tri* = *Smilacina trifolia*, *Sol spp* = *Solidago spp*, *Sphag* = *Sphagnum spp*, *Tara off* = *Taraxacum officinale*, *Trie bor* = *Trientalis borealis*, *Typ lati* = *Typha latifolia*, *Vac ang* = *Vaccinium angustifolium*, *Vac myr* = *Vaccinium myrtilloides*, *Vac vit* = *Vaccinium vitis-idaea*, *Vio spp* = *Viola spp*.

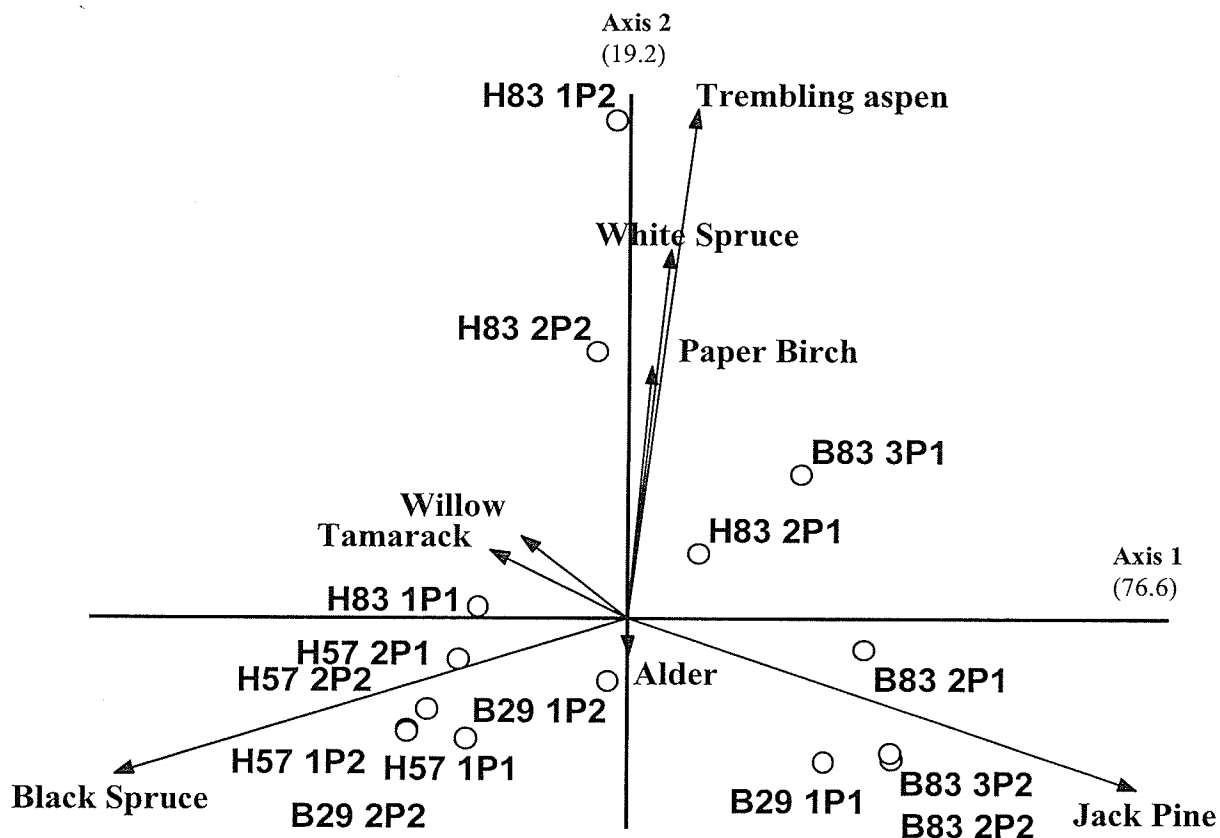


Figure 9. Tree species in all plots: PCA ordination diagram with plots (O) and tree species (arrows).

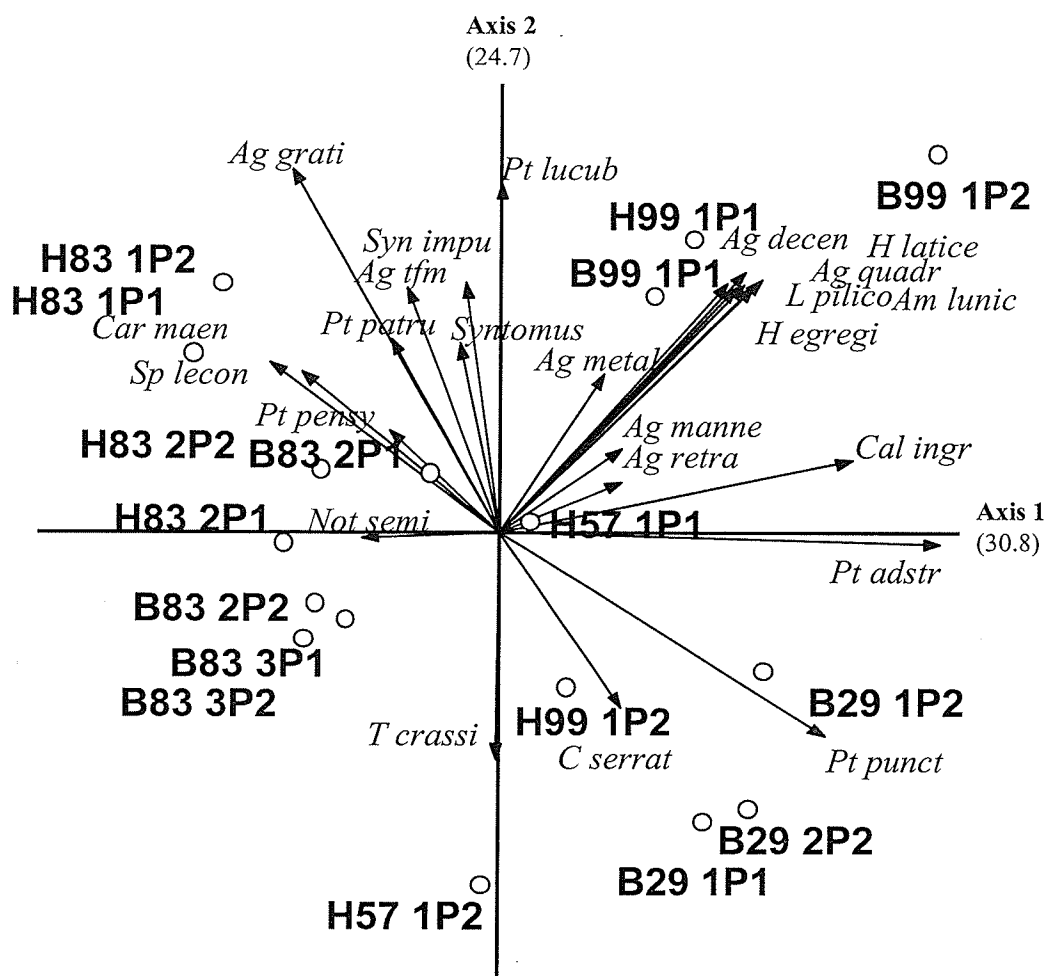


Figure 10. 2000 carabid data: PCA ordination diagram with plots (O) and carabid species (arrows). Carabid beetle species are: *A grati* = *Agonum gratiosum*, *A manner* = *Agonum mannerheimi*, *A metall* = *Agonum metallescens*, *A retra* = *Agonum retracts*, *A tfm* = *Agonum tfm*, *Am lunic* = *Amara lunicollis*, *Cal ingr* = *Calathus ingratus*, *Car serr* = *Carabus serratus*, *H egregi* = *Harpalus egregius*, *H latice* = *Harpalus laticeps*, *Loricera* = *Loricera pilicornis*, *Not semi* = *Notiophilus semistriatus*, *P adstri* = *Pterostichus adstrictus*, *P lucubl* = *Pterostichus lucublandus*, *P pensyl* = *Pterostichus pensylvanicus*, *P puncta* = *Pterostichus punctatissimus*, *Pl decent* = *Platynus decentis*, *S quadri* = *Sericoda quadripunctatum*, *Synt ame* = *Syntomus americanus*, *Synuchus* = *Synuchus impunctatus*.

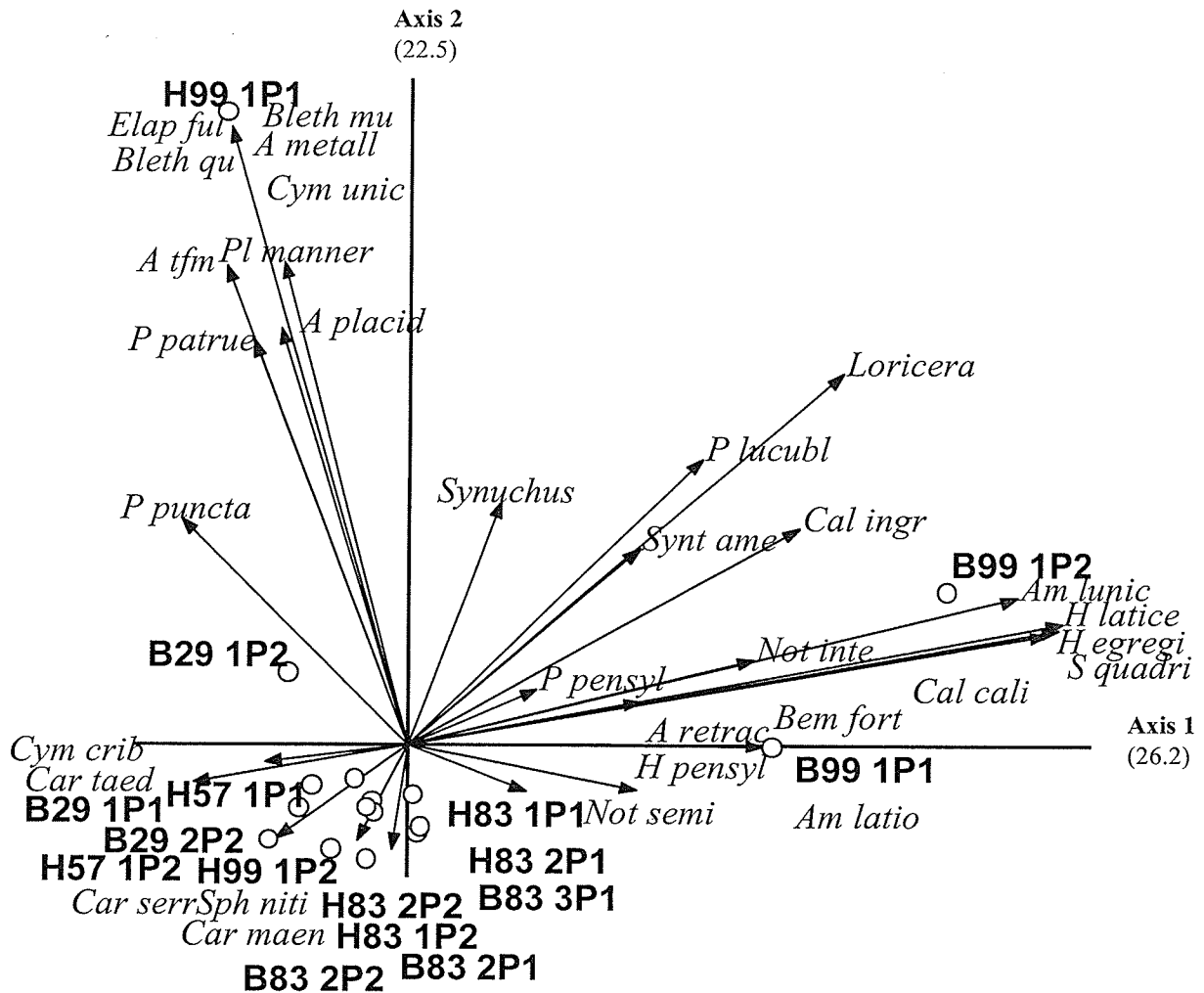


Figure 11 . 2000 carabid data with common species removed: PCA ordination diagram with plots (O) and carabid species (arrows). Carabid beetle species are: *Pl manner* = *Platynus mannerheimi*, *A metall* = *Agonum metallescens*, *A placid* = *Agonum placidum*, *A retrac* = *Agonum retractum*, *A tfm* = *Agonum tfm*, *Am latio* = *Amara latior*, *Am lunic* = *Amara lunicollis*, *Cal cali* = *Calosoma calidum*, *Cal ingr* = *Calathus ingratus*, *Car maen* = *Carabus maeander*, *Car serr* = *Carabus serratus*, *Car taed* = *Carabus taedatus*, *Cym crib* = *Cymindis cribricollis*, *H egregi* = *Harpalus egregius*, *H latice* = *Harpalus laticeps*, *Loricera* = *Loricera pilicornis*, *Not semi* = *Notiophilus semistriatus*, *P lucubl* = *Pterostichus lucublandus*, *P patrue* = *Pterostichus patruelis*, *P pensyl* = *Pterostichus pensylvanicus*, *S quadri* = *Sericoda quadripunctatum*, *Sph niti* = *Sphaeroderus nitidicollis*, *Synt ame* = *Syntomus americanus*, *Synuchus* = *Synuchus impunctatus*.

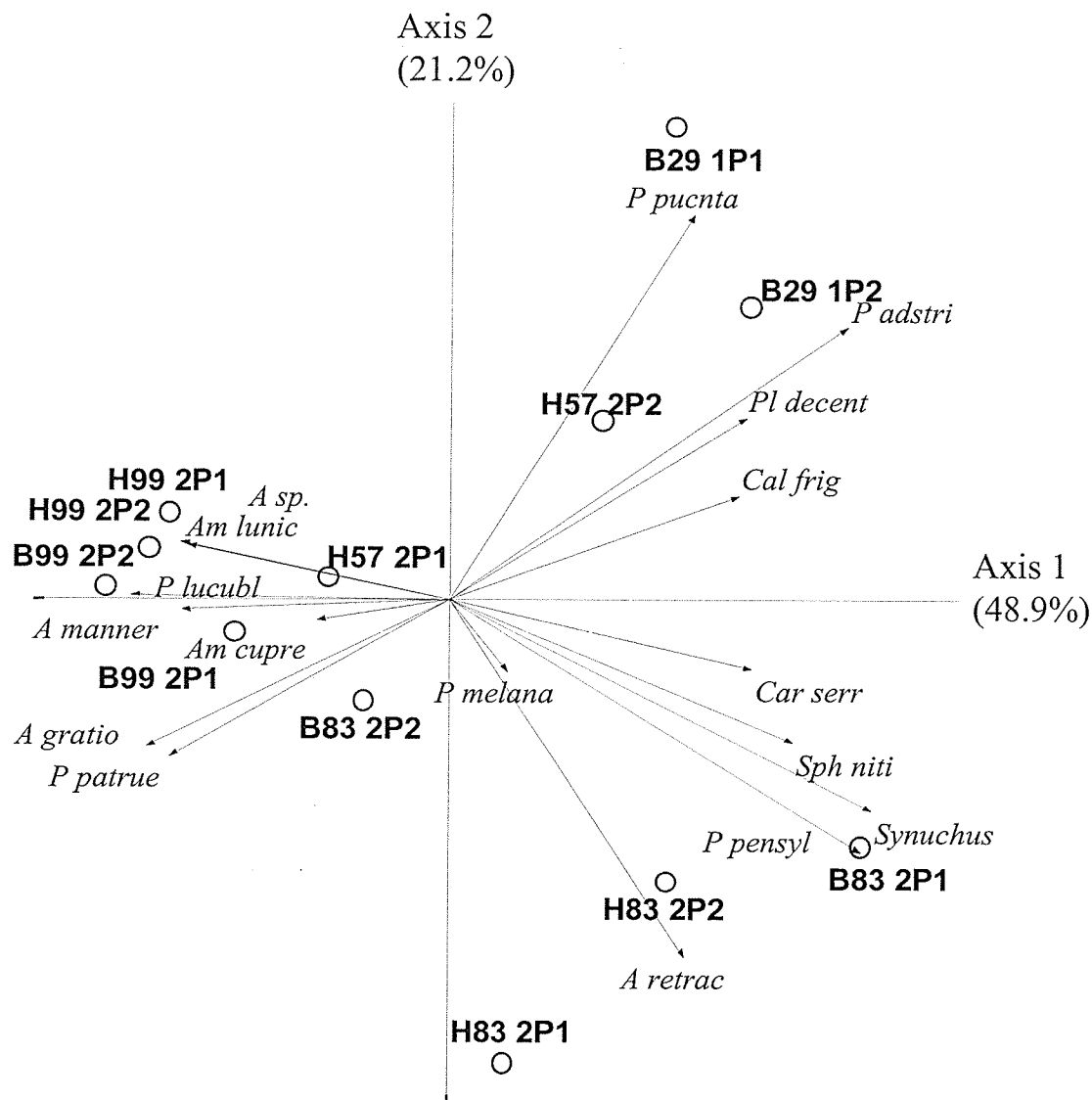


Figure 12. 2002 carabid data: PCA ordination diagram with plots (O) and carabid species (arrows). Carabid beetle species are: *A gratio* = *Agonum gratiosum*, *A manner* = *Agonum mannerheimi*, *A retrac* = *Agonum retractum*, *A sp* = *Agonum* species, *Am lunic* = *Amara lunicollis*, *Am cupre* = *Amara cupreolata*, *Cal frig* = *Calosoma frigidum*, *Cal ingr* = *Calathus ingratus*, *Car serr* = *Carabus serratus*, *P adstri* = *Pterostichus adstrictus*, *P melana* = *Pterostichus melanarius*, *P patrue* = *Pterostichus patruelis*, *P lucubl* = *Pterostichus lucublandus*, *P pensyl* = *Pterostichus pensylvanicus*, *P puncta* = *Pterostichus punctatissimus*, *Pl decent* = *Platynus decentis*, *Synt ame* = *Syntomus americanus*, *Synuchus* = *Synuchus impunctatus*.

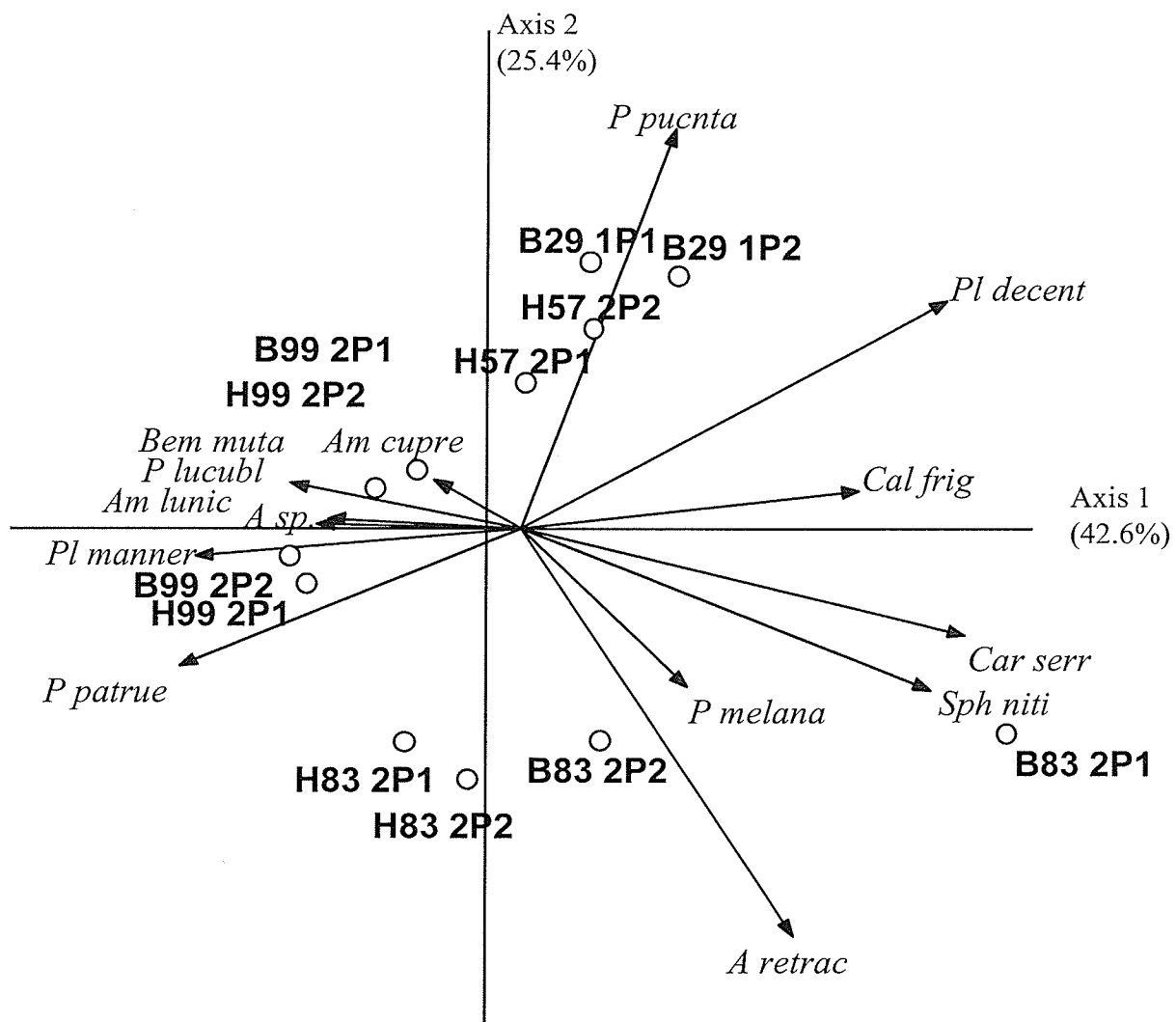


Figure 13 . 2002 carabid data with common species removed: PCA ordination diagram with plots (O) and carabid species (arrows). Carabid beetle species are: *Pl manner* = *Platynus mannerheimi*, *A retrac* = *Agonum retractum*, *A sp* = *Agonum* species, *Am lunic* = *Amara lunicollis*, *Am cupre* = *Amara cupreolata*, *Cal frig* = *Calosoma frigidum*, *Car serr* = *Carabus serratus*, *P patrue* = *Pterostichus patruelis*, *P lucubl* = *Pterostichus lucublandus*, *P puncta* = *Pterostichus punctatissimus*, *Pl decent* = *Platynus decentis*.

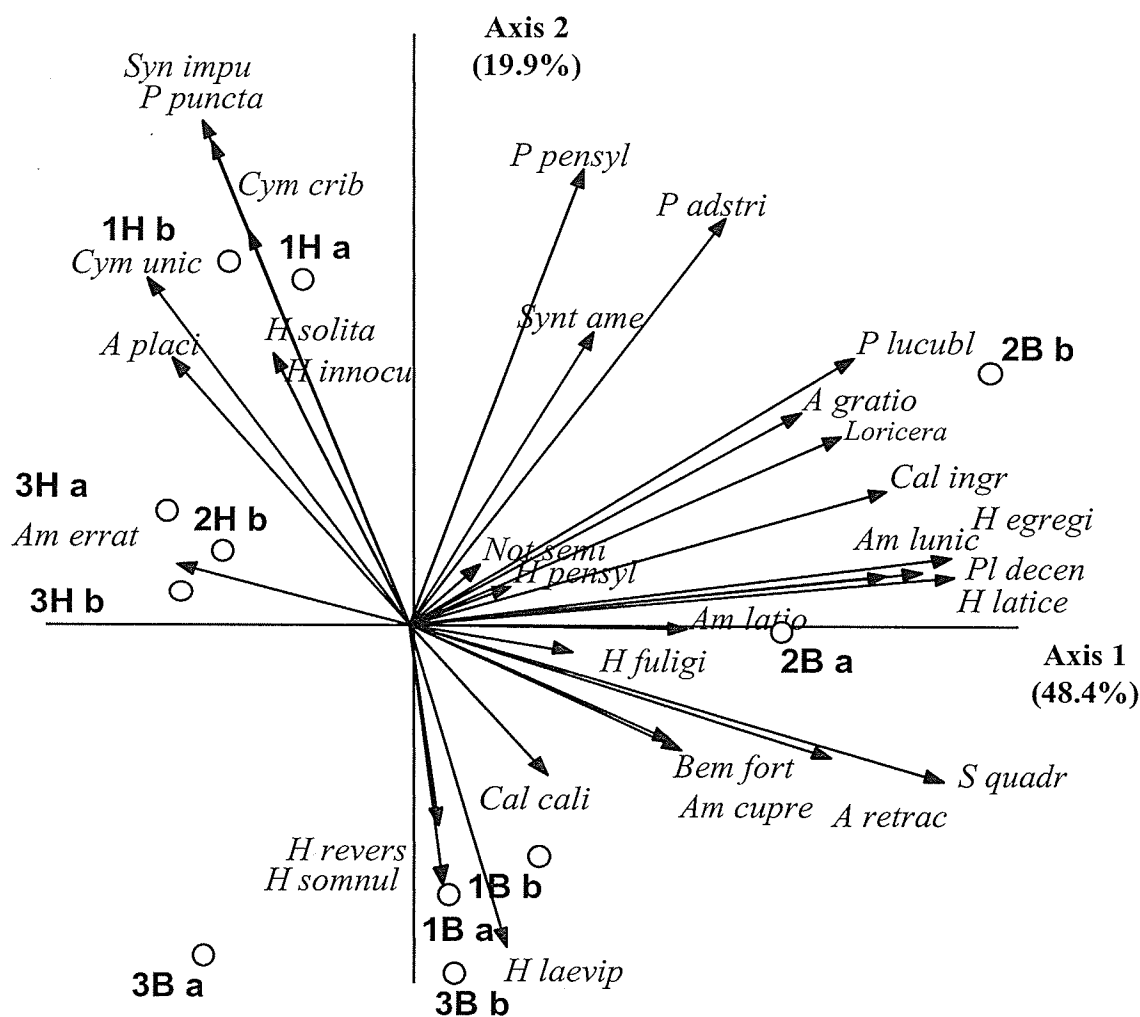
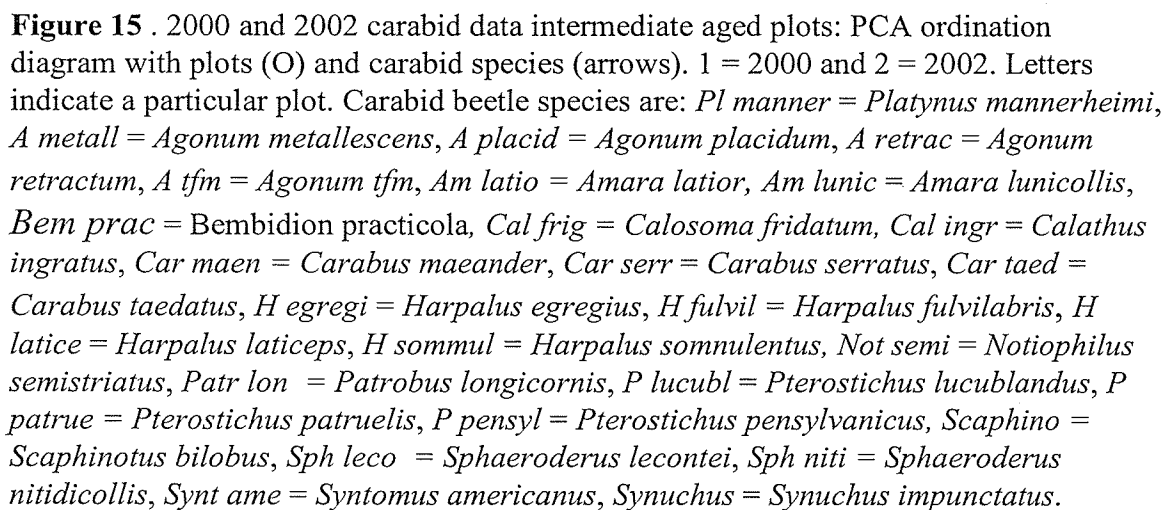


Figure 14 . Carabid data of young plots: PCA ordination diagram with plots (O) and carabid species (arrows). Numbers indicate collecting year: 1 = 1999, 2 = 2000, 3 = 2001. Letters indicate a particular plot. Carabid beetle species are: *A gratio* = *Agonum gratiosum*, *A placi* = *Agonum placidum*, *A retrac* = *Agonum retractum*, *Am cupre* = *Amara cupreolata*, *Am errat* = *Amara erratica*, *Am lunic* = *Amara lunicollis*, *Bem fort* = *Bembidion fortetrium*, *Cal cali* = *Calosoma calidum*, *Cal ingr* = *Calathus ingratus*, *Cym crib* = *Cymindis cribicollis*, *Cym unic* = *Cymindis unicolor*, *H egregi* = *Harpalus egregius*, *H fuligi* = *Harpalus fulvilabris*, *H latice* = *Harpalus laticeps*, *H. pensyl* = *Harpalus pensylvanicus*, *H revers* = *Harpalus reversus*, *H somnul* = *Harpalus somnulentus*, *Loricera* = *Loricera pilicornis*, *Not semi* = *Notiophilus semistriatus*, *P adstri* = *Pterostichus adstrictus*, *P. lucubl* = *Pterostichus lucublandus*, *P pensyl* = *Pterostichus pensylvanicus*, *P puncta* = *Pterostichus punctatissimus*, *Pl decen* = *Platynus decentis*, *S quadri* = *Sericoda quadripunctatum*, *Synt ame* = *Syntomus americanus*.



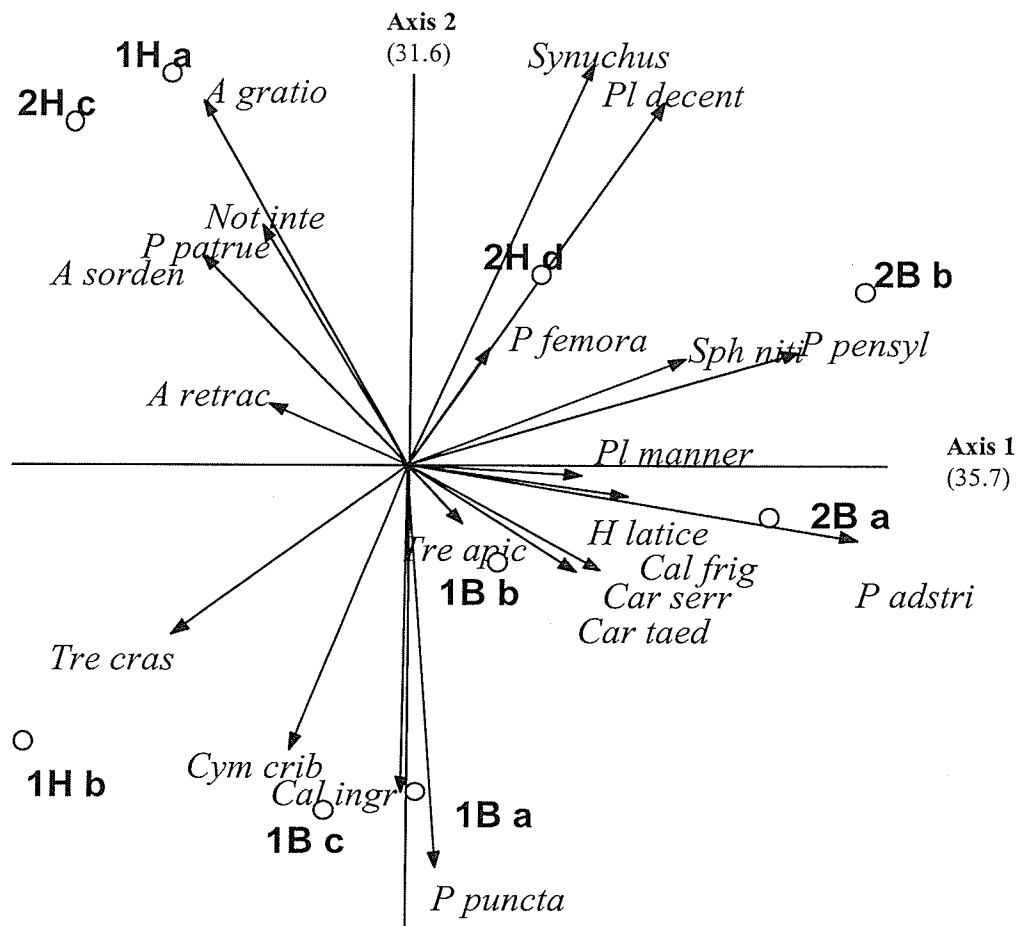


Figure 16 . 2000 and 2002 carabid data for old plots: PCA ordination diagram with plots (O) and carabid species (arrows). 1 = 2000 and 2 = 2002. Letters indicate a particular plot. Carabid beetle species are: *A gratio* = *Agonum gratiosum*, *Pl manner* = *Platynus mannerheimi*, *A retrac* = *Agonum retractum*, *Cal ingr* = *Calathus ingratus*, *Car serr* = *Carabus serratus*, *Car taed* = *Carabus taedatus*, *Cym crib* = *Cymindis cribricollis*, *H latice* = *Harpalus laticeps*, *P adstri* = *Pterostichus adstrictus*, *P femora* = *Pterostichus femoralis*, *P pensyl* = *Pterostichus pensylvanicus*, *P puncta* = *Pterostichus punctatissimus*, *Pl decent* = *Platynus decentis*, *Sph niti* = *Sphaeroderus nitidicollis*, *Synt ame* = *Syntomus americanus*, *Synuchus* = *Synuchus impunctatus*, *Tre apic* = *Trechus apicalis*, *Tre cras* = *Trechus crassiscapus*.

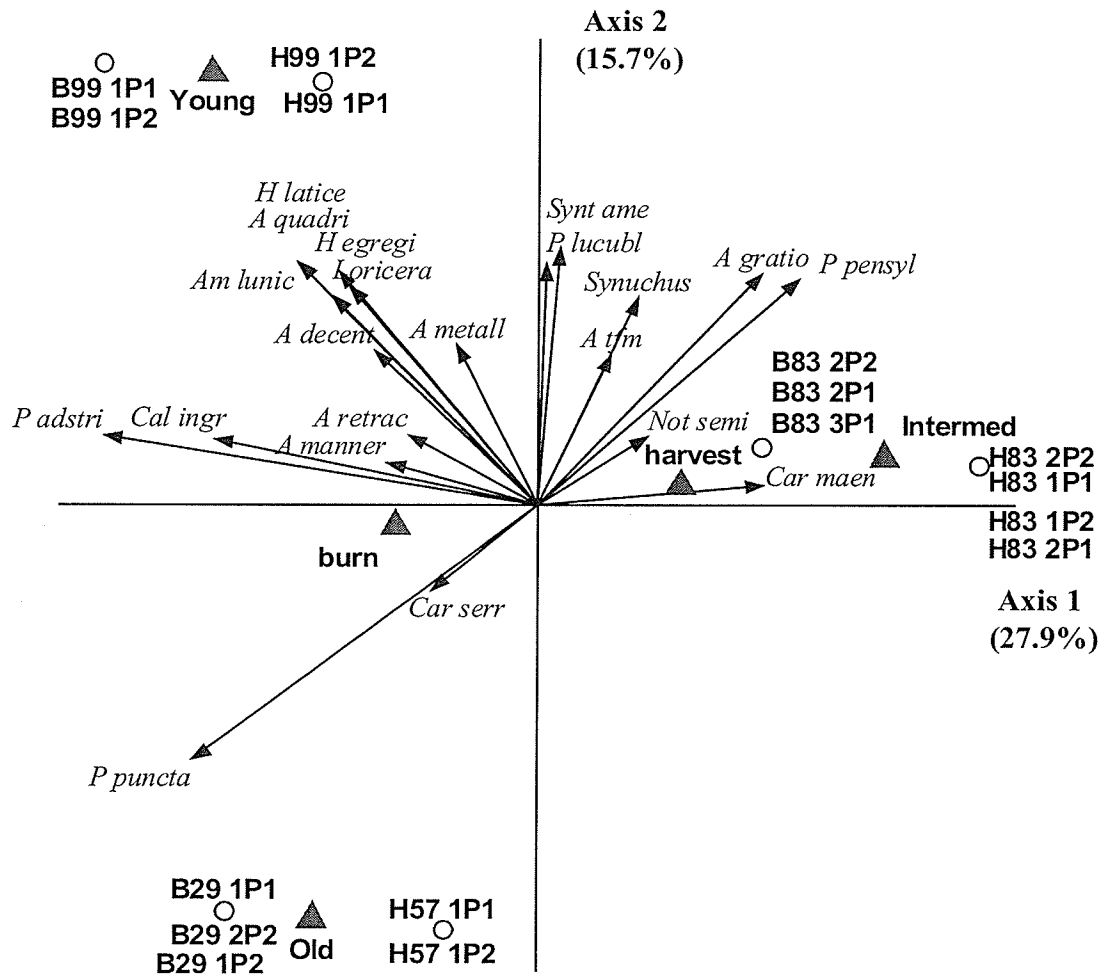


Figure 17. 2000 carabid and age class/disturbance type (environmental data): RDA ordination diagram with plots (O), carabid species (arrows) and environmental data (▲) Carabid beetle species are: *A gratio* = *Agonum gratiosum*, *A manner* = *Agonum mannerheimi*, *A metall* = *Agonum metallescens*, *A retrac* = *Agonum retractum*, *A tfm* = *Agonum tfm*, *Am lunic* = *Amara lunicollis*, *Cal ingr* = *Calathus ingratus*, *Car serr* = *Carabus serratus*, *H egregi* = *Harpalus egregius*, *H latice* = *Harpalus laticeps*, *Loricera* = *Loricera pilicornis*, *Not semi* = *Notiophilus semistriatus*, *P adstri* = *Pterostichus adstrictus*, *P lucubl* = *Pterostichus lucublandus*, *P pensyl* = *Pterostichus pensylvanicus*, *P puncta* = *Pterostichus punctatissimus*, *Pl decent* = *Platynus decentis*, *S quadri* = *Sericoda quadripunctatum*, *Synt ame* = *Syntomus americanus*, *Synuchus* = *Synuchus impunctatus*.

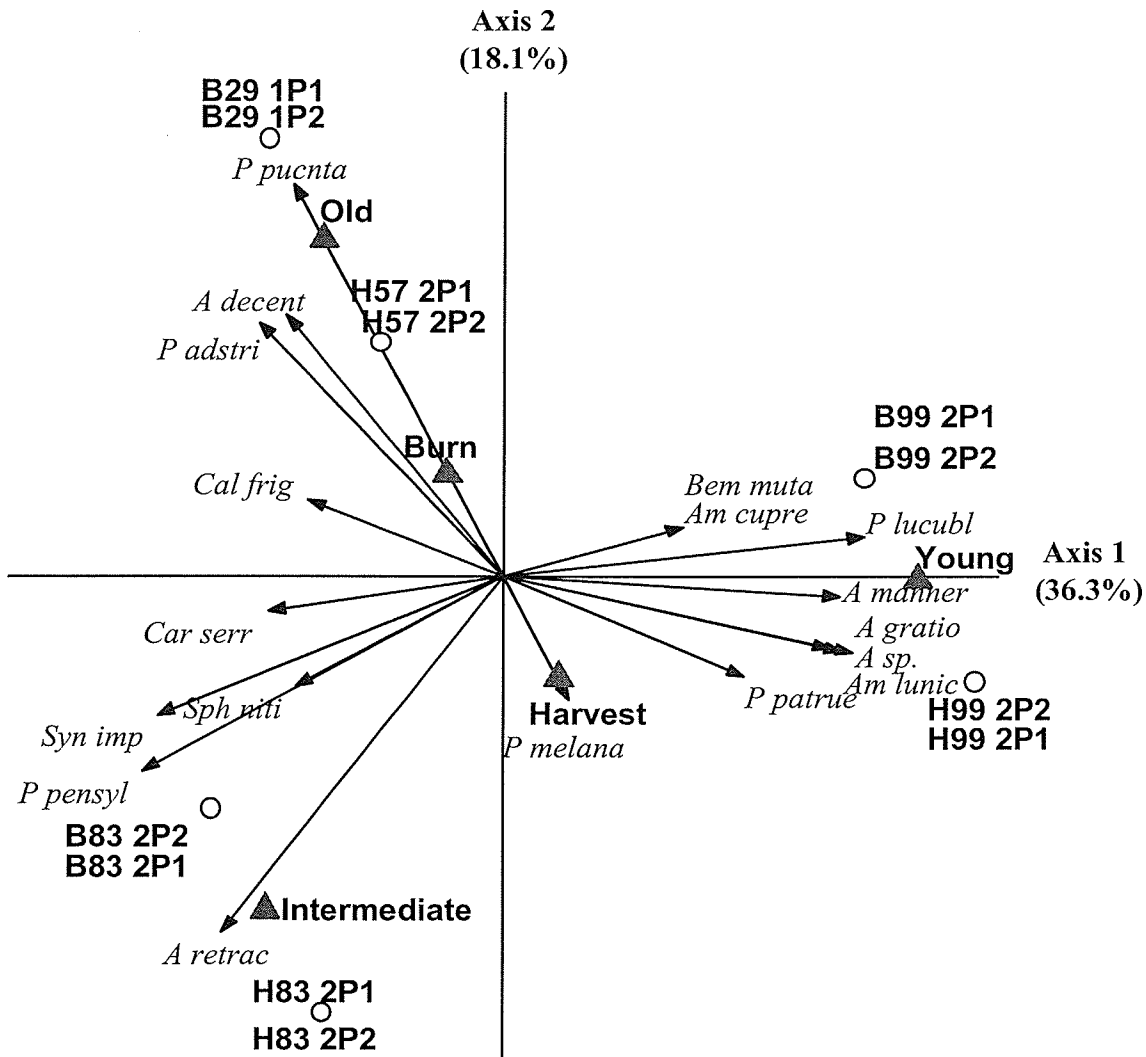


Figure 18. 2002 carabid and age class/disturbance type (environmental data): RDA ordination diagram with plots (O), carabid species (arrows) and environmental data (▲) Carabid beetle species are: *A gratio* = *Agonum gratiosum*, *A manner* = *Agonum mannerheimi*, *A retrac* = *Agonum retractum*, *A sp.* = *Agonum* species, *Am lunic* = *Amara lunicollis*, *Car serr* = *Carabus serratus*, *H egregi* = *Harpalus egregius*, *H latice* = *Harpalus laticeps*, *P adstri* = *Pterostichus adstrictus*, *P lucubl* = *Pterostichus lucublandus*, *P pensyl* = *Pterostichus pensylvanicus*, *P puncta* = *Pterostichus punctatissimus*, *Pl decent* = *Platynus decentis*, *Sph niti* = *Sphaeroderus nitidicollis*, *Synuchus* = *Synuchus impunctatus*.

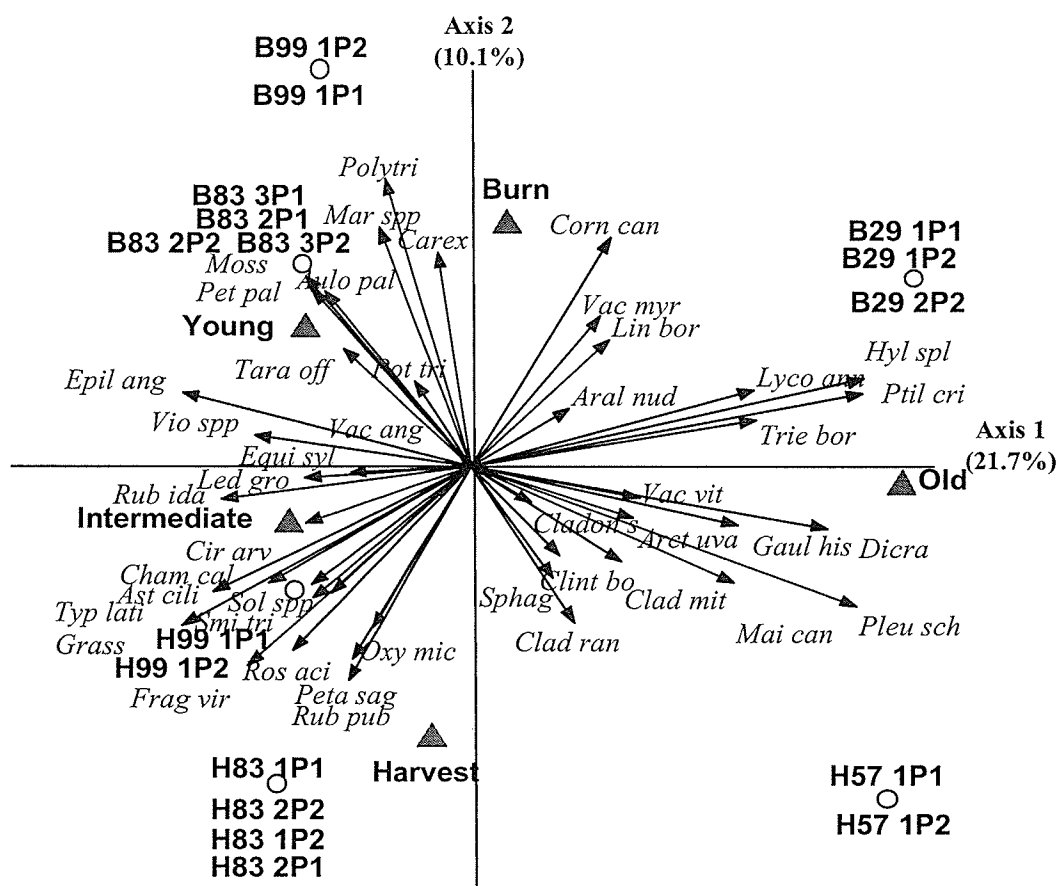


Figure 19. 2000 vegetation and age class/disturbance type (environmental data): RDA ordination diagram with plots (O), vegetation species (arrows) and environmental data (▲) Vegetation species are: *Aral nud* = *Aralia nudicaulis*, *Arct uva* = *Arctostaphylos uva-ursi*, *Ast cili* = *Aster ciliolatus*, *Aulo pal* = *Aulocomium palustre*, *Carex* = *Carex spp*, *Cham cal* = *Chamaedaphne calyculata*, *Cir arv* = *Cirsium arvense*, *Clad mit* = *Cladina mitis*, *Clad rang* = *Cladina rangiferina*, *Cladon spp* = *Cladonia spp*, *Clint bor* = *Clintonia borealis*, *Corn can* = *Cornus canadensis*, *Dicra* = *Dicranum spp*, *Epil ang* = *Epilobium angustifolium*, *Equi syl* = *Equisetum sylvaticum*, *Frag virg* = *Fragaria virginiana*, *Gaul hisp* = *Gaultheria hispidula*, *Grass* = *Grass spp*, *Hyl spl* = *Hylocomium splendens*, *Led gro* = *Ledum groenlandicum*, *Lin bor* = *Linnaea borealis*, *Lyco ann* = *Lycopodium annotinum*, *Mai can* = *Maianthemum canadense*, *Mar spp* = *Marchantia spp*, *Moss* = *Moss spp*, *Oxy mic* = *Oxycoccus microcarpus*, *Pet pal* = *Petasites palmatus*, *Peta sag* = *Petasites sagittatus*, *Pleu sch* = *Pleurozium scheberi*, *Polytri spp* = *Polytrichum spp*, *Pot tri* = *Potentilla tridentata*, *Ptil cris* = *Ptilium crista-castrensis*, *Ros aci* = *Rosa acicularis*, *Rub ida* = *Rubus idaeus*, *Rub pub* = *Rubus pubescens*, *Smi tri* = *Smilacina trifolia*, *Sol spp* = *Solidago spp*, *Sphag* = *Sphagnum spp*, *Tara off* = *Taraxacum officinale*, *Trie bor* = *Trientalis borealis*, *Typ lati* = *Typha latifolia*, *Vac ang* = *Vaccinium angustifolium*, *Vac myr* = *Vaccinium myrtilloides*, *Vac vit* = *Vaccinium vitis-idaea*, *Vio spp* = *Viola spp*.

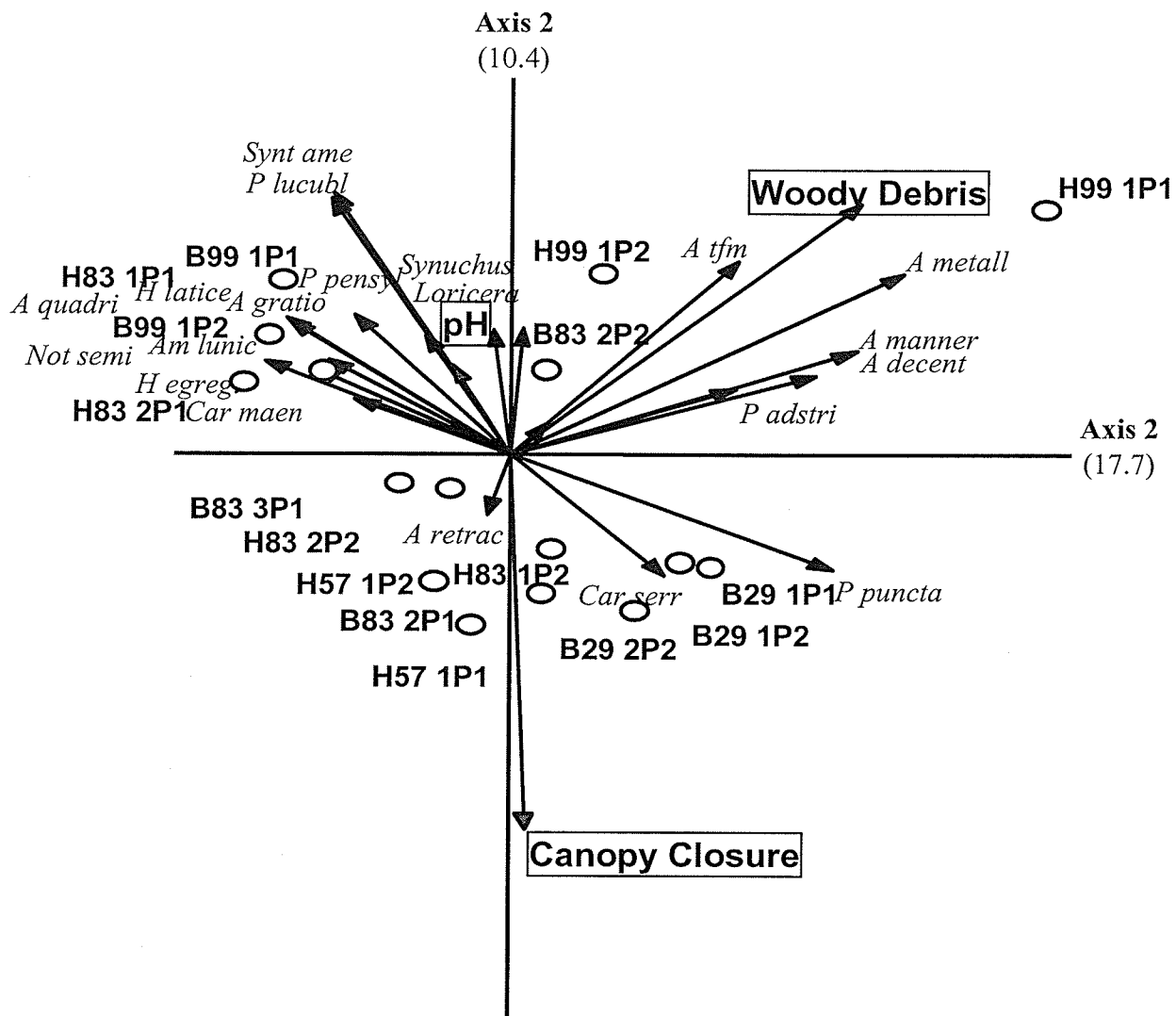


Figure 20. 2000 carabid and age class/disturbance type (environmental data): RDA triplot ordination diagram with plots (O), carabid species (solid arrows), environmental (boxes). Carabid beetle species are: *A gratio* = *Agonum gratiosum*, *A manner* = *Agonum mannerheimi*, *A metall* = *Agonum metallescens*, *A retrac* = *Agonum retractum*, *A tfin* = *Agonum tfin*, *Am lunic* = *Amara lunicollis*, *Cal ingr* = *Calathus ingratus*, *Car serr* = *Carabus serratus*, *H egregi* = *Harpalus egregius*, *H latice* = *Harpalus laticeps*, *Loricera* = *Loricera pilicornis*, *Not semi* = *Notiophilus semistriatus*, *P adstri* = *Pterostichus adstrictus*, *P lucubl* = *Pterostichus lucublandus*, *P pensyl* = *Pterostichus pensylvanicus*, *P puncta* = *Pterostichus punctatissimus*, *Pl decent* = *Platynus decentis*, *S quadri* = *Sericoda quadripunctatum*, *Synt ame* = *Syntomus americanus*, *Syn imp* = *Synuchus impunctatus*.

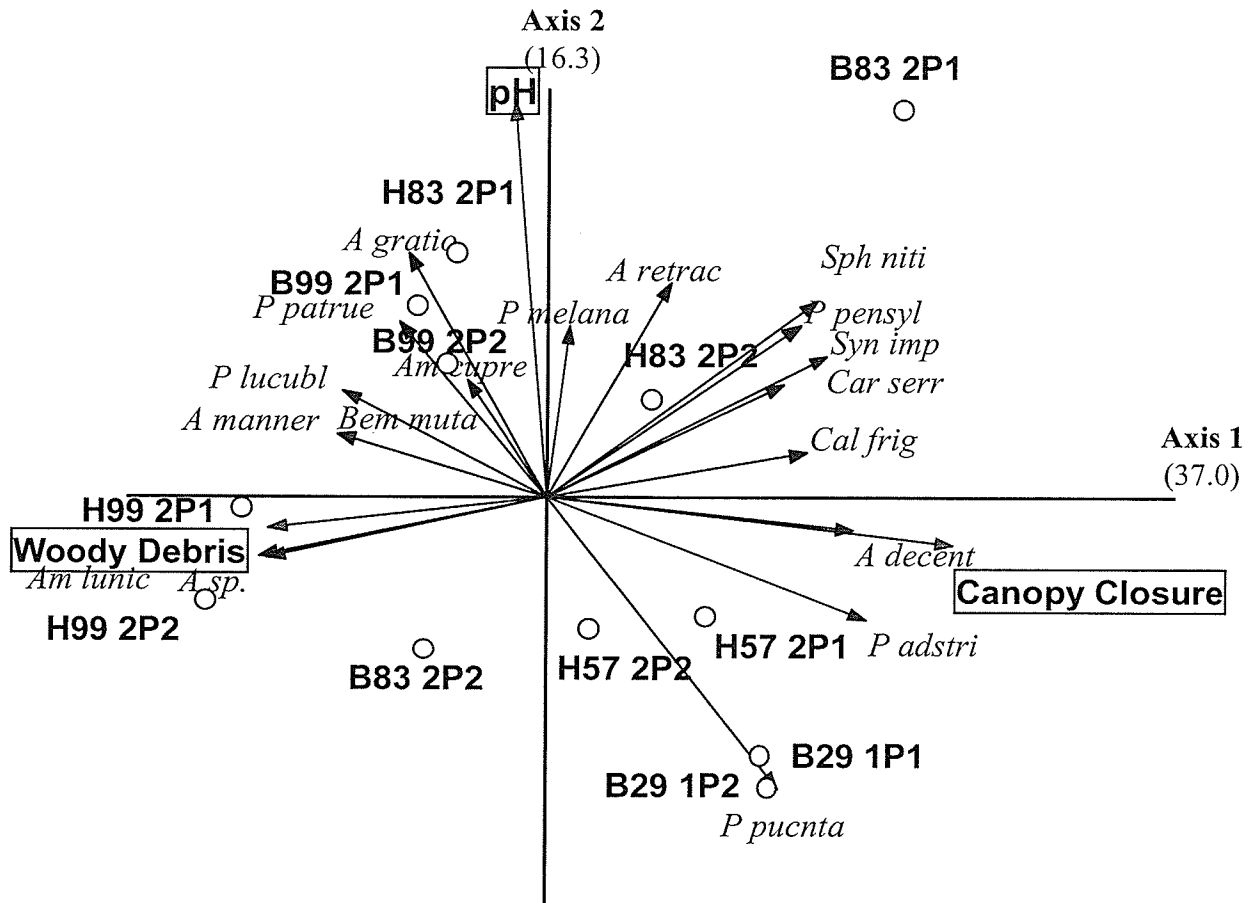


Figure 21. 2002 carabid and age class/disturbance type (environmental data): RDA triplot ordination diagram with plots (O), carabid species (solid arrows), environmental (boxes). Carabid beetle species are: *A. gratio* = *Agonum gratiosum*, *A. manner* = *Agonum mannerheimi*, *A. retrac* = *Agonum retractum*, *A. sp.* = *Agonum* species, *Am. lunic* = *Amara lunicollis*, *Car. serr* = *Carabus serratus*, *H. egregi* = *Harpalus egregius*, *H. latice* = *Harpalus laticeps*, *P. adstri* = *Pterostichus adstrictus*, *P. lucubl* = *Pterostichus lucublandus*, *P. pensyl* = *Pterostichus pensylvanicus*, *P. puncta* = *Pterostichus punctatissimus*, *Pl. decent* = *Platynus decentis*, *Sph. niti* = *Sphaeroderus nitidicollis*, *Syn. imp* = *Synuchus impunctatus*.

Chapter 5 - Discussion

5.1 - Disturbance Type and Age Class Effects on Environmental Variables

Soil pH, canopy closure, and herbaceous vegetation and shrubs did not differ between burned and harvested sites. Disturbance type did, however, have an effect on the percent cover of dead woody materials. The substantial amount of residual slash in young harvested plots contributed to a higher percent cover in these plots. The percent cover of dead woody material decreased as harvested sites increased in age.

The majority of ground cover was composed of charred plant materials following a burn,. Uncharred needles eventually fall from the trees after a fire (Begin and Marguerie 2002), and in this study, needles contributed significantly to the ground cover in burned intermediate sites, though a majority of these leaves were most likely the result of the self pruning of the branches and general needle fall.

Environmental variables were influenced to a greater degree by age class than by disturbance type. Densiometer and light meter readings showed that canopy closure increased with age of site. This result was also observed in jack pine forests (Lafreniere 1994).

Increases in canopy closure would result in lower subcanopy temperatures, which in turn would cause less evaporation of soil moisture, but possibly only during the day. Increased canopy closure along with a high water table can lead to old sites becoming dark, cool and moist—a favourable environment for moss establishment (Bisbee *et al.* 2001). In this study, moss had become well-established in old sites, regardless of disturbance type.

Measurements taken using a densiometer showed less variation than did measurements taken with a light meter. The variation (between measurements observed) in the light meter measurements could be due to cloud cover. Although efforts were made to standardize light meter readings (e.g. readings not taken when the sun was obviously obscured), thin clouds or haze may have been present. Since the densiometer does not depend on weather conditions, it is the preferred method to measure canopy closure, especially over methods such as digital and film hemispherical photography (Englund *et al.* 2000).

Herbaceous vegetation was not significantly different between burns and harvests, or between age classes with respect to mean percent cover, number of species, or Shannon's diversity indices. However, ordination analyses showed that young sites had a number of differences in their herbaceous vegetation composition compared to the intermediate and old sites. Previous studies by Halpern and Spies (1995) and Niemela (1999) also found vegetation composition to be initially different in harvest and fires, but as time progressed, ecosystems became increasingly similar. The PCA of plant species in 2000 showed sites were grouped mainly according to age class. On the other hand, plots H83 1P1 and H83 1P2 were separated from the other intermediate sites in terms of their location in the ordination diagram. A possible reason why these plots were different could be that H83 1P1 and H83 1P2 were located on Dark Gray Chernozem soils, while other intermediate harvest sites were located on by organic soils. The vegetation composition in other sample plots may have been affected by differences in soil type.

Vegetation characteristics varied between young, intermediate, and old plots. In young plots after a burn or a harvest, there is an initial increase in the water table,

possibly caused by the loss of water through transpiring vegetation (Kimmings 1997, Roy *et al.* 2000). Increased amounts of standing water often result in the establishment of grassy species. Research has shown a trend towards the establishment of wind-disseminated pioneer species (Ahlgren and Ahlgren 1960) such as graminoids. The water table decreases as grasses and sedges become established (Sims and Mueller-Dombois 1968). The biomass of grasses in the young plots appeared to be much greater even though grasses were observed in all age classes and disturbance types.

Mosses occurred in the young harvested plots, however the presence of mosses is characteristic of old sites. The mosses observed in the young plots could be “leftover” from before the plots were harvested. Mosses may decrease in abundance due to lack of habitat and competition from other plant species adapted to open areas as young plots mature (Sousa 1984). Plant species that are well adapted to open areas (*Vaccinium myrtilloides* and *Equisetum sylvaticum* (Johnson *et al.* 1995)) were found to be dominant in the young harvested and burned plots in this study.

Wet areas that had little or no canopy cover were dominated by grasses in intermediate plots. Lichen species were found developing on exposed rock surfaces in both burned and harvested sites. Sphagnum mosses were also beginning to re-establish themselves in intermediate sites.

The ground cover in old plots consisted mainly of mosses, but these were interspersed with a small number of herbaceous species (*Cornus canadensis* and *Maianthemum canadense*).

Old plots had less shrub species and a lower Shannon’s diversity index values than did intermediate and young plots. Reasons for decreased diversity of shrubs could

be due to less favourable conditions in old plots, such as the competition for light and nutrients by shrubs and well-established trees. The only shrub species that was well established in old plots was *Ledum groenlandicum*.

In contrast to the findings in this study regarding plots of all three age classes, Johnston and Elliott (1996) and Nguyen-Xuan *et al.* (2000) found differences in herbaceous plant composition when comparing burned and harvested areas of black spruce in northwestern Ontario within the first ten years following a disturbance. In this thesis, there were no major differences in shrub and tree data between disturbance types in any of the age classes; similarly, no differences were observed by Carleton and MacLellan (1994) or Johnston and Elliott (1996). Tree and shrub composition and diversity showed no marked differences between age classes. The species composition of the canopy cover did not seem to effect the composition of the understory vegetation in any of the age classes sampled. Intermediate burn plots had canopy consisting mainly of jack pine, whereas black spruce dominated the canopy in intermediate harvested plots; however, the understory plants were similar in both disturbance types.

5.2 – Disturbance Type and Age Class Effects on Carabid Beetles Species

The first two years after a disturbance show marked differences in carabid beetle assemblages. By the third year of sampling, the species composition of the young burns and harvests started to converge. PCA of beetle species of the young plots from 1999, 2000 and 2001, indicated beetle species composition in burned plots differed from harvested plots. This was also true for intermediate aged plots. In old plots there was minimum separation of disturbance types. This suggests that for species composition

there was not much of a temporal effect. However, in young plots the presence of species and numbers of pyrophilous species seemed to decrease with time. In 1999, the year of the fire, pyrophilous species were still moving into burned areas, causing their number to be lower. The year after the fire (2000) was when the highest numbers of pyrophilous species were collected. However, in 2000 *S. quadripunctatum* were caught in high number in the spring. Numbers of individuals decrease dramatically after 2000. This could be due to either a less attractive environment or increased competition from other species moving into the area.

Normally, the presence of forest generalist carabid species tends to not be affected after a harvest. On the other hand the number of species adapted to open habitats would increase, and mature forest species either decrease or disappear. Initial increases in carabid beetle numbers and species due to generalist species have been observed in other similar studies within the first few years after a harvest (Niemela *et al.* 1993, Niemela *et al.* 1994a, Beaudry *et al.* 1997, Pearce *et al.* 2003), or burn (Holliday 1991, Holliday 1992). The number of *Amara* and *Harpalus* species generally increased in young plots; this was also found to be the case in earlier studies (Holliday 1991, Niemela *et al.* 1993, Lafreniere 1994).

Generalist species that were found to increase directly after disturbances in this study included: *P. adstrictus*, *P. decentis*, and *S. impunctatus*. *Pterostichus adstrictus* was found in high numbers in both young burned and harvested plots during 2000. Niemela *et al.* (1994b) reported *P. adstrictus* occurred in high numbers during early successional stages in Canada and Finland. Niemela *et al.* (1994a) and Lindroth (1966) described *P. adstrictus* as a common forest species found in northern coniferous regions.

Platynus decentis was found in all plots, although it was found in highest numbers in the young harvests in 2000. Reported to be hydrophilous by Lindroth (1966), it may have an attraction to wet stands of black spruce.

Synuchus impunctatus was common during burned plots in 2000, and in intermediate plots in 2002. This species is thought to be a forest generalist (Beaudry *et al.* 1997). Lindroth (1966) reported *S. impunctatus* to be associated with *Rubus* spp. In this study, *Rubus* spp. was present in intermediate harvested plots and in young burned or harvested sites; this may have resulted in the tendency for slightly higher numbers of *S. impunctatus* in these plots.

In addition to generalist species moving into recently disturbed areas, pyrophilous ('fire-loving') species are pioneer species that colonize an area after a fire. In this study, *Sericoda quadripunctatum* was a pyrophilous species that was restricted to young burned sites and was only found within the first three years post-fire. The habitat of *S. quadripunctatum* is burned wood or under the bark (Lindroth 1966, Holliday 1984, Holliday 1991). Other carabid species that seemed to be pyrophilous were *H. laticeps* and *Amara lunicollis*. *Harpalus laticeps* was reported in large numbers from burned sites in previous studies (Holliday 1991, Lafreniere 1994). In this study, both *S. quadripunctatum* and *H. laticeps* had highest numbers the year following the fire, although it seems *H. laticeps* may have taken longer to establish during the year of the fire. *Amara lunicollis* was found mostly in burned sites but has not been reported as a pyrophilous species in other studies. The habitat of *A. lunicollis* is reported to be wet grass and peaty soil (Lindroth 1968), both of which were present in burn sites in this study.

All intermediate sites were similar in composition of carabid species regardless of their disturbance type. They shared many of the same carabid species such as *A. gratiosum*, *P. pensylvanicus*, and *S. impunctatus*.

Although, the old burned plots were 71 years old compared to old harvested plots (43 years), this 28-year difference did not translate into large differences in species assemblages. Old burned and old harvested sites were characterized by the presence of old-growth species, such as *Platynus mannerheimi* and *P. punctatissimus*. *Pterostichus punctatissimus* appears to be an old growth specialist, since it was only present in old plots. Lindroth (1966) suggested that *P. punctatissimus* has an association with moss on tree-stumps, which were abundant in older spruce trees. *Platynus mannerheimi* is an old growth species that survived a clearcut for up to two years post harvest, before quickly disappearing due to loss of habitat or competition (Niemela 1997). In this study, there were old growth species that may have been left-over after disturbance found in young plots including *P. mannerheimi* and *P. punctatissimus*.

Pterostichus adstrictus was found in higher numbers in old burned sites during both 2000 and 2002. This may be attributed to the increased amounts of woody debris that had been made available in old plots by windstorms in 2002. Oviposition and the larval habitat of *P. adstrictus* is associated with dead rotting logs or under the bark (Goulet 1974). Eggs of *P. adstrictus* are sensitive to desiccation and following drier years, population tend to decrease due to death of the eggs (Goulet 1974). The summers of 2000 and 2001 were cooler and wetter which may have added to a more favourable habitat in 2002 in older plots for egg survival.

5.3 – Habitat Characteristics and Seasonal Effects on Carabid Species Assemblages

Many forest carabids depend on decaying woody material and leaf litter for their habitat (Spence *et al.* 1996, Pearce *et al.* 2003). In this study, *P. decentis* was found associated with high percent ground cover of dead wood material. *Pterostichus adstrictus* was found associated with woody debris, which is the larval habitat (Goulet 1974). Other species that appeared to be associated with higher amounts of dead woody material were; *Agonum tfm*, *Agonum metallescens*, *Platynus mannerheimi*, and *P. decentis*. *Agonum metallescens* was only found in H99 1P1, the plot with the highest amount of dead woody material.

In Alberta, *P. pensylvanicus* is often found in areas with deciduous forest litter (Goulet 1974). However, in Ontario *P. pensylvanicus* has been reported exclusively from coniferous forests (Goulet 1974). The location of the present study site is near the Ontario border. After coniferous harvesting, the leaf litter tends to change from a coniferous to a deciduous composition (Begin and Marguerie 2002) and *P. pensylvanicus* was generally found in harvested intermediate sites that had more deciduous cover than other sites. The habitat preference for *P. pensylvanicus* in Manitoba could be a combination of coniferous areas with some deciduous trees contributing to the forest litter. Holliday (1991) believes that in Manitoba, *P. pensylvanicus* is less of a habitat specialist, and can be found in both deciduous and coniferous forests.

Canopy cover is associated with of stand age. Therefore, any species found to be associated with particular canopy cover values were those that occurred only in plots of particular ages.

Charred woods require habitat for many pyrophilous carabid species (Esseen *et al.* 1997). Pyrophilous species may have an important influence on forest succession and should be conserved. To conserve carabid species during harvesting, there should be a fire, either in the vicinity of harvest or in the harvest itself, to encourage pyrophilous species which are attracted to the heat or smoke during or following a fire (Holliday 1991). Prescribed burning might be a solution to the loss of pyrophilous species. Burning of harvested sites could also create an organic layer more suitable for a black spruce seedbed (Chrosciewicz 1976). As harvests may have different fuel types compared to an unharvested forest, fire behavior may differ from a natural forest fire and it is unknown if pyrophilous species would be attracted to this habitat.

Some carabid species could be associated with certain plant species.

Pterostichus adstrictus was captured in sites with high percent cover of *Cornus canadensis*. *Pterostichus pensylvanicus* and *A. gratiosum* seem to be associated with *Viola* spp. Little is known about the biology of *A. metallescens* other than that it is considered to be hydrophilous, often found near open water, and associated with *Equisetum* and grass spp. (Lindroth 1966). These plant species were found in young harvested sites, where the only population of *A. metallescens* was observed. In this study, *A. gratiosum* was found on moist ground with peat/sphagnum, or more often on clay soils with sedges, and this finding confirms the findings of Lindroth (1966). Conversely, carabid species may not have a direct association with plant species, but instead carabid and certain species may have similar habitat requirements.

In Finland, beetle associations were attributed to tree species that were strongly linked to soil moisture (Niemela *et al.* 1994a). In this study, it was observed that tree

species were not a major factor in carabid assemblages, however soil moisture may have been. Where the dominant tree species did not appear to be black spruce, such as the case with burned intermediate plots, many black spruce existed in the size class of 1m to 3m in height, therefore showing these plots were black spruce – type habitat. Carabid beetles from intermediate burned sites were similar to beetles captured in intermediate harvested sites.

Carabid species seem to show peaks of abundance during the collecting season. Peaks were similar in 2000 and 2002. These peaks may have corresponded to specific lifecycle events, such as adult emergence or to a mating period. The general timing of population peaks in some species corresponded to the findings of earlier studies. For example, *S. impunctatus* has been reported not to appear before the end of May (Lindroth 1966), and in this study was not present until the beginning of July. Holliday (1991) also observed *S. impunctatus* to be at its highest numbers in July. *Pterostichus adstrictus* and *P. pensylvanicus* show the same high peaks in numbers in May as reported by Goulet (1974) and Holliday (1991). However, Goulet (1974) and Holliday (1991) also reported high numbers in late fall. In this study plots were not sampled past early September, so if these second peaks did occur they were not observed.

Some species also seemed to be absent for periods of time such as *S. americanus*, which was found in 1999, 2000 and 2001 in, but was absent in 2002. Beaudry *et al.* (1997) also reported *S. americanus* absent from one collecting year to the next. Geography also influences emergence times and the length of an individual's life cycle (Butterfield 1996) and it would be necessary to collect for the entire season in an area, to achieve a better picture of carabid diversity.

5.4 – Disturbance Type and Age Class Effects on Diversity of Carabid Beetles

A reason for increased diversity in young plots was that when carabids are displaced from an area by disturbance they are quickly replaced by carabids moving in from surrounding undisturbed areas (Apigian and Wheelwright 2000, Pearce *et al.* 2003). Old sites were similar in having a small number of species and, Niemela *et al.* (1994b) also found catches were higher in sites cut less than 10 years ago compared to older sites.

The overall numbers of beetles found were lower than those found other studies. In 2000, 1347 carabid beetles were collected and 786 in 2002. Overall numbers of carabid species were lower in 2002 compared to the 2000. This may have been related to the weather. The year 2000 was cooler and wetter compared to 2002 which tended to be hotter and dryer. Differences in weather may have caused carabids to move into open areas when it was cooler and darker/cooler old sites when the weather was hotter. Carabid species have shown differences in abundance due to changes in temperature and humidity (Neve 1994). Lafreniere (1994) found 1998 carabids in one year and 2863 in the following year in jack pine stands, although sampling time varied in his study. However, black spruce stands or moist sites generally have less carabids compared to other stand types (Holliday 1991, Niemela *et al.* 1994a).

The numbers of individuals and numbers of species of carabids was different among age classes in 2000, due to high numbers of individuals and species present in young sites. However, numbers of individuals and species decreased from young disturbed sites by 2002 and there was no longer a significant difference between age classes. This follows the general pattern of recently disturbed sites having higher

diversity as found in previous studies (Niemela *et al.* 1993, Niemela 1997), a results of the numbers of individuals and species increase directly following a disturbance.

Overall, within age classes there tended to be higher numbers of individuals in burned sites in both 2000 and 2002. In contrast, differences in numbers between years may be due to plots in 2000 being different from those in 2002.

The log series alpha index values were not significantly different among age classes for 2000 and 2002 carabid beetle catches. Since high values indicate there are more individuals of more species and there were no differences between age classes or disturbance types this means that number were similar in all plots. However, this does not mean that they are the same species even if the number of species are similar. Plots with similar log series alpha values could potentially have completely different beetle assemblages. This diversity index can be useful in indicating differences between systems, but to rely on it alone could allow differences such as species assemblages to go undetected. This is why ordination techniques should be used along with diversity indices.

The Berger Parker index showed no significant differences between age classes or disturbance types in the 2000 or 2002 data. A low value of the Berger Parker index indicates higher diversity and lower species dominance (Southwood 1978, Magurran 1988). There was no significant difference between disturbance types or age classes in the evenness values. Evenness values like the Berger Parker index results shoed populations in most plots were similar.

Chapter 6 - Synthesis

The alpha diversity of carabid beetles did not differ between age classes or disturbance types in the sampled black spruce forest stands. However, the diversity indices employed in this study did not always detect the differences in species assemblages. Therefore, diversity indices should always be conducted along with ordinations in order to reveal any differences in assemblages. Ordination analysis showed that earlier forest stages may have had differences in carabid beetle species assemblages during the first two years post-disturbance; this was a result of an increase in generalist species and pyrophilous species in the burned stands. After the first two years, there appeared to be no differences between species assemblages from either burned or harvested black spruce stands.

Disturbance type and age class had an influence on habitat variables. Percent cover of dead woody material differed between disturbance types and age classes, the highest amounts of dead woody material occurred in young harvested sites. Canopy closure increased with site age and was generally greatest in burned sites. The soil pH of old plots was lower compared to the soil pH in both intermediate and young plots. Herbaceous plant species did not differ between harvested and burned sites, but did show some species composition differences when ordination techniques were employed.

Changes in habitat characters were most likely the determining factor in the composition of carabid beetle species assemblages. Patterns in herbaceous plant species were similar to the patterns observed in carabid assemblages where plots grouped

together in ordination into the three different age classes based on herbaceous species and carabid species.

Since, pyrophilous species were only present in the recently burned areas the ecology and biology of pyrophilous carabids must be studied further to fully understand these species' contributions to boreal forest succession, and whether their absence from a system could have detrimental effects on the natural system. Although we have some knowledge of the habitats of most carabids (Lindroth 1961, Goulet 1974), we still must learn the exact habitat requirements of all carabid species since such information is lacking (Niemela 1990). Habitat information would be helpful in determining if a habitat of a specific species is missing after a disturbance.

More studies are required to establish baseline taxonomic data for invertebrate boreal forest fauna, and to examine the long-term effects of harvesting on forest succession. The current goal in forest management is to regenerate forests after harvesting so forests will follow similar successional pathways and contain similar diversity levels as found after fire. Therefore, more studies are required to determine if current forest management techniques are conserving biodiversity and replicating natural successional pathways.

References

- Abildsnes, J., B. A. Tommeras. 2000. Impact of experimental habitat fragmentation on ground beetles (Coleoptera, Carabidae) in a boreal spruce forest. *Annales Zoologici Fennici*. **37**: 201-212.
- Adis, J. 1979. Problems of interpreting arthropod sampling with pitfall traps. *Zoologischer Anzeiger*. **202**: 177-184.
- Ahlgren, I. F., C. E. Ahlgren. 1960. Ecological effects of forest fires. *Botanical Review*. **26**: 483-533.
- Anderson, A. N. 1999. Editorial – My bioindicator or yours? Making the selection. *Journal of Insect Conservation*. **3**: 61-64.
- Apigian, K., N. T. Wheelwright. 2000. Forest ground beetles (Coleoptera: Carabidae) on a boreal island: habitat preferences and the effects on experimental removal. *The Canadian Entomologist*. **132**: 627-634.
- Baars, M.A. 1979. Catches in pitfall traps in relation to mean densities of carabid beetles. *Oecologia*. **41**: 25-46.
- Barber, H. S. 1931. Traps for cave-inhabiting insects. *Journal of the Elisha Mitchell Science Society*. **46**: 25-46.
- Basedow, T. 1994. Phenology and egg production in *Agonum dorsale* and *Pterostichus melanarius* (Col., Carabidae) in winter wheat fields of different growing intensity in Northern Germany. In *Carabid beetles: ecology and evolution*. Eds. K. Desender, M. Dufrière, M. Loreau, M.L. Luff, J.-P. Maelfait. Kluwer Academic Publishers, Netherlands. Pp 101-107.
- Beaudry, S., L. C. Duchesne, B. Cote. 1997. Short-term effects of three forestry practices on carabid assemblages in a jack pine forest. *Canadian Journal of Forest Research*. **27**: 2065-2071.
- Begin, L., L. Filion. 1999. Black spruce (*Picea mariana*) architecture. *Canadian Journal of Botany*. **77**: 664-672.
- Begin, Y., D. Marguerie. 2002. Characterization of tree macroremains production in a recently burned conifer forest in northern Quebec, Canada. *Plant Ecology*. **159**: 143-152.
- Behan-Pelletier, V., G. Newton. 1999. Linking soil biodiversity and ecosystem function – the taxonomic dilemma. *BioScience*. **49**: 149-153.

- Bergeron, Y., S. Gauthier, V. Kafka, P. Lefort, D. Lesieur. 2001. Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. *Canadian Journal of Forest Research*. **31**: 384-391.
- Bisbee, K. E., S. T. Gower, J. M. Norman, E. V. Nordheim. 2001. Environmental controls on ground cover species composition and productivity in a boreal black spruce forest. *Oecologia*. **129**: 261-270.
- Bousquet, Y. 1986. The number of clip setae on the protibia as a diagnostic character between *Pterostichus pennsylvanicus* LeConte and *P. adstrictus* Eschscholtz. *Coleopterists Bulletin*. **40**: 353-354.
- Bousquet, Y. 1991. Checklist of beetles of Canada and Alaska. Research Branch Agriculture Canada publication 1861/E.
- Bray, J. R., J. T. Curtis. 1957. An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs*. **27**: 325-349.
- Brown Jr., K. S. 1997. Diversity, disturbance, and sustainable use of Neotropical forests: insects as indicators for conservation monitoring. *Journal of Insect Conservation*. **1**: 25-42.
- Buddle, C. M., H. E. J. Hammond. 2003. Comparison of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) collected in pan and pitfall traps. *The Canadian Entomologist*. **135**: 609-611.
- Butterfield, J. 1996. Carabid life-cycle strategies and climate change: a study on an altitude transect. *Ecological Entomology*. **21**: 9-16.
- Carleton, T. J., P. MacLellan. 1994. Woody vegetation responses to fire versus clear-cutting logging: a comparative survey in the central Canadian boreal forest. *Ecoscience*. **1**: 141-152.
- Choromanska, V., T. H. DeLuca. 2002. Microbial activity and nitrogen mineralisation in forest mineral soil following heating: evaluation of post-fire effects. *Soil Biology and Biochemistry*. **34**: 263-271.
- Chrosiewicz, Z. 1976. Burning for black spruce regeneration on a lowland cutover site in southeastern Manitoba. *Canadian Journal of Forest Research*. **6**: 179-186.
- Colunga-Garcia, M., S. H. Gage, D. A. Landis. 1997. Response of an assemblage of Coccinellidae (Coleoptera) to diverse agricultural landscape. *Environmental Entomology*. **26**: 797-804.

- Den Boer, P. J., W. Den Boer-Daanje. 1990. On life history tactics in carabid beetles: are there only spring and autumn breeders? *In* The role of ground beetles in ecological and environmental studies. Ed. N. E. Stork, Intercept, Hampshire. Pp. 247-258.
- Dufrene, M., M. Baguette, K. Desender, J. P. Maelfait. 1990. Evaluation of carabids as bioindicators: a case in Belgium. *In* The role of ground beetles in ecological and environmental studies. Ed. N. E. Stork, Intercept, Hampshire. Pp. 377-381.
- Elmholt, S. 1996. Microbial activity, fungal abundance, and distribution of *Penicillium* and *Fusarium* as bioindicators of a temporal development of organically cultivated soils. *Biological Agriculture & Horticulture*. 13: 123-140.
- Englund, S. R., J. J. O'Brian, and D. B. Clark. 2000. Evaluation of digital and film hemispherical photography and spherical densiometry for measuring forest light environments. *Canadian Journal of Forest Research*, 30: 1999-2005.
- Esseen, P., A. B. Ehnstrom, L. Ericson, K. Sjoberg. 1997. Boreal forests. *Ecological Bulletin*. 11: 325-338.
- Evans, M. E. G. 1994. The carabid body plan: a functional interpretation. *In* Carabid beetles: ecology and evolution. Eds. K. Desender et al. Kluwer Academic Publishers, Netherlands. Pp 25-31.
- Fedorenko, D. N. 1999. Some data on fauna and populations of ground beetles (Coleoptera, Carabidae) in the Polish part of the Karkonosze National Park. *Biology Bulletin*. 26: 558-563.
- Fisher, R. A., A. S. Corbet, C. B. Williams. 1943. The relationship between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology*. 12: 42-58.
- Goodall, D. W. 1973. Sample similarity and species correlation. *In* Ordination of plant communities. Ed. R. H. Whittaker. W. Junk, The Hague. Pp. 99-149.
- Goulet, H. 1974. Biology and relationships of *Pterostichus adstrictus* Eschscholtz and *Pterostichus pensylvanicus* LeConte (Coleoptera: Carabidae). *Quaestiones entomologicae*. 10: 3-33.
- Greenslade, P. J. M. 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *Journal of Animal Ecology*. 33: 301-310.
- Grum, L. 1994. Habitat preference and competition among *Carabus*. *In* Carabid beetles: ecology and evolution. Eds. K. Desender et al. Kluwer Academic publishers, Netherlands. Pp. 295-298.

- Halpern, C. B., T. A. Spies. 1995. Plant species diversity in natural and managed forests of the pacific northwest. *Ecological Applications*. **5**: 913-934.
- Haydon, D. T., J. K. Friar, E. R. Pianka. 2000. Fire-driven dynamic mosaics in the Great Victoria Desert. *Landscape Ecology*. **15**: 373-381.
- Hengeveld, R. 1980. Polyphagy, oligophagy, and food specialization in ground beetles (Coleoptera, Carabidae). *Netherlands Journal of Zoology* **30**:564-584
- Hill, M. O. 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology*. **54**: 427-432.
- Holliday, N. J. 1984. Carabid beetles (Coleoptera: Carabidae) from a burned spruce forest (*Picea* spp.). *The Canadian Entomologist*. **116**: 919-922.
- Holliday, N. J. 1991. Species responses of carabid beetles (Coleoptera: Carabidae) during post-fire regeneration of the boreal forest. *The Canadian Entomologist*. **123**: 1369-1389.
- Holliday, N. J. 1992. The carabid fauna (Coleoptera: Carabidae) during postfire regeneration of boreal forest: properties and dynamics of species assemblages. *Canadian Journal of Zoology*. **70**: 440-452.
- Humphrey, J. W., C. Hawes, A. J. Peace, R. Ferris-Kaan, M. R. Jukes. 1999. Relationship between insect diversity and habitat characteristics in plantation forests. *Forest Ecology and Management*. **113**: 11-21.
- Johnson, D., L. Kershaw, A. MacKinnon, J. Pojar. 1995. *Plants of the western boreal forest and aspen parklands*. Lone Pine Publishing, Alberta. 392 pp.
- Johnson, E.A., and J. S. Rowe. 1975. Fire in the wintering ground of the Beverley Caribou Herd. *American Midland Naturalist* **94**: 1-14.
- Johnson, E. A., K. Miyanishi, N. O'Brien. 1999. Long-term reconstruction of the fire season in the mixedwood boreal forest of Western Canada. *Canadian Journal of Botany*. **77**: 1185-1188.
- Johnson, L. C., J. R. Matchett. 2001. Fire and grazing regulate belowground processes in tallgrass prairie. *Ecology*. **82**: 3377-3389.
- Johnston, M. H., Elliott, J. A. 1996. Impacts of logging and wildfire on an upland black spruce community in northwestern Ontario. *Environmental Monitoring and Assessment*. **39**: 283-297.
- Jukes, M. R., A. J. Peace, R. Ferris. 2001. Carabid beetle communities associated with coniferous plantations in Britain: the influence of site, ground vegetation and stand structure. *Forest Ecology and Management*. **148**: 271- 286.

- Keenan, R. J., J. P. Kimmins. 1993. The ecological effects of clearcutting. *Environmental Review*. **1**: 121-144.
- Kempton, R. A., L. R. Taylor. 1974. Log-series and log-normal parameters as diversity discriminants for the Lepidoptera. *Journal of Animal Ecology*. **43**: 381-399.
- Kenkel, N. C., D. A. Derksen, A. G. Thomas, P. R. Watson. 2002. Multivariate analysis in weed science research. *Weed Science*. **50**: 281- 292.
- Kimmins, J. P. 1997. *Forest ecology a foundation for sustainable management*. Second Edition. Prentice Hall, New Jersey. 596pp.
- Krause, C., M. Fournier. 1997. Development and initiation of the root system of old black spruce (*Picea mariana* (Mill.) B.S.P.) and balsam fir (*Abies balsamea* (L.) Mill.) trees. In: *Biology of root formation and development*. New York, Plenum Press. Pp. 279-280.
- Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications*. **2**: 203-217.
- Koleff, P., K. J. Gaston, J. J. Lennon. Measuring beta diversity for presence-absence data. *Journal of Animal Ecology*. **72**: 367-382.
- Kucera, C. L., J. H. Ehrenreich. 1962. Some effects on annual burning on central Missouri prairie. *Ecology*. **43**: 334-336.
- Lafreniere, R. C. 1994. Impact of regeneration techniques on ecological diversity in planted and natural forest stands: species and ecosystem diversity among carabid beetles (Coleoptera: Carabidae) in jack pine stands. M.Sc., University of Manitoba. 163 pp.
- Larsen, C. P. S. 1997. Spatial and temporal variations in boreal forest fire frequency in northern Alberta. *Journal of Biogeography*. **24**: 663-673.
- Lemmon, P. E. 1956. A spherical densiometer for estimating forest overstory density. *Forest Science*. **2**: 314-320.
- Lindenmayer, D. B. 1999. Future directions for biodiversity conservation in managed forests: indicator species, impact studies and monitoring programs. *Forest Ecology and Management*. **115**: 277-287.
- Lindroth, C. H. 1961. The ground beetles of Canada and Alaska. Part 2. *Opuscula Entomologica. Supplementa*, **20**: 1-200.
- Lindroth, C. H. 1963. The ground beetles of Canada and Alaska. Part 3. *Opuscula Entomologica. Supplementa*, **24**: 201-408.

- Lindroth, C. H. 1966. The ground beetles of Canada and Alaska. Part 4. *Opuscula Entomologica. Supplementa*, **29**: 409-648.
- Lindroth, C. H. 1968. The ground beetles of Canada and Alaska. Part 5. *Opuscula Entomologica. Supplementa*, **33**: 649-944.
- Lindroth, C. H. 1969. The ground beetles of Canada and Alaska. Part 6. *Opuscula Entomologica. Supplementa*, **34**: 945-1192.
- Little, T. I., D. J. Pluth, I. G. W. Corns, D. W. Gilmore. 2002. Post-fire forest floor development along toposequences of white spruce, trembling aspen, and mixedwood communities in west-central Alberta. *Canadian Journal of Forest Research*. **32**: 892-902.
- Loreau, M. 1990. The significance of intra- and interspecific competition in carabid beetles. *In* The role of ground beetles in ecological and environmental studies. Ed. N. E. Stork, Intercept, Hampshire. Pp. 31-38.
- Maelfait, J.-P., K. Desender. 1990. Possibilities of short-term carabid sampling for site assessment studies. *In* The role of ground beetles in ecological and environmental studies. Ed. N. E. Stork, Intercept, Hampshire. Pp. 217-225.
- Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton: Princeton University Press. 179 pp.
- Margalef, R. 1958. Information theory in ecology. *General Systematics* **3**:36-71.
- Milne, L., M. Milne. 1995. National Audubon Society field guide to North American Insects and Spiders. Alfred A. Knopf, Inc. New York. 989 pp.
- Miyanishi, K., E. A. Johnson. 2001. Comment – a re-examination of the effects of fire suppression in the boreal forest. *Canadian Journal of Forest Research*. **31**: 1462-1466.
- Nagy, B. R., B. G. Warner. 1999. Recent change in a degraded raised bog in southern Ontario, Canada. *Ecologie*. **30**: 71-77.
- National Research Council. 2000. Ecological indicators for the nation. Washington, D.C.: National Academy Press. 180 pp.
- Neve, G. 1994. Influence of temperature and humidity on the activity of three *Carabus* species. *In* Carabid beetles: ecology and evolution. Eds. K. Desender, M. Dufrêne, M. Loreau, M.L. Luff, J.-P. Maelfait. Kluwer Academic publishers, Netherlands. Pp 189-192.
- Nguyen-Xuan, T., Y. Bergeron, D. Simard, J. W. Fyles, D. Pare. 2000. The importance of forest floor disturbance in the early regeneration patterns of the boreal forest of western

and central Quebec: a wildfire versus logging comparison. *Canadian Journal of Forest Research*. **30**: 1353-1364.

Niemela, J. 1990. Spatial distribution of carabid beetles in the Southern Finnish Taiga: the question of scale. In: *The role of ground beetles in ecological and environmental studies*. Intercept, Andover, UK. 143-155.

Niemela, J. 1997. Invertebrates and boreal forest management. *Conservation Biology*. **11**: 601-610.

Niemela, J. 1999. Management in relation to disturbance in the boreal forest. *Forest Ecology and Management*. **115**: 127-134.

Niemela, J., D. Langor, J. Spence. 1993. Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. *Conservation Biology*. **7**: 551-561.

Niemela, J., J. R. Spence, D. Langor, Y. Haila, H. Tukia. 1994a. Logging and boreal ground-beetle assemblages on two continents: implications for conservation. In: *Perspectives in insect conservation*. Eds. Gaston, K., M. Samways. Intercept Publications, Andover, 29-50 pp.

Niemela, J. H. Tukia, E. Halme. 1994b. Patterns of carabid diversity in Finnish mature taiga. *Annales Zoologici Fennici*. **31**: 123-129.

Nimis, P. L., S. Martellos. 2001. Testing the predictivity of ecological indicator values. A comparison of real and 'virtual' relevés of lichen vegetation. *Plant Ecology*. **157**: 165-172.

Noss, R. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* **4**: 335-364.

Nyilas, I. 1994. Habitat distribution of *Brachinus* species in alkaline and salty steppes and loess grassland (Coleoptera: Carabidae). In *Carabid beetles: ecology and evolution*. Eds. K. Desender, M. Dufrêne, M. Loreau, M.L. Luff, J.-P. Maelfait. Kluwer Academic publishers, Netherlands. Pp 193-199.

Oliver, I., A. J. Beattie. 1993. A possible method for the rapid assessment of biodiversity. *Conservation Biology*. **7**: 562-568.

Paquin, P., N. Duperre. 2001. Beetles of the boreal forest: a faunistic survey carried out in western Quebec. *Proceedings of the Entomological Society of Ontario*. **132**: 57-98.

Pearce, J. L., L. A. Venier, J. McKee, J. Pedlar, D. McKenney. 2003. Influence of habitat and microhabitat on carabid (Coleoptera: Carabidae) assemblages in four stand types. *The Canadian Entomologist*. **135**: 337-357.

- Pearson, D. L. 1995. Selecting indicator taxa for the quantitative assessment of biodiversity. *In* Biodiversity measurement and estimation. *Ed.* D. L. Hawksworth. Chapman and Hall, London, UK. Pp. 75-79.
- Pereg, D., S. Payette. 1998. Development of black spruce growth forms at the treeline. *Plant Ecology*. **138**: 137-147.
- Perry, D. J., J. Bousquet. 2001. Genetic diversity and mating system of post-fire and post-harvest black spruce: an investigation using codominant sequence-tagged-site (STS) markers. *Canadian Journal of Forest Research*. **31**: 32-40.
- Pielou, E. C. 1975. Ecological diversity. Wiley, New York. London. Pp. 165.
- Pielou, E. C. 1984. The interpretation of ecological data. A primer on classification and ordination. Wiley, New York.
- Pitkanen, S. 1998. The use of diversity indices to assess the diversity of vegetation in managed boreal forests. *Forest Ecology and Management*. **112**: 121-137.
- Rainio, J., Niemela, J. 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodiversity and Conservation*. **12**: 487-506.
- Richardson, R. J., N. J. Holliday. 1982. Occurrence of carabid beetles (Coleoptera: Carabidae) in a boreal forest damaged by fire. *The Canadian Entomologist*. **114**: 509-514.
- Rosenberg, D. M., H. V. Danks, D. M. Lehmkuhl. 1986. Importance of insects in environmental impact assessment. *Environmental Management*. **10**: 773-783.
- Roy, V., J. C. Ruel, A. P. Plamondon. 2000. Establishment, growth and survival of natural regeneration after clearcutting and drainage on forested wetlands. *Forest Ecology and Management*. **129**: 253-267.
- Safford, L. O., J. C. Bjorkbom, J. C. Zasada. 1990. *Silvics of North America*, Vol.1. USDA For. Ser., Washington D. C. Agric. Handb.
- Scott, G. A. 2001. Soils and vegetation: A laboratory manual for the geography of soils and vegetation (23.2203/6). University of Winnipeg Printing Services. Pp 47-48.
- Shay, J., D. Kunec, B. Dyck. 2001. Short-term effects of fire frequency on vegetation composition and biomass in mixed prairie in south-western Manitoba. *Plant Ecology*. **155**: 157-167.
- Sims, H. P., D. Mueller-Dombois. 1968. Effect of grass competition and depth to water table on height growth of coniferous tree seedlings. *Ecology*. **49**: 597-603.

Smith, C. K., M. R. Coyea, A. D. Munson. 2000. Soil carbon, nitrogen, and phosphorus stocks and dynamics under disturbed black spruce forests. *Ecological Applications*. **10**: 775-788.

Soil Classification Working Group. 1998. The Canadian system of soil classification. Agriculture and Agri-Food Canada Publ. No. 1646. Third Edition. 187 pp.

Sousa, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics*. **15**: 353-391.

Southwood, T. R. E. 1978. *Ecological methods: with particular reference to the study of insect populations*. Chapman and Hall, New York. 524 pp.

Spence, J. R. 2001. The new boreal forestry: adjusting timber management to accommodate biodiversity. *Trends in Ecology and Evolution*. **16**: 591-593.

Spence, J. R., J. K. Niemela. 1994. Sampling carabid assemblages with pitfall traps: the madness and the method. *Canadian Entomologist* **126**: 881-894.

Spence, J. R., D. W. Langor, J. Niemela, H. A. Carcamo, C. R. Currie. 1996. Northern forestry and carabids: the case for concern about old-growth species. *Annales Zoologici Fennici*. **33**: 173-184.

Spence, J. R., D. W. Langor, H. E. J. Hammond, G. R. Pohl. 1997. Beetle abundance and diversity in a boreal mixed-wood forest. In: *Forests and Insects*. Eds. Watt, A. D., N. E. Stork, M. D. Hunter. Chapman & Hall, London. 287-301 pp.

Ter Braak, C. J. F., P. Smilauer. 2002. CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5). New York, Microcomputer Power, 500pp.

Terrell-Nield, C. E. 1990. Distribution of leg-colour morphs of *Pterostichus madidus* (F.) in relation to climate. In *The role of ground beetles in ecological and environmental studies*. Ed. N. E. Stork, Intercept, Hampshire. Pp. 39-49.

Thiele, H.-V. 1977. *Carabid beetles in their environments. A study on habitat selection by adaptations in physiology and behavior*. Springer – Verlag, Berlin. xvii+369 pp.

Thomas, A. W. 2001. Moth diversity in northeastern, North American, red spruce forest. Natural Resources Canada Information Report M-X-210E. 42pp.

Thomas, G. 2000. Bio-DAP: Ecological diversity and its measurement. A biodiversity analysis package. Downloaded from <http://nhsbig.inhs.vivc.edu/www/populations.html>.

Vance, E. D., F. S. Chapin. 2001. Substrate limitations to microbial activity in taiga forest floors. *Soil Biology and Biochemistry*. **33**: 173-188.

Villani, M. G. L. L. Allee, A. Díaz, P. S. Robbins. 1999. Adaptive strategies of edaphic arthropods. *Annual Review of Entomology*. **44**: 233-256.

Ward, P. C., A. G. Tithecott. 1993. Impact of fire management on the boreal landscape of Ontario. Ministry of Natural Resources, Aviation, Flood and Fire Management Branch Publ. 305, Sault Ste. Marie, Ont.

Ward, P. C., W. Mawdsley. 2000. Fire management in the boreal forests of Canada. In *Fire, climate change, and carbon cycling in the boreal forest*. Eds. E. S. Kasischke, B. J. Stocks. Springer, New York. Pp. 66-84.

Weber, M. G., S. W. Taylor. 1992. The use of prescribed fire in the management of Canada's forested lands. *The Forestry Chronicle*. **68**: 324-334.

Wierzchowski, J., M. Heathcott, M. D. Flannigan. 2002. Lightning and lightning fire, central cordillera, Canada. *International Journal of Wildland Fire*. **11**: 41-51.

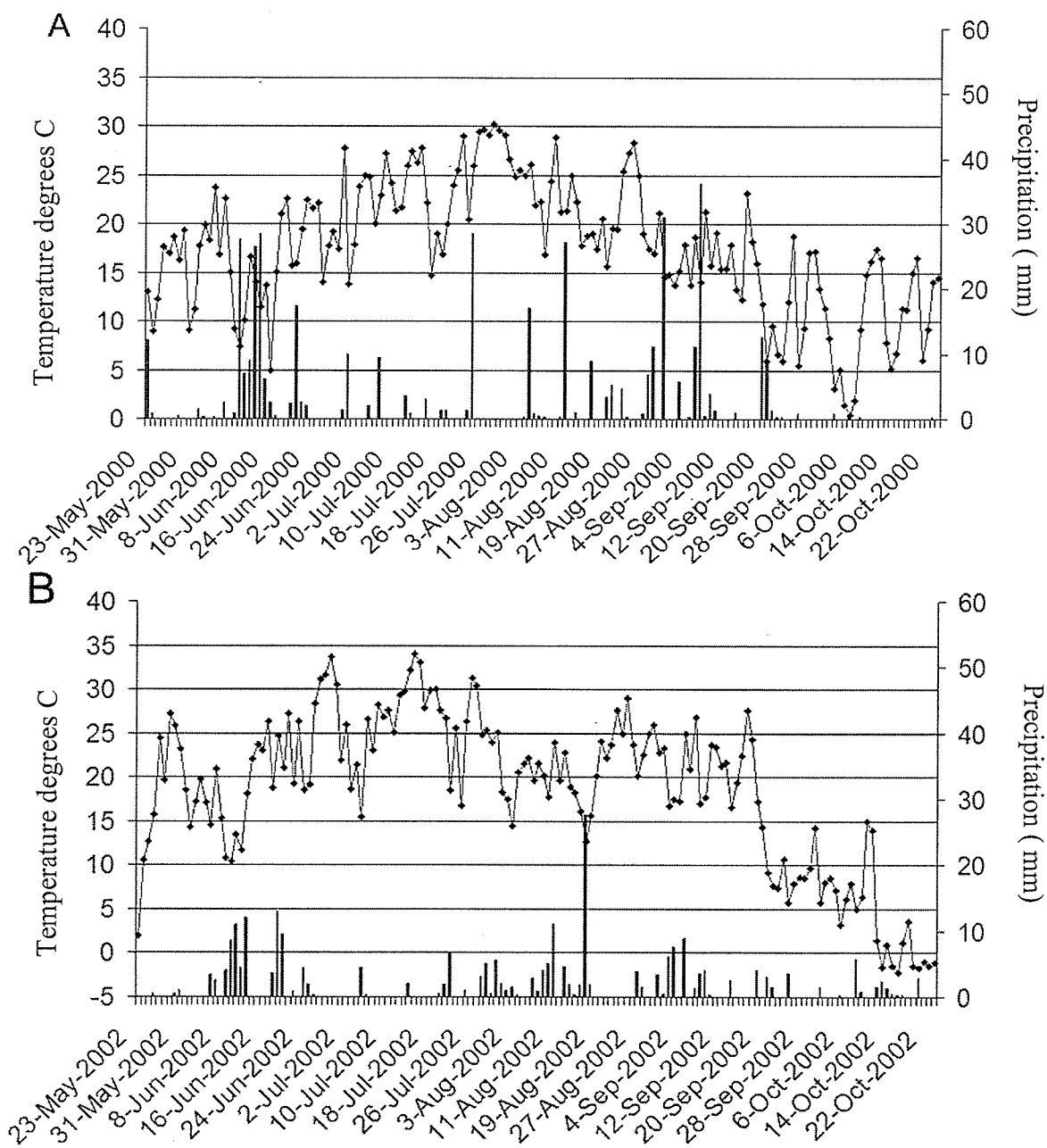
Wilkinson, L. 1998. SYSTAT: the system for statistics. Systat Inc. Evanston, Illinois.

Williams, P. H., K. J. Gaston. 1994. Measuring more of biodiversity: can higher-taxon richness predict wholesale species richness? *Biological Conservation*. **67**: 211-217.

Wilson, M. V., A. Shmida. 1984. Measuring beta diversity with presence-absence data. *Journal of Ecology*. **72**: 1055-1064.

Zoladeski, C. A., R. J. Delorme, G. M. Wickare, I. G. W. Corns, and D. T. Allan. 1998. Forest ecosystem toposequences in Manitoba. Canadian Forest Service Special Report 12. 63 pp.

Appendix 1. Climate data for A) 2000 and B) 2002. Daily maximum temperatures on the first Y-axis is represented by lines and total daily precipitation on the second Y-axis is represented by bars.



Appendix 2. Species list with authorities and percent cover of herbaceous species collected in 2000. Mean number of percent cover were calculated from 20 1m X 1m quadrats.

Herbaceous Species	B29 1P1	B29 1P2	B29 2P2	B83 2P1	B83 2P2	B83 3P1	B83 3P2	B99 1P1	B99 1P2	H57 1P1	H57 1P2	H83 1P1	H83 1P2	H83 2P1	H83 2P2	H99 1P1	H99 1P2	Sum
<i>Achillea millefolium</i> L.	0	0	0	0	0	0	0	0	0	0	0	0.47	0.12	0	0	0	0	0.59
<i>Actaea rubra</i> (Ait.) Willd.	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0.1
<i>Andromeda polifolia</i> L.	0	0	0	0	0.2	0	0.15	0	0	0	0	0	0	0	0	0	0	0.35
<i>Anemone canadensis</i> L.	0	0	0	0	0	0	0	0	0	0	0	0.45	0.75	0	0	0	0	1.2
<i>Aquilegia canadensis</i> L.	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0.2
<i>Aralia hispida</i> Vent.	0	0	0	0	0	0	0	0.95	0.5	0	0	0	0	0	0	0	0	1.45
<i>Aralia nudicaulis</i> L.	0.25	0	2.45	0	0	0.3	0	0.1	0.7	0.3	0	0	0.4	0	0.45	0.2	0	5.15
<i>Arctostaphylos uva-ursi</i> (L.) Spreng.	0	0	2	0	0	0	0	0	0	0.15	0	0	0	0.55	0	0	0	2.7
<i>Aster ciliolatus</i> Lindl.	0	0	0	0.67	0	0	0	0.3	0.25	0	0	12.5	2.3	0	1.5	0	0	17.52
<i>Aster</i> spp.	0	0	0	0.05	0	0	0	0.15	0.01	0	0	0	2.1	0	0	0	0	2.32
<i>Athyrium filix-femina</i> (L.) Roth	0	0	0	0	0	0	0	0	0	0	0	0	0.8	0	0	0	0	0.8
<i>Aulacomnium palustre</i> (Hedw.) Schwaegr.	0	0	0	3.75	0.9	0.2	3.7	0	0	0	0	0	0	0	0	0	0	8.55
<i>Betula glandulosa</i> Michx.	0	0	0	0	0	0	0.05	0	0	0	0	0	0	0	0	0	0	0.05
<i>Betula papyrifera</i> Marshall (seedlings)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05	0	0.02	0.07
<i>Bidens cernua</i> L.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Calla palustris</i> L.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Carex</i> spp.	0	0.55	0	0	0	0	0	1.2	5.51	0	0	0	0	0.25	0	0	0	7.51
<i>Chamaedaphne calyculata</i> (L.) Moench	0	0	0	0	0.65	0	0	0	0	0	0	0	0	1.55	0.2	0	0.2	2.6
<i>Chimaphila umbellata</i> (L.) W. Bart.	0.15	0	0.05	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0.21
<i>Cirsium arvense</i> (L.) Scop.	0	0	0	0	0	0	0	0.05	2	0	0	2.65	0.45	0	0.2	0	0	5.35
<i>Cladonia mitis</i> (Sandst.) Hustich	0	0	2.75	0	0	0	0	0	0	0.6	0	0	0	0	2.35	0	0	5.7
<i>Cladonia rangiferina</i> (L.) Nyl.	0	0.1	4.7	0.21	0.15	0.31	0.52	0.2	0	5.46	1.07	0	0	2.7	3.86	1.6	0.11	20.99
<i>Cladonia stellaris</i> (Opiz) Brodo.	0	0	0	0	0	0.05	0	0	0	0	0	0	0	0	0	0	0	0.05
<i>Cladonia borealis</i> S. Stenroos	0	0	0.05	0.15	0	0.14	0.02	0	0	0	0.01	0	0	0.02	0.01	0	0	0.4
<i>Cladonia</i> spp.	0	0	0.01	1.16	0.05	0.7	0.27	0	0	0.85	0.69	0	0	0.1	0	0	0	3.83
<i>Clintonia borealis</i> (Ait.) Raf.	0.1	0	0.25	0	0	0.5	0	0	0	0.5	0	0	0	0	1.25	0	0.15	2.75
<i>Coptis trifolia</i> (L.) Salisb.	0.16	0.21	0.81	0	0	0	0	0	0	0.6	0	0	0	0	0	0.16	0.32	2.36
<i>Cornus canadensis</i> L.	3.85	6.8	6.15	1.3	0.35	1.4	0.4	6.3	0.26	0	0	0	0	0.55	2.55	0.91	0	30.82
<i>Cornus stolonifera</i> Michx.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Corydalis sempervirens</i> (L.) Pers.	0	0	0	0	0	0	0	0	0	0	0	0.15	0.01	0	0	0	0	0.16
<i>Corylus cornuta</i> Marsh.	0	0	0	0	0	0	0	0.01	0.39	0	0	0	0	0	0	0	0	0.4
<i>Crustose lichen</i>	0	0	0	0	0	0	0	0	0	0	0	0.35	0.15	0	0	0	0	0.5
<i>Cypripedium acaule</i> Aiton	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Dicranum</i> spp.	9.9	6.2	8.95	0	0.16	2.86	0	0	0	6.3	4.76	0	0	0.21	0.66	2.75	0.85	43.6
<i>Diervilla lonicera</i> Mill.	0	0	0.05	0	0	0.6	0	0	0	0	0	0	0	0	0	0	0	0.65
<i>Dracocephalum paviflorum</i> Britt.	0	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0.01
<i>Elymus canadensis</i> L.	0	0	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0.01
<i>Epilobium angustifolium</i> L.	0	0	0.1	0.5	0	0.26	0.41	3	3.35	0	0	4.6	0.55	0	0.9	0.35	0.3	14.32
<i>Epilobium glandulosum</i> Lehm.	0	0	0	0	0	0	0	0	0.71	0	0	0	0	0	0	0	0	0.71
<i>Equisetum arvense</i> L.	0	0	0	0	0	0	0	0	0	0	0	0	0	0.4	1.05	0	0	1.45
<i>Equisetum fluviatile</i> L.	0	0	0	0	0.02	0	0	0	0	0	0	0	0	0	0	0	0	0.02
<i>Equisetum pratense</i> Ehrh.	0	0	0	0	0	0	0	0	0	0.01	0	0	0.1	0	0	0	0	0.11
<i>Equisetum sylvaticum</i> L.	0	0.55	0.2	0.06	0.02	0.16	0	4.4	4.23	0.72	0	0.75	0.7	0.95	0.8	0.51	0.1	14.15
<i>Foliose lichen</i>	0	0	0.1	0	0.3	0.55	0	0	0	0.35	0	0	0	0	0	0	0	1.3
<i>Fragaria virginiana</i> Duchesne	0	0	0.05	1.25	0	0	0	0	0.3	0	0	14.95	1.8	0.55	1.3	0	0.57	20.77
<i>Fungus</i>	0.09	0.57	0.15	0.04	0	0	0	0.01	0	0	0	0	0	0.05	0	0	0	0.91
<i>Galium boreale</i> L.	0	0	0	0.01	0	0	0	0	0.15	0	0	1.56	0.55	0	0	0	0	2.27
<i>Galium triflorum</i> Michx.	0	0	0	0	0	0	0	0	0.75	0	0	0	0.35	0	0	0	0	1.1
<i>Gaultheria hispida</i> (L.) Muhl.	0.01	1.25	0.3	0	0	0	0	0.01	0	0.31	0.09	0	0	0	0.05	0.26	0.35	2.63
<i>Goodyera repens</i> (L.) R.Br.	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0.01
<i>Grass</i> spp.	0.01	0.26	0.06	0.06	3.51	0.76	3.4	15.25	1.7	0.87	1.37	13.3	18.46	3.15	5.2	1.06	2.43	70.85
<i>Gymnocarpium dryopteris</i> (L.) Newman	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01
<i>Hylacomium splendens</i> (Hedw.) Schimp	0.6	1.4	1.15	0	0	0	0	0	0	0.3	0	0	0	0	0	0	0	3.45
<i>Kalmia polifolia</i> Wangenh.	0	0	0	0	0	0.01	0	0	0	0	0.01	0	0	0	0	0	0	0.02
<i>Larix laricina</i> (Du Roi) K. Koch (seedlings)	0	0	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0.01
<i>Lathyrus ochroleucus</i> Hook.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3
<i>Lathyrus venosus</i> Muhl.	0	0	0.15	0.56	0	0.01	0	0	0.25	0	0	0.65	0.05	0	0.25	0	0	1.92
<i>Ledum groenlandicum</i> Oeder	0	0.55	0	0	1.55	0	0.4	1.25	0.2	0.2	0	0	0	2.55	0.8	6.2	2	15.7
<i>Linnaea borealis</i> Gronov.	0.15	0.1	1.1	1.4	0	0.11	0	0	0.15	0.12	0	0	0	0	0.4	0	0	3.53
<i>Lycopodium annotinum</i> L.	0.2	3.4	1.1	0	0	0	0	0	0.25	0.2	0	0	0	0	0.65	0	0	5.8

Appendix 2. (Continued)

	B29 1P1	B29 1P2	B29 2P2	B83 2P1	B83 2P2	B83 3P1	B83 3P2	B99 1P1	B99 1P2	H57 1P1	H57 1P2	H83 1P1	H83 1P2	H83 2P1	H83 2P2	H99 1P1	H99 1P2	Sum
Herbaceous Species																		
<i>Lycopodium obscurum</i> L.	0	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05
<i>Lycopus uniflorus</i> Michx.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1
<i>Maianthemum canadense</i> Desf.	1.01	1.15	3.71	1.12	0	0.21	0.11	0	0	0.21	1.17	0.25	0.95	0.7	0.35	0.1	0	11.04
<i>Marchantia</i> spp	0	0	0	0	0	0	0	0.9	2.4	0	0	0	0	0	0	0	0	3.3
<i>Melampyrum lineare</i> Lam.	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01
<i>Monotropa uniflora</i> L.	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01
<i>Moss</i> spp	0	0.3	0	0.5	0.05	0.31	4.35	3	15.45	0.4	0	0.15	0.5	0.25	0.2	0	0	25.46
<i>Oxycoccus microcarpus</i> Turcz.	0	0	0	0	0.5	0	0.15	0.15	0	0.2	0.18	0	0	1.26	0.26	0.15	0.1	2.95
<i>Peltigera</i> spp	0	0	0	0.25	0	0	0	0	0	0	0	0	0	0	0	0	0	0.25
<i>Petasites palmatus</i> (Ait.) Gray	0	0	0	1.15	0	0	0	1.2	2.65	0.01	0	0.35	0.1	0	0	0	0	5.46
<i>Petasites sagittatus</i> (Pursh) A. Gray	0	0	0	0	0	0	0	0	0	0	0	1.55	2.15	0	0	0	0	3.7
<i>Picea mariana</i> (Mill.) BSP. (seedlings)	0	0.06	0.21	0.06	0.47	0	0	0.01	0	0	0	0.05	0.05	0	0.1	0	0.01	1.02
<i>Pinus banksiana</i> Lamb. (seedlings)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.03	0.03
<i>Pleurozium schreberi</i> (Brid.) Mitt	45.7	35.25	31.1	0.45	0.4	0.2	0	0	0.15	24.2	27.9	0.6	0.65	2.1	0.35	7.85	2.2	179.1
<i>Polygonum-like</i> unknown	0	0	0	0	0	0	0	1.15	0.1	0	0	0	0	0.5	0	0	0	1.75
<i>Polytrichum</i> spp	0.1	3.35	1.56	0.83	4.16	17.36	17.9	1.4	1.05	0	0	0	0	0.7	2.25	0.05	0	50.71
<i>Populus tremuloides</i> Michx. (seedlings)	0.2	0	0.01	0.15	0	0.11	0	0	0.16	0.1	0	0	0	0	0	0	0	0.73
<i>Potentilla palustris</i> (L.) Scop.	0	0	0	0	0.05	0	0	0	0	0	0	0	0	0.15	0.45	0	0.1	0.75
<i>Potentilla tridentata</i> Ait.	0	0	0.32	0	0.02	1.15	0.7	0	0	0	0	0	0	0.4	0	0	0	2.59
<i>Prunus pensylvanica</i> L.	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0.01
<i>Pteridium</i>	0	0	0	0	0	1	0	0	0	0	0	0	0.2	0	0.6	0	0	1.8
<i>Ptilium crista-castrensis</i> (Hedw.) De Not.	16.2	2.35	2.5	0	0	0	0	0	0	1.7	0	0	0	0	0	0	0	22.75
<i>Pyrola</i> spp	0	0	0.01	0	0	0	0.1	0	0	0.2	0	0	0	0	0	0	0.01	0.32
<i>Pyrola virens</i> Schreb.	0	0	0	0	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0.2
<i>Ribes</i> spp	0	0	0	0	0	0	0.1	0.25	1.25	0	0	0.35	0.1	0	0	0.02	0.05	2.12
<i>Rosa acicularis</i> Lindl.	0	0	0.15	0.21	0	0.4	0	0	0.01	0.05	0	1.15	0.35	0	0.5	0.31	0.21	3.34
<i>Rubus acaulis</i> Michx.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Rubus chamaemorus</i> L.	0	0	0	0	0	0	0	0	0	0	1.13	0	0	0	0	0	0	1.13
<i>Rubus idaeus</i> L.	0	0	0	0	0	0	0	0.8	2.4	0	0	0.8	0.25	0.55	0.15	0.35	0.11	5.41
<i>Rubus pubescens</i> Raf.	0.05	0.35	0.25	4.6	0	0.25	0.01	0	0.15	0.7	0	1.8	5.6	0.55	1.1	0.66	0.5	16.57
<i>Salix</i> spp	0	0	0	0	0	0	0.41	0.1	0.35	0	0	0	0	0	0	0	0	0.86
<i>Sanicula marilandica</i> L.	0	0	0	0	0	0	0	0	0	0	0	1.7	0.25	0	0	0	0	1.95
<i>Scirpus cyperinus</i> (L.) Kunth	0	0	0	0	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0.01
<i>Smilacina trifolia</i> (L.) Desf.	0	0	0	0	0.05	0	0.1	0.35	0.85	0.1	0.2	0.2	0.35	0.67	0.7	0	0	3.57
<i>Solidago</i> spp	0	0	0	0	0	0	0	0.1	0.05	0	0	2.5	0.8	0	0	0	0	3.45
<i>Sonchus arvensis</i> L.	0	0	0	0	0	0	0	0.05	0.3	0	0	0	0	0	0	0	0	0.35
<i>Sphagnum</i> spp	0	7.41	2.05	0	22.4	6.65	7.2	0.1	0.4	17.7	39.1	0	0	40.75	28.1	0.3	3.55	175.71
<i>Spiraea alba</i> Du Roi	0	0	0.05	0	0	0.15	0.31	0	0	0	0	0	0	0	0.06	0	0	0.57
<i>Stereocaulon tomentosum</i> E. Fries	0	0	0	0	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0.05
<i>Taraxacum officinale</i> (Dahlst.) Raunk.	0	0	0	0	0	0	0	0.5	1.5	0	0	0.95	0	0	0	0	0	2.95
<i>Thalictrum dasycarpum</i> Fisch. & Avé-Lall.	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0	0.01
<i>Thalictrum venulosum</i> Trel.	0	0	0	0.01	0	0	0	0	0	0	0	0.7	0.26	0	0	0	0	0.97
<i>Trientalis borealis</i> (Hook.) Hultén	0.56	1.25	0.4	0	0	0.2	0	0	0	0.11	0	0	0.05	0	0.3	0.05	0.01	2.93
<i>Typha latifolia</i> L.	0	0	0	0	0.65	0	3.15	0	0.26	0	0	3.3	0.25	0.85	1.65	0	0.15	10.26
Unknown 1	0	0	0	0.45	0	0	0	0	0	0	0	0	0	0	0	0	1	1.45
<i>Vaccinium angustifolium</i> Ait.	0	0.25	1.7	0.05	0.66	0.72	0.66	0	0	0.01	0.06	0	0	1.61	2.1	0	0	7.82
<i>Vaccinium myrtilloides</i> Michx.	0.45	0.56	1.5	0	0.1	0	0.05	0.65	0	0.01	0	0	0	0	0	3.01	0.46	6.79
<i>Vaccinium vitis-idaea</i> L.	0.02	0.21	0.01	0	0.8	0	0.25	0.16	0.15	1.42	1.52	0	0.1	0	0.22	0.01	0.48	4.87
<i>Vicia americana</i> Muhl.	0	0	0	0	0	0	0	0	0.12	0	0	0.45	0	0	0	0	0	0.57
<i>Viola adunca</i> (Hook.) Fern	0	0	0	0.35	0	0.1	0.17	0	0	0.06	0	0	0	0	0	0	0	0.68
<i>Viola</i> spp	0	0.01	0	0.2	0.1	0	0	0.6	0.41	0	0	0	0.66	0	1.56	0	0.15	3.69
<i>Woodsia ilvensis</i> (L.) R. Br.	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01
Grand Total	99.47	100.05	100.02	100.02	97.22	100.09	100.35	100.05	100.13	100.25	100.31	101.09	96.37	99.97	99.46	99.87	100.9	1695.62

Appendix 3. Species list with authorities and percent cover of shrub species collected in 2000. Mean numbers of percent cover were calculated from 15 2m X 2m quadrats.

Shrub Species	B29 1P1	B29 1P2	B29 2P2	B83 2P1	B83 2P2	B83 3P1	B83 3P2	B99 1P1	B99 1P2	H57 1P1	H57 1P2	H83 1P1	H83 1P2	H83 2P1	H83 2P2	H99 1P1	H99 1P2	Total
<i>Abies balsamifera</i> (L.) Mill.	0	0	0	0	0	0	0	0	0	0.02	0	0	0	0	0	0	0	0.02
<i>Alnus crispa</i> (Vill.) DC.	0	1.25	0	0	0	0	0	0.25	0.06	0	0	0	0	0	11.7	2.2	0.75	16.21
<i>Alnus rugosa</i> (DuRoi) Spreng.	0	0	0	0.15	0.35	0	0	0	0	0.21	0	0	0	0.56	0	0	0	1.27
<i>Andromeda polifolia</i> L.	0	0	0	0	1.01	0	0.05	0	0	0	0	0	0	0.1	0	0	0	1.16
<i>Apocynum androsaemifolium</i> L.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.35	0	0.35
<i>Aralia hispida</i> Vent.	0	0	0	0	0	0	0	0.35	0.5	0	0	0	0	0	0	0	0	0.85
<i>Aralia nudicaulis</i> L.	0.2	0	0.9	1.05	0	0.35	0	0	0	0.15	0	0	0.3	0	0	1	0	3.95
<i>Betula glandulosa</i> Michx.	0	0	0	0	3.5	0	3.75	0	0	0	0	0	0	0.4	1.15	0	0.45	9.25
<i>Betula papyrifera</i> Marsh.	0	0	0	0	0	0	0	1	0	0	0	0	0	1.75	0.75	0	0	3.5
<i>Chamaedaphne calyculata</i> (L.) Moench	0	0	0	0	5.51	0	1.25	0.15	0	0.01	0.25	0	0	8.55	8.3	0	0	24.02
<i>Cornus stolonifera</i> Michx.	0	0	0	0	0	0	0	0	0	0.01	0	2.7	2.1	0	0	0	0	4.81
<i>Corylus cornuta</i> Marsh.	0	0	0	0	0	0	0	0	0	0	0	0.35	0.25	0	0	0.1	0	0.7
<i>Diervilla lonicera</i> Mill.	0	0	0	2.5	0	5.45	0	0.15	0	0	0	0	0	0	0	0	0	8.1
<i>Epilobium angustifolium</i> L.	0	0	0	0	0	0.02	0	0	0	0	0	0	0	0	0	0	0	0.02
<i>Fraxinus pennsylvanica</i> Marsh.	0	0	0	0	0	0	0	0	0	0	0	0.5	0	0	0	0	0	0.5
<i>Gymnocarpium dryopteris</i> (L.) Newman	0	0	0	0	0	0.05	0	0	0	0	0	0	0	0	0	0	0	0.05
<i>Kalmia polifolia</i> Wangenh.	0	0	0	0	0	0	0	0	0	0	0.01	0	0	0	0.05	0	0	0.06
<i>Larix laricina</i> (Du Roi) K. Koch	0	0	0	0	0.05	0	0	0	0	0	0.1	0	0	0.2	0.45	0	0	0.8
<i>Ledum groenlandicum</i> Oeder	0.01	2.9	0.1	0	1.8	0.01	0	9.5	1.25	6.26	2.61	0	0	7.85	3.85	4.15	5.16	45.45
<i>Picea mariana</i> (Mill.) BSP.	0.3	0	0.2	0.95	2.45	1.9	0.65	0	0	0.61	2.05	0.8	0.9	0.5	0.4	0.15	0.15	12.01
<i>Pinus banksiana</i> Lamb.	0	0	0	0	0.8	0.2	0.1	0	0	0	0	0	0	0	0.25	0	0	1.35
<i>Populus tremuloides</i> Michx.	0.05	0.03	0.15	0	0	0.2	0.2	2.52	1.32	0.01	0	0.9	0.2	0.15	0.16	0	0	5.89
<i>Prunus pensylvanica</i> L.	0	0	0	0.3	0	0	0.05	0.05	0.06	0	0	0	0	0.05	0	0	0.05	0.56
<i>Prunus virginiana</i> L.	0	0	0	0	0	0	0	0	0	0	0	0	0.55	0	0	0	0	0.55
<i>Ribes</i> spp	0	0	0	0	0	0	0	0.2	1	0	0	0.1	0.07	0.05	0.01	0	0	1.43
<i>Rosa acicularis</i> Lindl.	0.02	0	0.01	0.5	0	0.05	0	0	0.76	0	0	0.56	1.27	0	0	0.7	0.15	4.02
<i>Rubus idaeus</i> L.	0	0	0	0.36	0	0	0	4.1	2.9	0	0	0.05	0.85	0	0	0.05	0.1	8.41
<i>Salix</i> spp	0	0.2	0	0	3.25	0.11	4.15	0.75	0.7	0.01	0.01	2.65	4.25	0	0	0	0	16.08
<i>Spiraea alba</i> Du Roi	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.01
<i>Vaccinium angustifolium</i> Ait.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0.1
<i>Vaccinium myrtilloides</i> Michx.	0.75	0.25	0.26	0	0	0.03	0.15	0	0	0.05	0	0	0	0	0	0.55	0.35	2.39
<i>Viburnum edule</i> (Michx.) Raf.	0	0	0	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05
<i>Viburnum opulus</i> L.	0	0	0	0	0	0	0	0	0	0	0	0.3	0.4	0	0	0	0	0.7
<i>Viburnum rafinesquianum</i> Schultes	0	0	0	0	0	0	0	0	0	0	0	2.05	2.65	0	0.05	0	0	4.75
Total Mean Percent Cover	0.09	0.31	0.11	0.39	1.25	0.56	0.69	1.27	0.57	0.49	0.34	0.73	0.92	1.34	1.82	0.61	0.48	179.37

Appendix 4. Species list of carabid beetles collected in 1999. Total catches for each plot.

Carabid Species	B29 1P1	B29 1P2	B29 2P2	B83 2P1	B83 2P2	B83 3P1	B83 3P2	B99 1P1	B99 1P2	H57 1P1	H57 1P2	H83 1P1	H83 1P2	H83 2P1	H83 2P2	H99 1P1	H99 1P2	Total
Agonum cupreum	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	2
Agonum cupripenne Say	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Agonum gratiosum	0	2	0	15	2	1	10	5	1	5	0	40	36	10	11	2	5	146
Agonum metallescens	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Agonum obsoletum Say	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Agonum placidum	0	0	0	0	0	0	0	0	0	1	0	2	0	0	6	0	1	10
Agonum retracts	0	4	0	9	0	2	0	1	0	2	0	1	1	2	1	0	0	23
Agonum simile Kirby	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Agonum tlm	0	0	0	0	0	0	0	0	0	0	0	4	4	0	0	0	0	8
Agonum thoreyi Dejean	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Amara impunctatus/littoralis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Amara lunicollis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Bembidion fortetistratum	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	2
Bembidion mutatum Gemminger & Herold	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2
Bembidion praticola	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Calathus ingratus	5	3	15	0	0	2	0	0	5	2	0	0	0	0	1	2	0	35
Calosoma calidum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Carabus maeander	0	0	0	0	0	0	0	0	0	0	0	2	11	0	0	0	0	13
Carabus serratus	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	3
Carabus taedatus	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Chlaenius alteratus Horn	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Chlaenius sericeus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Cymindis cribricollis	0	0	1	0	0	0	0	0	0	2	0	0	0	1	0	0	0	1
Cymindis unicolor Kirby	1	2	1	0	0	0	0	0	0	2	5	0	0	0	0	1	1	13
Dyschirius globulosus Say	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2
Harpalus fulvibris	0	2	0	0	0	0	0	0	0	0	0	2	1	0	0	0	1	6
Harpalus innocuus LeConte	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
Harpalus laevipes Zetterstedt	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Harpalus laticeps	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	2	1	6
Harpalus nigrifrons C.R. Sahlberg	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	6
Harpalus ochropus Kirby	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Harpalus reversus Casey	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2
Harpalus solitarius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
Harpalus somnulentus	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	2
Harpalus sp.	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	3
Larva	1	0	1	0	3	0	1	0	0	0	1	5	4	0	0	4	6	26
Notiophilus aquaticus L.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Notiophilus intermedius	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Notiophilus semistriatus	0	0	0	0	0	2	0	0	0	1	1	0	0	4	2	0	0	10
Patrobis foveicollis	0	0	0	2	0	0	0	0	0	0	0	3	1	0	0	0	0	6
Patrobis longicornis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Platynus decentis	1	0	0	1	0	0	0	0	0	10	0	0	3	0	0	0	0	15
Pterostichus adstrictus	37	23	30	3	0	1	0	7	16	19	0	0	0	0	2	48	17	203
Pterostichus femoralis (Kirby)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Pterostichus lucublandus	0	0	1	0	0	0	0	0	0	0	0	13	1	1	3	2	0	21
Pterostichus melanarius Illiger	0	0	0	0	0	0	0	0	0	0	0	6	1	0	0	0	0	7
Pterostichus patruelis	0	1	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	5
Pterostichus pennsylvanicus	0	4	6	8	4	12	4	1	0	4	1	18	4	20	57	1	5	149
Pterostichus punctatissimus	14	5	20	0	0	0	0	0	0	8	9	0	0	1	1	8	10	76
Sericoda quadripunctatum	0	0	0	0	0	0	0	9	29	0	0	0	0	0	0	0	0	38
Sphaeroderus lecontei	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	3
Sphaeroderus nitidicollis	0	3	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	6
Syntomus americanus	0	0	0	0	1	3	1	1	0	0	0	31	1	4	9	2	0	53
Synuchus impunctatus	7	5	3	2	1	0	0	1	4	16	2	5	18	3	15	14	17	113
Trechus apicalis	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3
Trechus crassiscapus	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Total	66	61	80	44	13	23	25	33	61	75	19	143	92	48	110	87	72	1052

Appendix 5. Species list of carabid beetles collected in 2000 with authorities. Total catches for each plot.

Carabid Species	B29 1P1	B29 1P2	B29 2P2	B83 2P1	B83 2P2	B83 3P1	B83 3P2	B99 1P1	B99 1P2	H57 1P1	H57 1P2	H83 1P1	H83 1P2	H83 2P1	H83 2P2	H99 1P1	H99 1P2	Total
Agonum affine Kirby	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Agonum canadense Goulet	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Agonum cupreum Dejean	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	2
Agonum gratiosum (Mannerheim)	0	1	0	11	15	2	6	19	6	13	0	32	28	4	16	15	1	169
Agonum lutulentum (LeConte)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Agonum metallescens (LeConte)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	58	0	58
Agonum placidum (Say)	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	3
Agonum retractum LeConte	0	2	2	6	1	7	1	3	2	5	0	0	0	0	1	1	1	32
Agonum superioris L.	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	2
Agonum tfm	0	0	0	0	0	0	0	0	0	0	0	3	3	0	2	11	0	19
Amara crassispina (LeConte)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Amara cupreolata Putzeys	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	2
Amara erratica (Duftschmidt)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Amara laticollis (Kirby)	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	4
Amara lunicollis Schiodte	0	0	0	0	0	0	0	2	12	0	0	0	0	0	1	0	0	15
Badister obtusus LeConte	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Bembidion fortetiatum (Motschulsky)	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	3
Bembidion praticola L.	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Blethisa multipunctata (L.)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2
Blethisa quadricollis Haldeman	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	3
Calathus ingratus Dejean	3	1	2	0	0	2	0	2	7	0	0	0	0	0	0	1	0	18
Calosoma calidum (Fabricius)	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	1	0	4
Carabus maeander Fischer	0	0	0	0	0	0	0	0	0	0	0	14	19	0	0	0	0	33
Carabus serratus Say	0	6	3	2	1	0	1	0	0	0	0	0	0	0	0	0	1	14
Carabus taedatus Fabricius	0	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Chlaenius pensylvanicus Say	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Chlaenius sericeus Forster	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Cymindis cricicollis Dejean	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	5
Dyschirius integer LeConte	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Elaphrus clairvillei Kirby	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Elaphrus fuliginosus Say	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	4
Harpalus egregius Casey	0	0	0	0	0	0	0	2	8	0	0	0	0	0	0	0	0	10
Harpalus solitarius Dejean	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Harpalus fulvibris Mannerheim	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	3
Harpalus laticeps LeConte	0	0	0	0	0	0	0	6	12	0	0	0	0	0	0	0	0	18
Harpalus pensylvanicus (DeGeer)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	2
Harpalus somnulentus Dejean	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Harpalus sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Larva	0	4	0	0	1	0	1	1	3	1	3	3	1	5	1	11	1	36
Loricera pilicornis (Fabricius)	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	1	0	6
Notiophilus intermedius L.	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	2
Notiophilus semistriatus Say	0	0	0	0	0	0	4	1	0	0	0	0	0	7	0	0	0	12
Patrobus foveocollis (Eschscholtz)	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	3
Patrobus longicornis (Say)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Platynus decentis (Say)	0	8	2	8	0	0	0	2	15	5	0	0	6	0	0	44	0	90
Platynus mannerheimi (Dejean)	0	10	0	0	5	0	0	0	1	0	0	0	0	1	1	10	0	28
Pterostichus adstrictus Eschscholtz	44	46	55	2	0	0	0	15	94	6	1	0	0	0	1	15	22	301
Pterostichus lucublandus (Say)	0	0	0	0	0	0	0	3	3	0	0	4	2	1	0	1	0	14
Pterostichus patruelis (Dejean)	0	0	0	0	0	0	0	1	0	0	0	0	1	1	3	1	0	7
Pterostichus pensylvanicus LeConte	3	15	20	14	4	17	3	4	5	0	0	12	26	11	25	3	2	164
Pterostichus punctatissimus (Randall)	12	13	15	0	0	0	0	1	1	3	9	0	0	0	0	7	1	62
Scaphinotus bilobus (Say)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Sericoda quadripunctatum (DeGeer)	0	0	0	0	0	0	0	21	29	0	0	0	0	0	0	0	0	50
Sphaeroderus lecontei Dejean	0	0	0	0	0	0	0	0	0	0	0	1	7	0	0	0	0	8
Sphaeroderus nitidicollis Chevrolat	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	2
Syntomus americanus (Dejean)	0	0	0	0	0	0	1	1	2	0	0	3	0	5	0	1	1	14
Synuchus impunctatus (Say)	1	2	0	7	0	5	1	2	6	16	0	5	4	13	6	14	10	92
Trechus apicalis Motschulsky	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Trechus crassiscapus L.	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	9
Total	64	112	101	55	27	34	18	98	215	51	21	81	103	52	61	211	43	1347

Appendix 6. Species list of carabid beetles collected in 2001. Total catches for each plot.

Carabid Species	B29 2P2	B99 1P1	B99 1P2	B99 2P1	B99 2P2	H57 1P1	H57 1P2	H57 2P1	H57 2P2	H83 1P1	H83 1P2	H83 2P1	H83 2P2	H99 1P1	H99 1P2	H99 2P1	H99 2P2	Total
<i>Agonum cupripenne</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	2
<i>Agonum gratiosum</i>	0	3	17	28	24	10	3	8	5	1	4	8	36	3	3	4	5	162
<i>Agonum placidum</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	2
<i>Agonum retracts</i>	0	0	3	2	1	3	1	0	0	0	0	0	4	0	0	1	0	15
<i>Agonum superioris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
<i>Agonum tlm</i>	0	1	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	3
<i>Amara cupreolata</i>	0	0	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	4
<i>Amara erratica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
<i>Amara impuncticollis or littoralis</i>	0	0	1	1	0	0	0	0	0	2	0	0	0	0	0	0	0	4
<i>Amara lunicollis</i>	0	0	3	0	0	0	0	0	0	0	0	1	0	0	1	0	0	5
<i>Amara schwarzi or latior</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
<i>Amara sp.</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
<i>Bradyellus semipubescent L.</i>	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2
<i>Calathus ingratus</i>	5	0	0	1	0	0	0	0	0	0	0	0	6	0	0	0	0	12
<i>Calosoma calidum</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2
<i>Carabus maeander</i>	0	0	0	0	0	0	0	0	0	2	6	0	0	0	0	0	0	8
<i>Carabus serratus</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Cymindis cimbicollis</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
<i>Cymindis unicolor</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	3
<i>Dyschirius sp.</i>	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	2
<i>Elaphrus claviger</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Harpalus bicolor Fabricius</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
<i>Harpalus egregius</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Harpalus fulvipes</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
<i>Harpalus laevipes</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Harpalus laticeps</i>	1	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
<i>Harpalus nigriventris</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Harpalus pensylvanicus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
<i>Harpalus somnulentus</i>	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
<i>Harpalus sp.</i>	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Larva	0	1	20	13	8	5	1	2	1	1	1	2	1	5	1	11	1	74
<i>Notiophilus semistriatus</i>	0	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	0	4
<i>Patrobis septentrionis Dejean</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
<i>Platynus decentis</i>	0	0	3	0	0	8	8	0	1	0	1	0	2	0	0	0	1	24
<i>Agonum mannerheimi</i>	0	0	0	0	0	3	4	0	0	0	1	5	2	0	0	0	4	19
<i>Pterostichus lucublandus</i>	0	0	0	0	1	0	0	0	0	2	1	0	1	0	0	0	0	5
<i>Pterostichus adstrictus</i>	65	2	15	0	0	33	13	0	1	0	0	0	0	14	10	2	5	160
<i>Pterostichus femoralis</i>	0	0	0	0	0	0	0	0	0	0	1	3	0	0	0	0	0	4
<i>Pterostichus melanarius</i>	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	3
<i>Pterostichus patruelis</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Pterostichus pensylvanicus</i>	35	0	0	3	0	2	5	0	0	1	0	25	45	2	2	2	0	122
<i>Pterostichus punctatissimus</i>	20	1	0	0	0	4	10	2	1	0	0	0	0	1	2	2	0	43
<i>Scaphinotus bilobus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
<i>Senecoda quadripunctata (DeGeer)</i>	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
<i>Senecoda quinquepunctatum</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Sphaeroderus lecontei</i>	0	0	0	0	0	0	0	0	0	3	2	0	0	0	0	0	0	5
<i>Sphaeroderus nitidicollis</i>	0	0	0	0	0	2	0	0	0	0	0	1	2	0	0	0	0	5
<i>Syntomus americanus</i>	0	0	0	5	5	0	0	0	0	2	0	0	3	2	0	2	0	19
<i>Synuchus impunctatus</i>	11	1	0	0	0	23	4	0	6	0	2	30	8	18	11	0	0	114
<i>Trechus apicalis</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
<i>Trechus crassiscapus</i>	0	0	0	0	0	1	5	1	1	0	0	0	0	0	0	0	0	8
Total	138	12	77	57	42	98	54	14	16	15	25	75	118	53	32	24	18	870

Appendix 7. Species list of carabid beetles collected in 2002. Total catches for each plot.

Carabid Species	B29 1P1	B29 1P2	B83 2P1	B83 2P2	B99 2P1	B99 2P2	H57 2P1	H57 2P2	H83 2P1	H83 2P2	H99 2P1	H99 2P2	Total
<i>Agonum cupreum</i>	0	0	0	0	0	1	0	0	0	0	0	0	1
<i>Agonum gratiosum</i>	0	1	10	0	23	40	11	0	4	2	12	10	113
<i>Agonum retractum</i>	0	0	10	6	0	0	0	0	3	4	0	0	23
<i>Agonum sordens</i> Kirby	0	0	0	0	0	0	1	0	0	0	0	0	1
<i>Agonum</i> sp.	0	0	0	0	0	0	0	0	0	0	1	3	4
<i>Agonum</i> tfm	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Amara cupreolata</i>	0	0	0	0	2	0	0	0	0	0	0	0	2
<i>Amara lunicollis</i>	0	0	0	0	0	0	0	0	0	0	1	2	3
<i>Badister obtusus</i>	0	0	0	0	0	1	0	0	0	0	0	0	1
<i>Bembidion mutatum</i>	0	0	0	0	1	0	0	0	0	0	0	0	1
<i>Calathus ingratus</i>	0	0	0	1	0	0	0	0	0	0	0	0	1
<i>Calosoma frigidum</i>	1	0	1	0	0	0	0	0	0	0	0	0	2
<i>Carabus serratus</i>	0	2	7	1	0	0	0	0	0	0	0	0	10
<i>Carabus taedatus</i>	0	1	0	0	0	0	0	0	0	0	0	0	1
<i>Elaphrus fuliginosus</i>	0	0	0	0	0	0	0	0	0	0	0	1	1
<i>Harpalus laticeps</i>	1	0	0	0	0	0	0	0	0	0	0	0	1
Larva	0	0	1	0	0	2	0	1	0	0	0	2	6
<i>Platynus decentis</i>	4	8	20	1	2	1	4	7	0	0	0	1	48
<i>Platynus mannerheimi</i>	0	2	0	0	1	6	0	0	1	1	2	2	15
<i>Pterostichus adstrictus</i>	111	74	25	0	1	1	1	11	0	9	2	0	235
<i>Pterostichus femoralis</i>	0	0	0	0	0	0	0	1	0	0	0	0	1
<i>Pterostichus luctuosus</i> (Dejean)	0	0	0	0	0	0	0	0	0	0	0	1	1
<i>Pterostichus lucublandus</i>	0	0	0	0	2	1	0	0	0	0	0	1	4
<i>Pterostichus melanarius</i>	0	0	1	0	0	0	0	0	0	0	1	0	2
<i>Pterostichus patruelis</i>	0	0	0	0	1	7	1	0	2	1	2	0	14
<i>Pterostichus pensylvanicus</i>	3	7	33	5	5	0	1	5	17	31	0	0	107
<i>Pterostichus pucnatissimus</i>	5	5	0	0	0	0	1	1	0	0	0	0	12
<i>Sphaeroderus nitidicollis</i>	0	1	7	0	0	0	0	0	0	1	0	0	9
<i>Synuchus impunctatus</i>	3	13	47	0	0	0	3	7	48	33	0	0	154
Grand Total	128	114	162	14	39	60	23	33	75	82	21	23	774