Effects of timber harvesting and forest fire on the ecological diversity of carabid beetles (Coleoptera: Carabidae) in aspen dominated mixedwood forests (*Populus tremuloides* Michx.) in western Manitoba.

By

Jeffrey K. Shaddock

A thesis submitted to the University of Manitoba in partial fulfilment
of the requirements for the degree Master of Science in the
Faculty of Graduate Studies

THE UNIVERSITY OF MANITOBA

FACULTY OF GRADUATE STUDIES

*****

COPYRIGHT PERMISSION

Effects of timber harvesting and forest fire on the ecological Diversity of carabid beetles (Coleoptera: Carabidae) in aspen Dominated mixedwood forests (Populus tremuloides Michx) In Western Manitoba.

BY

Jeffrey K. Shaddock

A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of Manitoba in partial fulfillment of the requirement of the degree

Master Of Science

For my parents, Donna and Mark, without whose love and support, this would never have been possible.

Acknowledgements

I would like to express my sincere thanks and gratitude to my supervisor, Dr. Richard Westwood, for his tremendous help and support over the duration of the research that makes up this thesis. I would also like to thank the members of my committee, Dr. Richard Staniforth for his expert advice and encouragement and Dr. Neil Holliday.

I am indebted to all those who assisted with field work over three summers of research: Joe Ackerman, Karen Skibo, Mason Kulbaba, Brin Jones, Sheri Streilein, Heather Tomkins, Tansy Shymko and Eva Walker. I also wish to acknowledge the support and help of fellow students who helped in numerous other aspects of the project: Rachel Boone, Lisa Capar, Brock Epp, Karen Budnick, Yacine Bara and Andrea Thomson.

Donna Grassia, Vern Bauman and Paul Leblanc of Lousiana-Pacific Canada Ltd. helped in the establishment of field sites and provided continued support throughout the duration of this study. Mr. Herb Bresky and Mr. Garth Riehl, graciously allowed access to study sites via their property. I thank Dr. Yves Bousquet and Dr. Henri Goulet for their help identifying the most difficult carabid beetle specimens. The Mixedwoods Forest Research & Advisory Committee (MFRAC) provided accommodations at the Goldeneye Research Station in Duck Mountain Provincial Park.

Funding for this project was provided by NSERC, Lousiana-Pacific Canada Ltd., and the Manitoba Model Forest.

Lastly, I would like to thank all of my friends and family who are not directly connected to this project, but who provided immense support over the duration of the study. Those deserving special mention include Stephen Shaddock, Martin Riley, and Peter and Lillian Whitehill.

Abstract

Shaddock, J.K., University of Manitoba, 2005.

Effects of timber harvesting and forest fire on the ecological diversity of carabid beetles (Coleoptera: Carabidae) in aspen dominated mixedwood forests (*Populus tremuloides* Michx.) in western Manitoba.

Major Professor: Dr. A.R. Westwood

Carabid beetles (Coleoptera: Carabidae) were sampled in burned and timber harvested mixedwood forests to determine the effects of disturbance type on carabid beetle communities. Three forest age classes within each disturbance type were compared: sites burned in 1980, 1961 and 1932; and sites harvested in 1995, 1980 and 1967. A total of 13873 carabid beetles, representing 51 species, were caught using pitfall traps during varying summer sampling periods in 2000, 2001 and 2002. The catch frequency of carabid beetles was generally higher in burned forests compared to harvested forests, although there was a high degree of variation within burned forests. The differences in catch frequency between disturbance types were due primarily to high catch frequencies of forest generalist carabid beetle species, such as *Platynus decentis* (Say), *Pterostichus adstrictus* Eschscholtz, and *Synuchus impunctatus* (Say) in burned forests. There were no significant differences detected between burned and timber harvested sites in the number of species of carabid beetles, log α diversity, evenness, or the Berger-Parker (dominance) index. The Jaccard index of β diversity indicated that the differences between the carabid beetle communities of burned and harvested sites were greatest in the most recently disturbed sites, and least in older sites. Each disturbance resulted in an initial increase in the number of species of carabid beetles that are known to inhabit open areas, such as *Agonum cupreum* Dejean, *Agonum cupripenne* Say, and *Cymindis cribricollis* Dejean; and an initial decline in the catch frequency of forest generalist species. It is unclear whether these effects are caused by timber harvesting or are normal for any large-scale disturbance. Forest generalist carabid beetle species were slower to return to harvested sites than to burned sites. The catch frequency of carabid beetles was highest in May/June, steadily declined over the collection period, and was lowest in August. Older forests had significantly higher catch frequencies of carabid beetles and lower levels of diversity than more recently disturbed forests, possibly due to differences in the quantity of leaf litter and coarse woody debris.

Table of contents

List of figures

List of tables

List of appendices

Introduction

The loss and fragmentation of natural habitats due to anthropogenic disturbances such as logging, agriculture, altered fire regime and urban development are suspected to be the primary causes of a recent rapid decline in the world's biodiversity (MacArthur and Wilson 1967; Wilson 1988). Reduced levels of biodiversity are problematic, with consequences including reduced habitat and nutrients for other organisms, diminished sources of potential pharmaceuticals, and the loss of natural pest control agents (Ledig 1988; Reid and Miller 1989; Wilson 1992). As a result, the importance of biodiversity and its conservation as a part of sustainable forest management has increased over the past decade (Government of Canada 1995). This has resulted in an increased need to monitor indicator taxa and assess the impact of different forestry practices.

Carabid beetles (Coleoptera: Carabidae) have been used as indicators of overall forest diversity in Europe and North America (Lenski 1982; Jennings et al. 1986; Martel et al. 1991; Duchesne and McAlpine 1993; Niemelä et al. 1992, 1993, 1996; Addison and Barber 1997; Beaudry et al. 1997; Duchesne et al. 1999; Werner and Raffa 2000, 2003; Day and Carthy 1988; Butterfield 1997; Magura et al. 2001). These beetles are so widely used because they are relatively easy and cost effective to sample; their taxonomy is stable and well understood with taxonomic keys available; and some species are known to be sensitive to disturbances in forests (Werner and Raffa 2000). Most carabid beetles are generalist predators, however some are relatively specialized (Currie and Digweed 1996).

Several studies have reported that carabid beetle abundance, species richness and diversity may be affected by timber harvesting (Jennings et al. 1986; Niemelä et al. 1993; Duchesne et al. 1999; Werner and Raffa 2000). The vast majority of this research has been conducted in coniferous forests, with relatively little information available on deciduous and mixedwood forests. Only three studies in North America have previously looked at the effects of timber harvesting on carabid beetles in hardwood forests (Werner and Raffa 2000; Vance and Nol 2003; Moore et al. 2004). Vance and Nol (2003) reported significantly fewer carabid beetles in recently harvested hardwood forests in Ontario. Werner and Raffa (2000) reported no significant differences in species richness or abundance, and few differences in diversity in hardwood stands in Wisconsin and Michigan. Moore et al. (2004) reported that strip and clearcutting did not significantly affect the the overall catch frequency of carabid beetles relative to undisturbed forests in Quebec.

In Manitoba, the large-scale commercial harvesting of hardwood forests began in the mid-1990s (Manitoba Natural Resources 1996). This activity was concentrated in the Duck Mountain and Porcupine Provincial Forests. The objective of this study was to evaluate the effect of timber harvesting compared to forest fire on the relative abundance, species richness and diversity of carabid beetles in aspen dominated mixedwood forests.

Literature review

Aspen and the mixedwood boreal forest

The boreal forest is one of the world's largest ecosystems. It covers some 6.7 million km^2, includes one-third of the world's forested lands, and 14% of the world's forest biomass (Kauppi and Posch 1985). In Canada, the boreal forest covers 2.6 million km^2 (Danks and Foottit 1989) and is divided into three regions: the high-, mid- and low-boreal (Scott 1995). The mid-boreal forest is a transition between the temperate deciduous forests in the south, and northern coniferous forests (Zoltai 1975; Scott 1995). It is characterized by a mix of hardwood and softwood tree species and hence is also known as the mixedwood boreal forest (Scott 1995). The mixedwood boreal forest stretches from Minnesota, northward through central Manitoba, and northwest through Saskatchewan and northern Alberta (Scott 1995). The southern boundary of the mixedwood boreal is the southern limit of conifer distribution (Scott 1995); while the northern boundary, as defined by Zoltai (1975) is where at least one, but not more than three, of the four typical boreal conifer species is encountered; these include *Picea glauca* (Moench) Voss [white spruce], *Picea mariana* (Mill.) B.S.P. [black spruce], *Pinus banksiana* Lamb. [Jack pine] and *Larix laricina* (Du Roi) Koch.

The western edge of Manitoba is several hundred metres higher than the rest of the province. This increase in elevation is the remnant of glacial Lake Agassiz's western shoreline (Bird 1930). Today this elevated region is recognized as three distinct 'mountains' in Manitoba, namely Riding Mountain, Duck Mountain, and Porcupine Mountain. The two northern most 'mountains' of the escarpment (i.e. Duck Mountain and Porcupine Mountain) are islands of mid-boreal forest surrounded by land that has been converted for agricultural use.

Vegetation

The tree canopy in early successional stages in the mixedwood boreal forest is dominated by the hardwood deciduous tree species *Populus balsamifera* L. [balsam poplar or black poplar], *Populus tremuloides* Michx. [trembling aspen or white poplar] and to a lesser extent *Betula papyrifera* Marsh. [paper birch] (Looman 1987). While older stands are dominated by coniferous tree species such as *Picea glauca*.

The biology and life histories of *Populus tremuloides* and *Populus balsamifera* are very similar, and therefore both will be indicated by the term 'aspen'. Aspen is the most widely distributed tree in North America (Stevens et al. 1999). In Canada, aspen accounts for 10% of the national forest inventory (2¼ billion m^3) (Morley 1986). In the Prairie Provinces, aspen makes-up greater than 40% of the total forest cover (Manitoba Natural Resources 2001).

Aspen is dioecious and clonal; most reproduction is vegetative with new stems arising from the lateral roots of an established tree (Stevens et al. 1999). This reproductive pattern results in stands where each tree is genetically identical to those with which it shares a common root system. These groups of genetically identical trees are known as clones. Clones vary in size and longevity, but are capable of reaching large sizes. Stevens et al. (1999) described a single mature aspen clone in Utah that covered 43 ha and had 47,000 stems with an estimated weight of 6 x 10^6 kg. More commonly, clones consist of approximately 100 individual trees (Barnes 1966) and occupy 1 to 2 ha (Lindroth 1991). Despite being genetically identical, variation does occur between individual stems within clones. Differences have been observed in susceptibility to fungi, insect outbreak, frost damage and herbivory (Barnes 1966; Hwang and Lindroth 1997). Mature aspen are also particularly susceptible to fungal white heart rot (*Phellinus (Fomes) igniarius* (L.)) as well as many insect and disease pests (Bird 1930; Howse 1995).

Aspen are capable of seed production and new stems may be produced by germination. Stevens et al. (1999) reported on an intense fire in Yellowstone National Park that killed most of the aspen roots, resulting in an episode of aspen regeneration exclusively by seeds by surviving trees.

Aspen is a fast growing, relatively short-lived tree, reaching maturity at 60 years old and 15 – 20 meters tall (Johnstone et al. 2004). The majority of trees in a young stand do not reach their maximum size due to intense intraspecific competition (Bird 1930). Aspen will respond very quickly to disturbances, and usually grow 15-30 cm in the first year of growth (Perala 1990). When the tops of trees are killed or removed, new stems quickly arise from the lateral roots of the destroyed trees. Looman (1987) reported densities of up to 70 stems per m^2 within a few months of a forest fire, although fire severity does affect the density of regenerating stands (Wang 2003). Five- to ten-year old aspen stands remain extremely dense, often exceeding 100000 stems per ha (approximately 10 per m^2) (Johnstone et al. 2004). The density of mature stands in Manitoba ranges from 2500 – 6000 stems per ha (approximately 0.25 – 0.6 per m^2), depending on the number of coniferous stems in the same forest (Manitoba Natural Resources 2001).

A dense layer of deciduous shrubs is often present in the understory of aspen stands. Common genera encountered in the shrub layer include *Alnus* [alder], *Corylus* [hazelnut], and *Prunus* [cherry] (Bird 1930). Common herb species found at the forest floor include *Cornus canadensis* L. [bunchberry], *Fragaria virginiana* Duchesne [common strawberry] and *Aralia nudicalis* L. [wild sarsaparilla], the broad leaves of which often form a dense layer approximately 30 cm off the ground.

Disturbance

A disturbance is a discreet event that disrupts an ecosystem, community or population, and alters the resources, substrate or physical environment (White and Pickett 1985). Disturbance prone ecosystems have a wider variety of age classes, vegetation types and higher levels of biodiversity than comparable systems where disturbances have been suppressed (Duchesne et al. 1999).

The initial impacts of disturbances are often quite obvious: new species become established while others disappear. The habitat itself may be dramatically altered; for example, an intense forest fire may destroy thick layers of leaf litter leaving behind bare rock (Kimmins 1997). Disturbances can also have more subtle effects that are often overshadowed by the more obvious impacts (Andersen 1990). Local extinctions resulting from a disturbance may occur long after the disturbance and therefore go unnoticed and unrecorded (Lindenmayer 1999). These and other smaller effects, such as reductions in species abundance, are difficult to detect but may be just as important as more apparent impacts.

Disturbances can be grouped into one of two categories depending on the origin of the disturbance: natural or anthropogenic. Organisms have had thousands of years to adapt and evolve responses to natural disturbances. The result is that a naturally disturbed ecosystem often recovers quickly, and through succession a community that is similar to the original is re-established. Anthropogenic disturbances are different. Most current large-scale, uniquely human disturbances originate in the 20th Century and organisms have had little time to adapt and evolve in response to the change in ecosystem conditions they present.

Within the mixedwood boreal, the somewhat drier conditions that promote the replacement of conifers by *Populus tremuloides* and *Populus balsamifera*, also favour fire (Scott 1995). The other major disturbance in this forest type is timber harvesting, where aspen are harvested for oriented strand board (OSB) or kraft paper (Froning 1980; Scott 1995). As these forests mature, the hardwood species are gradually replaced by slower-growing, shade-tolerant coniferous tree species including *Picea glauca*, *Picea mariana* and *Pinus banksiana* (Looman 1987). In 80 – 100 year old stands, the conifers may over-top the aspen and after 120 years, the aspen may have completely died out (Scott 1995).

Succession

When an area is altered by a disturbance, it may be rapidly colonized by new species of plants and other organisms. Many of these species influence the environmental factors of the developing site, allowing additional species to become established. The sequence of changes that occur following a disturbance is called succession (Pickett et al. 1987; Krebs 1994; Ricklefs 2001). It is often assumed that specific organisms are adapted to recently disturbed areas and that these organisms will be the first to establish themselves. This view is partially correct, however it overlooks the importance of random colonization events in newly disturbed areas (MacArthur and Wilson 1967).

The original concept of succession was described by Cowles (1901) and later clarified by Clements (1936); it is now known as facilitative succession (Ricklefs 2001). This type of succession regarded the process as a movement towards a single end point, at which time the system would be self-sustaining and would remain at equilibrium until a new disturbance reset the community to a primary successional stage. In facilitative succession, each successive species relies on environmental conditions that are created by the species that preceded it (Connell and Slatyer 1977; Ricklefs 2001). The problem with this view of succession is that it fails to consider the random nature in which species colonize a disturbed area, and may affect the composition of the climax community.

Other mechanisms of succession have been described to address the shortcomings of facilitative succession (Connell and Slatyer 1977). Ricklefs (2001) describes the inhibition mechanisms of succession where one species inhibits the presence of another. Inhibition results in systems where the climax community is difficult to predict, and is as dependant upon which species arrive first (precedence) as the environmental conditions that pioneer species create (Ricklefs 2001). Research (summarized by Krebs 1994) has shown that random colonization in successional events is a much more important factor than previously considered, and that many communities never reach the predicted climax communities (McLeod 1980). Connell and Slatyer (1977) and Ricklefs (2001) describe a the tolerance mechanism of succession, where the establishment of a species is independent of the presence or absence of other species, and rather depends on the dispersal abilities and physical conditions of the environment, and competitive exclusion shapes the future of the community.

In the mixedwood boreal forest, a stand-replacing disturbance results in dense stands of sapling *Populus tremuloides* and *Populus balsamifera* (Scott 1995). Smithers (1961) observed a fire in central Alberta, and reported that where *P. tremuloides* and *P.*

balsamifera and coniferous seeds germinate at the same time, the aspen grow much more quickly, and therefore come to dominate the tree canopy of these forests for approximately 50 years (baring any further disturbances). In younger stands the understory is dominated by shade-tolerant coniferous species such as *Picea glauca*.

Forest fire

Fire is an important disturbance in many ecosystems. In grasslands (Anderson 1992), heathlands (Mallik and Gimingham 1985) some forest types (Johnson and Miyanishi 2004) fire is often the most common and influential disturbance. In grasslands, frequent fires prevent the encroachment of trees, allowing the grasslands to persist (Brown 1985). In many of the world's forests, including the boreal forest, fire has been the single most persistent and important disturbance (Perry 1994). Fires burn an estimated 2.5 million ha of Canadian forests each year (Government of Canada 1978 – 1995).

Forest fires are usually categorized according to the uppermost fuel stratum through which they burn (ground, surface or crown). Ground fires are limited to the soil, where they burn the organic material and humus (Martell 2001). Surface fires burn the litter of the forest floor and the shrub layer. These fires may result in some tree deaths, depending on the intensity and severity of the fire. Crown fires consume the upper stratum of the forest and are often very large, stand-replacing events (Perry 1994). In boreal forests, stand-destroying crown fires occur at roughly 50- to 200-year intervals, and in very moist sites, these intervals can reach up to 500 years (Bonnan and Shugart 1989). Frequent forest fires increase the number of potential plant and animal habitats over a large area, resulting in higher levels of biodiversity (Niemelä et al. 1996). All fires, regardless of size, share the common characteristic of being very patchy and random (Perry 1994). This randomness is due in large part to variations in site topography and weather conditions during the fire, which can result in areas of unburned forest surrounded by burned forest.

Fires vary in severity and frequency. The severity of a forest fire once it is ignited depends on two factors: weather and fuel. Weather is probably the key determinant of fire severity (Johnson and Larsen 1991). Historic records show that the most extensive wildfires in North American forests occur during dry periods (Clark 1990). Wind direction and speed direct the spread of the fire, leaving some areas with little damage, while the vegetation in others is totally destroyed (Fryer and Johnson 1988). The distribution and flammability of fuels are also important determinants of fire severity and frequency (Perry 1994). Older forests contain more fuel in the form of lichens, which may be very flammable (Boudreault et al. 2002; Rydgren et al. 2004), accumulated deadfall and coarse woody debris, making them more susceptible to fire. Different plant species can affect the degree to which the fire spreads through the crown. Some burn readily and propagate fire, while others are less combustible and inhibit the spread of fire. The overall flammability of a forest is influenced by a combination of the moisture content (weather), the amount of fuel (stand age) and the chemical composition of the trees (plant species) (Perry 1994).

When forests burn, the fire consumes woody and other dead plant material, kills or injures vegetation and animal life, and produces residual mineral products that may chemically alter the soil (Brown and Davis 1973). Depending on soil factors such as moisture and soil type, a fire may burn only the leaf litter and humus; or it may burn the entire organic layer down to rock or mineral soil (Kimmins 1997). Following a forest fire, most of the organic matter that had been present on the site in the form of vegetation remains on the site as ash. This material provides an important resource for the pioneer species that initiate succession (Lee 1998).

Timber harvests

In North America, more forested area is harvested for timber than is burned by fire (Kimmins 1997). Consequently, timber harvesting is now the major initiator of post-disturbance forest succession (Niemelä 1999). There are several unique aspects of timber harvesting that are not present in natural disturbances. The removal of surface material is one of the most important differences between timber harvesting and natural disturbances (Niemelä 1999). In harvest, the removal of surface material reduces the coarse woody debris left on the site (Niemelä 1999), which provides important habitat for many early successional species (Simon et al. 2002). The heavy machinery commonly used in timber harvests over the last 50 years may compact soil, limiting the growth of new plants and damaging the roots of seed trees (Greacen and Sands 1980), although, the recent introduction of new machinery that is very low-impact may help reduce the long-term impacts of timber harvesting (Conway 1992).

Timber harvests often leave the shrub layer relatively intact, causing the ground to be more heavily shaded than after a forest fire, where the shrub layer is frequently destroyed (Johnstone et al. 2004). Increased shade may alter the species that can become established on the new site. Landscape characteristics such as topography do not affect timber harvests in the same way they affect natural disturbances. On a larger scale, timber harvests are also more uniform than natural disturbances (Niemelä et al. 1993), which are characteristically more patchy (Brown and Davis 1973). Historically, residues on harvested sites are often pushed into large piles with tractors or bulldozers (a practice known as windrowing). Windrowing has been repeatedly shown to reduce tree growth after harvests compared to the effects of a natural disturbance (Atzet et al. 1989), and it is no longer practiced in most provinces (Manitoba Natural Resources 2001).

There have been advances over the past 20 years in timber harvesting to reduce the amount of damage that is caused to the site and vegetation. Among these improvements are considerations for the habitat of specific animals and plants (Kurttila et al. 2002). Using more modern (lighter) machinery, harvesting in the winter, or using soil rehabilitation techniques can help to reduce soil compaction (Ilstedt et al. 2004). Careful site planning restricts the amount of ground surface that is affected by heavy machinery. Topping and de-limbing the tree at the stump, rather than at the roadside, ensures that more coarse woody debris remains on the site (Palik et al. 2002). In several places, some harvested sites are intentionally burned to better emulate a natural disturbance, a process called 'prescribed burning' (Brunson and Shindler 2004; Fernandes and Botelho 2004). These changes are part of the disturbance modeling approach to timber harvesting, which attempts to emulate the effects of natural disturbances.

Carabidae

The Carabidae are one of the largest families of the Coleoptera, with over 35000 known species (Tripplehorn and Johnson 2004). In North America approximately 1700 species of carabid beetles in 150 genera have been recorded, making it the third largest Coleopteran family (Triplehorn and Johnson 2004). In the Province of Manitoba, approximately 320 species[1] have been recorded.

The taxonomy of the Carabidae is well understood and is relatively stable. Bousquet and Larochelle's (1993) catalogue of the North American fauna is the most recent. One of the most recent revisions is a reclassification of the Nearctic Pterostichini (Bousquet 1999).

Biology

Adult and larval carabid beetles are either omnivorous or carnivorous. Most carabid beetles are generalist predators feeding on various insect larvae, Collembola, earthworms,

---

[1] This number is synthesized from Lindroth (1961-1969); Bousquet and Larochelle (1993); and Bousquet (1999)

spiders, centipedes and isopods (Thiele 1977; Werner and Raffa 2000). Most predation occurs on the ground amongst the leaf litter, but some species will climb trees in search of food (Crowson 1981). Adults of most species are active at night, seeking refuge under stones and logs during the day (Loreau 1990). Breeding occurs in either the spring or autumn, with spring breeders over-wintering as adults, and autumnal breeders over-wintering as larvae (Dulge 1994).

Some species are capable of flight, and may be capable of flying up to 200 meters per day (Matalin 1994); in other species, the wings are highly reduced. Species incapable of flight are less likely to be pioneer species, and are more often associated with mature forests (Atzet et al. 1989). In species capable of flight, younger beetles tend to spend more time flying than older beetles (Matalin 1994). Younger beetles have higher reproductive potential and therefore are more likely to successfully re-establish the species in disturbed areas.

Ecology

In the boreal forest, carabid beetles are an important part of the functioning ecosystem. Apigian and Wheelwright (2000) considered a low density of carabid beetles to be 50000 – 250000 beetles per hectare. Carabid beetles play important roles in the regulation of Lepidopteran defoliators and they are an important food source for some insectivorous mammals (Crowson 1981). In addition to the references provided below, Natural

Resources Canada (2004) provides a list of many species of carabid beetles from Canada and the habitats in which they have been collected.

Not enough is known about the behaviour and ecology of carabid beetles to determine why particular species are more abundant in some forests than others (Pearce et al. 2003). This lack of knowledge is due in large part to the cryptic behaviour of most carabid beetles, which include living in the soil, under stones, in moss and rotting wood, and under leaves and bark (Loreau 1990). Studies in North American mixedwood forests have consistently found a similar carabid beetle community (e.g. Niemelä et al. 1992, 1993; Digweed et al. 1995; Werner and Raffa 2000, 2003; Pearce et al. 2003). Five species in these communities were consistently among the most frequently caught: *Agonum retractum* LeConte, *Calathus ingratus* Dejean, *Platynus decentis* (Say), *Pterostichus adstrictus* Eschscholtz and *Pterostichus pensylvanicus* LeConte.

Platynus decentis is a transcontinental North American forest insect that is often found under bark and logs (Lindroth 1961-1969; Niemelä et al. 1992). It is associated with mesic to hydric deciduous forests (Lindroth 1961-1969; Epstein and Kulman 1990), although it has also been recorded in coniferous forest stands (Holliday 1991). Werner and Raffa (2000, 2003) reported that *P. decentis* was most frequently caught in old growth forests compared to younger forests. *Platynus decentis* is sometimes very abundant relative to other carabid beetle species in the same area (Niemelä et al. 1992; Werner and Raffa 2000). This species has two distinct activity cycles per year (Bousquet at Pilon 1977). The first occurs during the spring, when reproduction occurs; the second extends from mid-August to the end of October and mainly represents the adult offspring from the first cycle (Bousquet at Pilon 1977). The adult is the only lifecycle stage that overwinters. Lindroth (1961-1969) believed the wings of this species were too small for the beetle to be capable of flight.

Pterostichus adstrictus has a circumpolar and transcontinental distribution in North America (Lindroth 1961-1969). It is one of the most common species of carabid beetles in northern coniferous forests (Lindroth 1961-1969), although it is not restricted to forests, and is one of the few carabid beetles where the adults can be described as "habitat generalists" (Niemelä et al. 1992). The preferred larval habitat is coarse woody debris, which provides protection from desiccation and temperature extremes (Goulet 1974). *Pterostichus adstrictus* is also a generalist predator that feeds on plant material, snails, and other small invertebrates (Digweed 1993). This species has a similar two-stage activity cycle to *Platynus decentis* (Bousquet at Pilon 1977). The adults are most frequently caught early in the summer and over-winter as adults.

Pterostichus pensylvanicus is morphologically very similar to *Pterostichus adstrictus* but its distribution is restricted to North American (Goulet 1974). Like *P. adstrictus*, *P. pensylvanicus* is also a generalist predator (Digweed 1993) that prefers to live under dead leaves and moss (Lindroth 1961-1969). *Pterostichus pensylvanicus* is a forest specialist, preferring aspen forests (Niemelä et al. 1992) with moist loose soil, which is preferred for oviposition (Goulet 1974). The preferred larval habitat is within leaf litter and in the soil (Goulet 1974). Adults are most frequently caught early to mid-summer. Some individuals are capable of flying.

Calathus ingratus is found across Canada and is one of the most common beetles in northern coniferous forests (Lindroth 1961-1969). It is primarily a forest beetle, living under dead leaves and moss (Lindroth 1961-1969). Like *Platynus decentis*, Niemelä et al. (1992) considered *C. ingratus* to be a forest generalist. Adults of this species have one activity cycle per year, which takes place predominantly in the summer (Bousquet at Pilon 1977). Reproduction takes place throughout the activity period, and overwintering occurs in either the larval or an adult stage (Bousquet at Pilon 1977; Carter 1980).

While the four species listed above are often abundant in hardwood boreal forests, few carabid beetle species have been identified as specialists of aspen forests. Species that have been identified as aspen forest specialists include *Agonum retractum*, *Calosoma frigidum* Kirby and *Carabus chamissonis* Fischer von Wadlheim (Niemelä et al. 1993). *Calosoma frigidum* has been found in all Canadian provinces. They over-winter as adults, feed mainly on caterpillars, are very good flyers and are capable of climbing trees (Lindroth 1961-1969). Adults of *Agonum retractum*, unlike many other members of the genus, are forest specialist living under bushes and ferns (Lindroth 1961-1969). Some individuals have wings large enough to fly. Adults are most frequently caught in mid summer and hibernate as adults. *Carabus chamissonis* is transcontinentally distributed in

Canada and over-winters as an adult (Lindroth 1961-1969). This species has an interesting distribution, as it is found both on the tundra and in aspen forests.

Sampling

The literature includes many methods for sampling adult carabid beetles, including litter washing (Spence and Niemelä 1994), Tullgren funnels (Spence and Niemelä 1994), quadrat counts (Greenslade 1964), and a variety of passive trapping methods including ramp traps, gutter traps and pitfall traps (Spence and Niemelä 1994). Litter sampling involves placing samples of litter from the forest floor in containers of water, and allowing beetles and other invertebrates to float to the surface where they are collected (Spence and Niemelä 1994). Tullgren funnel sampling involves placing litter samples from the forest floor under a heat source (usually a light bulb), which drives the invertebrates into a preservative fluid (Pande and Berthet 1971). Quadrat counts provide an estimate of absolute abundance for the time of sampling and involves sampling a defined space and identifying all individuals of species of interest within that area (Greenslade 1964). Passive sampling methods using traps usually involve the establishment of several traps throughout the sampling area. Traps may be submerged in the soil, so that the top is flush with the ground surface (pitfall traps, gutter traps) or may use a ramp to provide access to the trap (ramp traps). Ramp traps are often used when the traps cannot be submerged into the substrate, for example in rocky areas. Traps usually contain a fluid that acts as a killing agent and preservative.

Each method of sampling has its own biases and limitations. Litter sampling techniques can provide estimates of absolute abundance (Spence and Niemelä 1994), but they are relatively labour intensive, and the samples require rapid processing. Passive sampling allows the researcher to leave traps in place, and return at a later date to empty the contents. Pitfall trapping is the most common method of sampling carabid beetle communities (Spence and Niemelä 1994), due primarily to being inexpensive and labour efficient. The numerous studies that have used pitfall traps to capture carabid beetles have resulted in a large body of literature on the limitations of this method (Spence and Niemelä 1994). Variables that have been shown to influence the sampling effectiveness of pitfall traps include: soil humidity and temperature (Briggs 1960); the vegetation surrounding individual traps (Duffey 1972); trap diameter (Greenslade 1964); the shape of the trap (Adis 1979); trap construction material (Adis 1979); the presence of a cover over the trap and its size and shape (Adis 1979); and the type of killing-preservative agent (Adis 1979). Werner and Raffa (2003) include insect size, activity, habitat structure and season as factors that may also affect pitfall trap catches. Pearce et al. (2003) stressed the importance of soil disturbance around pitfall traps. This "digging-in" effect (Greenslade 1973) is greater in aspen and mixedwood forests than in forests with a floor of sphagnum, and may result in increased catches of some species (Pearce et al. 2003).

Pitfall trap catches rely on both population density and an organism's activity to provide a measure known as activity-density (Thomas et al. 1998). The catch frequency of individual species may be correlated with relative abundance (Desender and Maelfait

1986), but pitfall trapping does not provide information on the absolute abundance because catches are dependent on activity (Spence and Niemelä 1994). Pitfall trapping may provide adequate data for comparing relative catch frequency between areas sampled with the same method (Desender and Maelfait 1986), so long as factors affecting activity-density are understood. These factors include temperature, prey density, hunger level, or reproductive state (Thomas et al. 1998). Pitfall trapping tends to underestimate carabid beetle density, especially during warmer, drier months (Spence and Niemelä 1994). Compared to litter sampling, pitfall trapping is also biased towards larger-bodied species of carabid beetles because a larger beetle will tend to cover more ground and therefore is more likely to encounter (and fall into) a pitfall trap (Adis 1979). Pitfall traps may provide a better estimate of arboreal species than litter sampling techniques, especially for species that return to the ground at night and other nocturnal species (Crins 1980).

Analysis

Biodiversity and biodiversity measures

The literature seems to have an endless number of definitions for the term 'biodiversity'. Niemelä (1999) has described it as essentially a measure of the amount of heterogeneity in nature. Ecological diversity is difficult to define because it consists of two elements: the number of species (or 'species richness') in a habitat and the relative abundance of each species (or 'evenness') (Magurran 1988). Areas with more species and an equal number of individuals within each species are generally considered to be more biologically diverse than areas with fewer species, or when a few species account for a great proportion of individuals (Wilson 1992).

In ecosystems that experience frequent disturbances, high levels of landscape biodiversity act as buffers against disturbance (Wilson 1988). The more species that are present, the higher the likelihood that the disturbed site will be able to return to a pre-disturbance level of diversity (Wardel et al. 2004).

Numerous methods of measuring biodiversity have been presented in the literature. Excellent reviews of the measurement of biodiversity are provided by Pielou (1975), Southwood (1978), Magurran (1988) and Krebs (1989). There are other measures and types of biodiversity beyond those discussed here. Kimmins (1997) provides a review of other types of diversity, including genetic and regional diversity.

In ecological research, two of the most commonly measured types of diversity are alpha diversity (α) and beta diversity (β). Alpha diversity is a measure of diversity within a single habitat (in forests, this is often referred to as the stand level) (MacArthur 1965; Whittaker 1977). Beta diversity is the degree of similarity between habitats (in forests, this is often referred to as the landscape level) (MacArthur 1965; Whittaker 1977; Thomas 2001).

Biodiversity measures

Species richness is the number of species in a given area, and is currently the most widely used measure of diversity (Gray et al. 2001). Relative species abundance in a community, or 'evenness', is another element of diversity (Hurlbert 1971). The slope parameter of the log abundance of each species plotted against rank is one method of determining evenness. Values range from 0 to -1. A slope closer to 0 indicates that all species were present in relatively equal (or 'even') numbers, while a slope closer to -1 indicates the disparity between the relative abundances of individual species (Southwood and Brown 1979; Alatalo 1981). Sampled areas with evenness values that are closer to 0 are generally considered to have higher levels of biodiversity. Values represent the evenness of individual sites and should be considered in conjunction with the species richness (Gray et al. 2001).

Numerous proportional abundance diversity indices have been developed to indicate alpha diversity (for examples see Hill 1973, Magurran 1988). One of the most commonly used measures of alpha diversity is Fisher's α statistic, also known as the log-series α (Fisher et al. 1943). The log-series α represents the number of species and the number of individuals within each species. Sampled areas with more species and more individuals within each species have higher log-series α values (and are considered to have higher levels of biodiversity). Taylor et al. (1976) considered the log-series α superior to Simpson's index and the Shannon-Weiner statistic in some situations because it is less sensitive to sample size than either of these other two measures. A weakness of the log-series α is that although sites with greater evenness (see below) are usually considered more diverse, the α value may potentially be higher in a site that shows greater dominance (Magurran 1988). The log-series α is calculated using two equations: The first equation calculates the parameter ***x*** using iteration (which may range from 0 to 1, but in practice is almost always between 0.9 and 1.0 (Magurran 1988)):

$$S / N = \frac{(1-x)}{x(-\ln(1-x))}$$

Where ***S*** is the total number of species in the site, and ***N*** is the total number of individuals in the site.

The second equation calculates the parameter **α**:

$$\alpha = \frac{N(1-x)}{x}$$

Where ***N*** is the total number of individuals in the site, and ***x* is** the value that was derived in the previous equation.

The Shannon-Weiner index (or Shannon index) is another commonly used measure of alpha diversity. The Shannon index incorporates both species richness and evenness. Values range between 1.5 and 3.5, and higher values indicate higher biodiversity (Magurran 1988). This index assumes that samples are randomly collected from an infinitely large population, which limits its application in some situations (Magurran 1988). For example, different moth species are attracted to light traps with different frequencies (Southwood 1978), therefore the Shannon index would not be appropriate for data collected in this manner. The Shannon index is better suited to stationary organisms and is commonly used with percent cover data of plant species. The Shannon index (or ***H'****)* is calculated using the following equation:

$$H' = -\sum p_i \ln p_i$$

Where p_i is the proportional abundance of the ith species.

The Berger-Parker index is an alpha diversity measure that evaluates the level of species dominance in the sample, expressing the proportional importance of the most abundant (dominant) species (May 1986). Vales range from 0 to 1; higher values indicate greater single-species dominance, and therefore lower diversity (Magurran 1988). One of its strengths is that it can be used when sample sizes are small. May (1975) considered the Berger-Parker index to be one of the more useful indices, particularly when used in conjunction with the Shannon index. The Berger-Parker index (or d) is calculated using the following equation:

$$d = \frac{N_{\max}}{N}$$

Where N is the total number of individuals and N_{max} is the number of individuals in the most abundant species.

Beta diversity is also referred to as differentiation diversity or landscape diversity. While alpha diversity indices provide a value for each particular site, beta diversity indices provide a value that describes the level of similarity between two sites. Beta diversity indices can be particularly useful when used to compare similar habitats that have experienced two different disturbance types.

Beta diversity indices can be qualitative (exclusively presence/absence species data) or quantitative (species and their abundances). Values for beta diversity show the degree of similarity between two sites, with higher values indicating a greater degree of similarity. Values for some indices, such as the Jaccard index of similarity, range from 0 to 1. When the value is 0 the two sites have no species in common; when the value is 1, the two sites have identical sets of species (Magurran 1988). The Jaccard index (or C_J) is calculated as using the following equation:

$$C_J = \frac{j}{(a+b-j)}$$

Where j is the total number of species in both sites, a is the number of species in Site A, and b is the number of species in Site B.

The Jaccard index is an effective and widely used qualitative beta diversity index (Magurran 1988). As with all qualitative measures, the primary shortcoming of the Jaccard index is that it does not consider species abundance and could potentially indicate that two sites are very similar, when the structure of their communities (i.e. relative abundances of species) is actually very different (Magurran 1988). The index is a proportional value based on the number of species that the two sites have in common.

Beta diversity values such as the Jaccard index cannot be analyzed using statistical procedures that rely on differences in variance. These methods, such as analysis of variance, are not applicable because beta diversity values are not derived independently of each other (Pielou 1984). Cluster analysis, a method frequently used by systematists, has been used with The Jaccard index values (Saravia et al. 1998; Paulitz and Adams 2003). Cluster analysis attempts to group samples into sets (clusters), which can be based on the degree of similarity. The goal is that these clusters will correspond to features of the data set (Gower 1967). Hierarchical cluster analysis is one of the most commonly used methods of cluster analysis and is recommended when the sample size is less than 200 (Wilkinson et al. 2004). Cluster analysis results in diagrams that have the appearance of branching trees, the more similar two samples are, the closer together they occur on the tree. Distances between samples vary depending on the data being used, however with the Jaccard index, actual values are used to represent the degree of similarity (distance) between samples (Paulitz and Adams 2003).

Alpha and beta diversity are independent measurements, and two areas with high alpha diversity values may have a low measure of beta diversity (Kimmins 1997). The most reliable way to measure biodiversity, from a research perspective, is to use several measures and have a good understanding of the strengths and weaknesses of each. By carefully choosing several diversity indices, a tiling effect is created whereby the weaknesses of one index are covered by the strengths of another (Magurran 1988).

Temporal diversity refers to changes in biological communities over time (Kimmins 1997). Diversity components such as species richness and evenness are used to show changes in temporal diversity. Temporal diversity may apply to changes over a single year or growing season, to changes over decades, or even centuries (Kimmins 1997). A practical means of studying temporal diversity is to examine differences in similar environments that were altered at different, known intervals, a technique known as static age class research or chronosequencing (Wardle et al. 2004). For example, the effect of forest fire could be studied by working in similar forests that were burned in 1950, 1975 and 2000. This method would permit a relatively rapid assessment of processes that would have otherwise taken 50 years or more.

Ordination analysis

Over the past 30 years, the use of multivariate statistics has expanded tremendously (Grossman and Nickerson 1991; Kenkel et al. 2002). Ordination analysis is a method of multivariate analysis that represents multivariate data in two-dimensional space, while maximizing the amount of trended variation (Pielou 1984; Kenkel et al. 2002). Ordination serves to summarize community data (such as species abundance data) by producing a low-dimensional ordination space in which similar species and samples are plotted close together, and dissimilar species and samples are placed far apart. Ordination analysis also provides a means to simultaneously consider multiple data sets and look for correlations between them. The results of these analyses are presented graphically in relation to one or more ecological gradients, or to abstract axes that may represent such gradients (James and McCulloch 1990).

Generally, ordination techniques are used to search for relationships between species composition patterns and underlying environmental gradients that influence these patterns, in effect asking: "what factors structure the community?" (Jackson 1993). Ordination analysis attempts to simplify and graphically represent multiple raw data sets, with the hope of illuminating relationships among species, plots and environmental variables. Results are usually presented graphically as a biplot. The horizontal (first) axis usually expresses the greatest amount of linear variation in the data, and the vertical (second) axis usually expresses the second most linear variation.

The relative strength of the relationships between the variables that are presented is inferred from the eigenvalue associated with each axis. When displayed on biplot diagrams, eigenvalues are usually scaled so that they range from 0 to 1 and indicate the proportional amount of variance accounted for by a particular axis (Kenkel et al. 2002). Axes with high eigenvalues explain a high percentage of the variation in the data. Correspondingly, greater confidence can be placed in the relationships expressed by axes with high eigenvalues. As the type of data that ecologists analyze varies so considerably, there is no single recognized eigenvalue above which the relationships are considered significant (Jackson 1993). An implicit assumption when using ordination techniques is that researchers are able to distinguish meaningful patterns from random noise. These distinctions are based on (1) the number of variables; (2) the structure of the correlation matrices; and (3) the strength of the intervariable correlations (Jackson 1993). To avoid spurious correlations, it is important to confirm the relationships suggested in the analysis by referring back to the original data.

Principle component analysis

Principle component analysis (PCA) was one of the earliest ordination techniques applied to ecological data and remains one of the most widely used methods of ordination analysis (Jackson 1993; Kenkel et al. 2002). Both species and site ordinations result from a single analysis (James and McCulloch 1990). The results are graphically represented on a biplot where the amount of separation between two sites represents their level of similarity. Sites with similar species composition are grouped closer together than sites with different species composition.

PCA allows ecological researchers to look for similarities in response to different disturbances among multiple sites. Interpretation of PCA outputs in these cases usually involves identifying groupings of sites, which would indicate that they are responding to the disturbance in a similar way.

Redundancy analysis

Redundancy analysis (RDA) is a method of ordination analysis that incorporates the responses of species to environmental variables (ter Braak and Šmilauer 2002). RDA is essentially a more controlled version of PCA where species are constrained by designated environmental variables (ter Braak 1987; Legendre and Legendre 1998). The resulting output displays the relationships of species and sites, as well as the incorporation of environmental variables. As with PCA, the results of RDA are presented graphically on a biplot. The environmental variables are often displayed as arrows originating from the centre of the diagram; longer arrows indicate a more significant variable.

RDA permits the simultaneous examination of environmental variables, sites and species. It allows the researcher to connect species responses with specific environmental variables and relate those responses to other environmental variables.

Materials and Methods

Description of general study area

This study was conducted in central western Manitoba between May 2000 and September 2002. Study plots were located in Duck Mountain Provincial Park, Duck Mountain Provincial Forest and Porcupine Provincial Forest (Table 1) (Figure 1), which lie within the boreal plains, an ecotone between the boreal shield and prairie ecoregions (Scott 1995). A mixture of hardwood and softwood tree species characterizes this ecotone. The dominant tree species are trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and white spruce (*Picea glauca*). The two former species tend to be dominant on south-facing slopes, which are drier, while the latter tends to be dominant on north-facing slopes (Grossnickle 2000). Duck Mountain and Porcupine Mountain are part of the Manitoba escarpment, an upland region where elevations range from 670 m to greater than 790 m. The geomorphology consists of a hummocky moraine with steep slopes on the eastern edges of the upland and gradual slopes to the west (Knapik et al. 1988). Surface materials consist mostly of stony, calcareous till. Depressions are common and are often poorly drained, frequently resulting in the presence of shallow bogs (Knapik et al. 1988).

The soils of this region are Gray Luvisols (Zoladeski et al. 1995), which are characterized by eluvial and Bt horizons. They usually have L, F and H horizons and may have a degraded Ah or Ahe horizon (Soil Classification Working Group 1998).

The nearest weather station to the study area is located in Swan River, Manitoba (52°3'N, 101°13'W) within 65 km of all study plots. Appendix I shows the daily maximum temperatures, minimum temperatures, and precipitation for 2000, 2001 and 2002, as well as the 30-year averages.

Experimental design

The intent of this study was to compare the effects on carabid beetles of timber harvesting with those of a natural disturbance (forest fire) in aspen forests. Within each of these disturbance types, forest stands of three different age classes were identified for the purpose of this study. Years of disturbance were 1967, 1980 and 1995 for harvested forests, and 1932, 1961 and 1980 for burned forests.

For clarity, the term 'site' refers to a forest stand that experienced the same disturbance in the same year. Sites were coded according to disturbance type and the year the disturbance occurred. For example, site B32 burned (B) in 1932 (32). The term 'plot' refers to individual sampling areas within sites. Plots were designated by the site code, followed by an individual plot code. For example plot B32A1 was plot A1 within the B32 site. Plots were labeled A1, A2, B1 or B2; plots A1 and A2 were generally closer to one another, as were plots B1 and B2. Table 1 shows the number of plots within each site. The term 'paired sites' refers to two sites that experienced different disturbances (i.e. burn and harvest), at approximately the same time (e.g. B80 and H80). In order to determine whether the carabid beetle community responds differently to timber harvesting than to forest fire, much of the statistical analysis involves the comparison of paired sites. These pairings are: the B80 site with the H80 site, and the B61 site with the H67 site. Statistically significant differences between paired sites would indicate that the carabid beetle community may have responded differently to timber harvesting than to forest fire.

The time since disturbance for all plots was initially assessed using forest inventory maps provided by Manitoba Conservation's Forestry Branch, and were later confirmed using tree core samples. The longitude, latitude and elevation of all plots were determined using a Garmin GPS model 76.

Individual plots measured 70 m x 60 m (Figure 2); this size was dictated by the smallest timber harvest cut-block in which a plot was established. Each plot was subdivided by a numbered grid that was marked every 10 metres. The outer edges of plots were a minimum of 20 m from the nearest discontinuity such as a road, and a minimum of 500 m from those of the next study plot.

Vegetation sampling and measurement of environmental variables

Vegetation sampling was conducted in 2001. The plant community was stratified into tree, shrub and herb/moss layers. All woody vegetation greater than 2 m high was considered to be in the tree stratum. All woody and herbaceous vegetation less than 2 m, but greater than 30 cm high was considered to be in the shrub stratum. All vegetation, including moss, less than 30 cm in height, was considered to be in the herb/moss stratum.

The tree stratum was sampled in five randomly-chosen 10 m x 10 m quadrats in all plots except for the H95 site. In the H95 plots the tree stratum was composed of a dense growth of small saplings, so was sampled in five 2 m x 2 m quadrats. Quadrat locations were determined using a random number table to locate a point on the plot grid, and the compass direction from that point. Within each quadrat, the species, height and diameter at breast height (DBH) were determined for each tree except in the H95 plots, where DBH was not measured. DBH was measured using DBH calipers, and height was measured using a clinometer. Tree age was determined by taking a core sample from two trees per quadrat. Samples were taken approximately 30 cm from the base of each tree. This height avoided stem rot at the base of trees (which is common in aspen), and while limiting the number of growth rings missed to approximately two (Perala 1990). Trees that were selected were judged to have been representative of the quadrat, based on species and DBH.

A common method of classifying small areas of forest by vegetation and soil type is through the use of vegetation types (v-types). V-types use dichotomous keys to classify 10 m x 10 m forest areas according to overstory, shrub and herbaceous plant species composition, as well providing information on common soil types and acceptable management practices (Zoladeski et al. 1995). Although forest vegetation changes continuously along gradients, this method of classification provides a standardized means of describing and comparing forest stands. This model of forest classification is used by the forest industry in most Canadian provinces, and the inclusion of v-types facilitates the application of results by forestry companies and governments (Corns and Annas 1986; Sims et al. 1989). The vegetation type (v-type) of each tree sampling quadrat was identified according to Zoladeski et al. (1995).

Except in the H95 plots, canopy cover was measured to the nearest 5% using a Model C densiometer (Lemmon 1956). Measurements were taken in the centre of each tree sampling quadrat, with the densiometer held at a height of approximately 1.5 m.

The shrub stratum was sampled using ten 2 m x 2 m quadrats in each plot. Quadrat locations were selected using a random number table to locate a point on the plot grid; the compass direction and number of steps to the quadrat location from that point were also determined using the random number table. All shrubs were identified to species, the height of each plant was measured and the percent cover of each species was estimated to the nearest 5%.

The herb/moss stratum was sampled using ten 1 m x 1 m quadrats in each plot. Quadrat locations were selected in the same manner as for shrub quadrats. In each quadrat, the two most abundant species by percent cover were identified as well as the total percent cover of all herbs and mosses in the quadrat. Members of the family Poaceae were designated 'grass', and were not identified to genus or species.

Light intensity was measured August 13-15, 2002, within each plot at 10 random locations using a Gossen Tri-Lux foot-candle meter [Glossen GMBH, Erland, Germany] held at a height of approximately 1.5 m. Locations were selected using a random number table to locate a point on the plot grid; the compass direction and number of steps to the sampling location from that point were also determined using the random number table. Light intensity was measured on sunny days with minimal cloud cover. To standardize light intensity measurements, a reading was taken outside each plot in an open area (usually a roadway) that was used as a maximum light intensity value, and readings were recorded as percentages of the maximum light intensity. Care was taken to ensure that in-plot readings were taken in similar cloud cover conditions as the open area reading.

Carabid beetle sampling and identification

Adult carabid beetles were sampled in 2000, 2001 and 2002 on sampling dates shown in Table 1. Not all sites were sampled each year, and sampling was conducted over three years to ensure that all sites were samples at least two years (Table 1). Carabid beetles were sampled using pitfall traps, which consisted of two 473 cm^3 (16 oz.), 8 cm diameter plastic cups, one inside the other. This two-cup design minimized the disturbance to the area surrounding the trap while its contents were being removed. The traps were set so that the top of the inner cup was flush with the ground. Surrounding vegetation and leaf litter were left undisturbed. A plywood lid measuring approximately 10 cm x 10 cm covered each trap. The lids were elevated approximately 3 cm off the ground by 6 cm nails, one in each corner. Traps were filled approximately one-half full with 33% methanol (blue windshield wiper fluid) mixed with water in an approximately 1:1 ratio. This fluid acted as a killing agent and preservative.

Twelve pitfall traps were placed in each plot, in a 4 x 3 grid (Figure 2). The outer pitfall traps were located 20 m inside the edge of the plot, and the distance between adjacent traps was 10 m. Traps were emptied every two weeks, except in August 2000, when a flooded road delayed the collection of the H67 site for two weeks, and resulted in a four week interval.

Carabid beetles were identified using the keys of Lindroth (1961-1969). Taxonomic information was updated using Bousquet and Larochelle (1993). Dr. Y. Bousquet of Agriculture and Agri-Food Canada, Ottawa, identified specimens that could not be identified by the author.

Data analysis

Plot comparisons and pooling of data

Although three age classes were established in each of the two disturbance categories, only in the 1980 and 1961/67 age classes were burn and harvest plots of sufficiently similar age available for comparison. Therefore calculations that involve pooling data by disturbance type exclude the B32 and H95 plots.

Vegetation

Tree density (stems per m^2), the number of species in the tree stratum, the percentage of trees that were either *Populus tremuloides* or *Populus balsamifera* and the percentage of trees that were coniferous (*Picea glauca, Picea mariana*, *Pinus banksiana*, or *Abies balsamea* (L.) Mill.) were used to describe the composition of the tree stratum. Prior to analysis, the mean tree density was transformed ($\log_{10}$) to satisfy assumptions of normality and homogeneity of variance. The normality of all data, and hence the decision whether to log transform data, was assessed by examining the shape of the data sets (e.g. kurtosis, skewness), the one-sample Kolmogorov-Smirnov test and by determining Levene's statistic for use in ANOVA. Except for the H95 plots, the log-series α was used as an index of alpha diversity for the tree stratum. Light levels and canopy cover were used to indicate the density of the canopy. One-way Analysis of variance (ANOVA) with using SYSTAT General Linear Model (GLM) (Wilkenson 1998) was used to determine the effects of plot age and disturbance type on these variables. Contrast analysis was used to explore the differences between disturbance types within age classes. The coefficient of variation (c.v.) in the light intensity and canopy cover measurements within individual plots were calculated as follows:

$$c.v. = \left(\frac{\sigma}{\overline{x}} \right) \times 100$$

Where: **σ** is the standard deviation of the sample, and **x** is the mean.

The stem density, the percent cover of the shrub stratum and the number of species in the shrub stratum were used to describe the composition of the shrub layer. The Shannon-Weiner index (May 1975) was used to quantify the alpha diversity of the shrub layer, and was calculated using Bio~DAP software (Thomas 2000). ANOVA was used to determine the effects of plot age and disturbance type on these variables.

Carabid beetles

Carabid beetle data was entered in Microsoft Excel following the format described in Thomas (2001). The number of carabid beetles caught and the number of species of carabid beetles caught were used to indicate relative abundance and relative species richness in all plots. Tables present actual values, however, for all analyses involving the number of carabid beetles, values were transformed ($\log_{10}$) to satisfy assumptions of normality and homogeneity of variance. Alpha diversity was estimated using the log-series α diversity index (May 1975). Evenness was calculated using the slope parameter of a rank log abundance plot (Southwood and Brown 1979). Species dominance was calculated using the Berger-Parker index (Berger and Parker 1970). Beta diversity was measured using the Jaccard index of similarity (Southwood 1978). The Jaccard values for site-to-site comparisons are means of all possible plot-to-plot comparisons between the two sites being compared. Diversity statistics, including the log-series α, the Berger-

Parker index, and the Jaccard index were calculated using Bio~DAP software (Thomas 2000).

Conventional methods of estimating variance, such as standard error, are not applicable to comparisons among more than two Jaccard index values. When Jaccard index values are calculated, one site is half the pair multiple times, and therefore values are not independent of one another (Magurran 1988). This lack of independence between individual values invalidates the use of methods such as ANOVA. Consequently, tables which display mean Jaccard index values display the minimum and maximum values that contributed to the mean as an indicator of variation.

The most frequently caught carabid beetle species in each of the three collecting years were determined using the number of individuals from paired sites only (i.e. the 1980 and 1961/67 sites). Individual species were selected if their catch was greater than 1% of the total catch for that year from paired sites only.

The presence of all species that were caught predominantly or exclusively within a single plot was analyzed using the Poisson distribution. The probability of randomly catching an individual of a given species (λ) was the total number of individuals of that species caught, divided by the total number of plots that were sampled that year. If the Poisson probability of a species being caught in its actual frequency within a specific plot was less than 5%, its distribution was determined to be potentially non-random. Analysis was performed using the following equation:

$$P_{(k)} = \frac{(e^{-\lambda})(\lambda^{k})}{k!}$$

Where: $P_{(k)}$ is the probability of k occurrences given that λ is the probability of randomly encountering a given species in a plot.

Univariate analysis

ANOVA was used to determine the significance of the effect of time since disturbance and disturbance type on the following vegetation variables: stem density of the tree stratum and stem density of the shrub stratum; the number of species in the tree stratum and the number of species in the shrub stratum; the log-series α of the tree stratum; percent canopy cover; percent light intensity; percentage of tree stratum stems that were *Populus* spp.; the percent cover of the shrub stratum and the percent cover of the herb/moss stratum. ANOVA was also used to determine the effects of time since disturbance and disturbance type on the catch of carabid beetles; the number of species of carabid beetles; the log-series α index for carabid beetles; evenness; and the Berger-Parker index. One-way Analysis of variance (ANOVA) with using SYSTAT General Linear Model (GLM) (Wilkenson 1998) was used to determine the effects of plot age and disturbance type on these variables. Contrast analysis was used to explore the differences between disturbance types within age classes.

Paired t-tests were used to determine whether disturbance type affected individual species of carabid beetles in paired sites.

Multivariate analysis

Analysis of the Jaccard index values was performed using hierarchical clustering (Wilkinson 1998). Data were saved as a similarity matrix so that the actual values would be used as distances in the analysis. Average linkage, as opposed to centroid or single linkages, was used because it best represented the raw data.

Unless otherwise specified, all indirect gradient analysis was performed using CANOCO for Windows software version 4.5 with default settings (ter Braak and Šmilauer 2002). All species matrices were transformed ($y' = \log_{10} [y + 1]$) using the log transformation option in CANOCO.

Detrended correspondence analysis (DCA) using detrending by segments was performed on all data sets prior to further ordination analysis. As the resulting gradients never exceeded 4 standard deviation units in length, linear species response models were indicated (ter Braak and Šmilauer 2002) and so further analyses assumed a linear response model. Principle component analysis (PCA) was used for unconstrained analyses and redundancy analysis (RDA) was used to examine the relationship between species distributions and environmental variables. In PCA of the tree and shrub strata, log transformed data were used in an effort to reduce the dominating effects of the most abundant species. In PCA of carabid beetles, log transformed data were also used. For carabid beetles, the three sampling years were analyzed separately.

In all RDA, Monte Carlo permutation tests were used to determine the significance of relationships between environmental variables and the species data. For each test, 499 permutations were randomly generated, and variables with $p \leq 0.05$ were considered significant (ter Braak and Šmilauer 2002). The continuous environmental variables that were tested with carabid beetles using this method included: tree age, the number of tree species, the percentage of the trees that were *Populus* spp., the mean canopy cover, the mean light intensity, the Shannon-Weiner index for the shrub stratum, and the percent cover of the herb/moss stratum. These variables were selected because they provided the best estimates of the vegetation composition in all three strata, while minimizing overlap between multiple variables. Using forward selection, only significant environmental variables were retained in these analyses and are displayed on RDA figures.

In RDA of carabid beetles and treatment variables (i.e. time since disturbance and disturbance type) only paired sites were used in the analyses. Using unpaired sites in these analyses would have made for a non-orthogonal design, impeding the ability to discriminate between the effects of time since disturbance and disturbance type. All other

RDAs used all plots in the analyses; however, the unbalanced study design should be taken into account when these analyses are considered. Disturbance type and age class were displayed as nominal variables. Monte Carlo permutation tests were used to determine the significance of relationships between carabid beetles and treatment variables, but forward selection was not used on treatment variables and all are displayed on RDA figures.

Table 1: The disturbance type, year of disturbance, location, elevation, and dates of carabid beetle sampling for all plots.

Site	Plot	Disturbance type	Year of disturbance	Latitude (N)	Longitude (W)	Elevation (m)	Location[1]	2000		2001		2002	
								Pitfall traps installed	Pitfall traps removed	Pitfall traps installed	Pitfall traps removed	Pitfall traps installed	Pitfall traps removed
B32	B32A1	Burn	1932	51°35.666’	100°53.444’	743	DMPP	July 4	Aug. 30	May 22	Aug. 18	Not Sampled	
	B32A2	Burn	1932	51°35.353’	100°53.609’	725	DMPP	July 4	Aug. 30	May 22	Aug. 18	Not Sampled	
B61	B61A1	Burn	1961	51°38.080’	100°54.810’	669	DMPP	July 4	Aug. 30	May 22	Aug. 18	Not Sampled	
	B61A2	Burn	1961	51°38.699’	100°53.916’	774	DMPP	July 4	Aug. 30	May 22	Aug. 18	Not Sampled	
	B61B1	Burn	1961	51°40.963’	100°54.983’	744	DMPP	July 4	Aug. 30	May 22	Aug. 18	Not Sampled	
	B61B2	Burn	1961	51°41.266’	100°55.000’	736	DMPP	July 4	Aug. 30	May 22	Aug. 18	Not Sampled	
B80	B80A1	Burn	1980	52°16.959’	101°30.189’	671	PMPF	July 4	Aug. 30	May 22	Aug. 18	May 22	Aug. 14
	B80A2	Burn	1980	52°18.689’	101°30.226’	638	PMPF	July 4	Aug. 30	May 22	Aug. 18	May 22	Aug. 14
	B80B1	Burn	1980	52°19.660’	101°33.268’	632	PMPF	July 4	Aug. 30	May 22	Aug. 18	May 22	Aug. 14
	B80B2	Burn	1980	52°19.651’	101°33.893’	645	PMPF	July 4	Aug. 30	May 22	Aug. 18	May 22	Aug. 14
H67	H67A1	Harvest	1967	51°49.194’	101°18.326’	622	DMPF	July 4	Aug. 30	May 22	Aug. 18	Not Sampled	
	H67A2	Harvest	1967	51°48.942’	101°18.167’	649	DMPF	July 4	Aug. 30	May 22	Aug. 18	Not Sampled	
	H67B1	Harvest	1967	51°48.490’	101°17.422’	640	DMPF	July 4	Aug. 30	May 22	Aug. 18	Not Sampled	
	H67B2	Harvest	1967	51°48.324’	101°17.030’	640	DMPF	July 4	Aug. 30	May 22	Aug. 18	Not Sampled	
H80	H80A1	Harvest	1980	52°02.440’	100°55.317’	645	DMPF	Not Sampled		May 22	Aug. 18	May 22	Aug. 14
	H80A2	Harvest	1980	52°02.480’	100°54.895’	654	DMPF	Not Sampled		May 22	Aug. 18	May 22	Aug. 14
H95	H95A1	Harvest	1995	51°54.246’	101°11.203’	601	DMPF	July 4	Aug. 30	May 22	Aug. 18	Not Sampled	
	H95A2	Harvest	1995	51°53.966’	101°11.267’	598	DMPF	July 4	Aug. 30	May 22	Aug. 18	Not Sampled	
	H95B1	Harvest	1995	51°48.662’	101°18.426’	640	DMPF	Not Sampled		May 22	Aug. 18	Not Sampled	
	H95B2	Harvest	1995	51°36.191’	101°28.389’	718	DMPF	July 4	Aug. 30	May 22	Aug. 18	Not Sampled	

[1] DMPP – Duck Mountain Provincial Park; DMPF – Duck Mountain Provincial Forest; PMPF – Porcupine Mountain Provincial Forest

Figure 1: Research area and location of study plots.

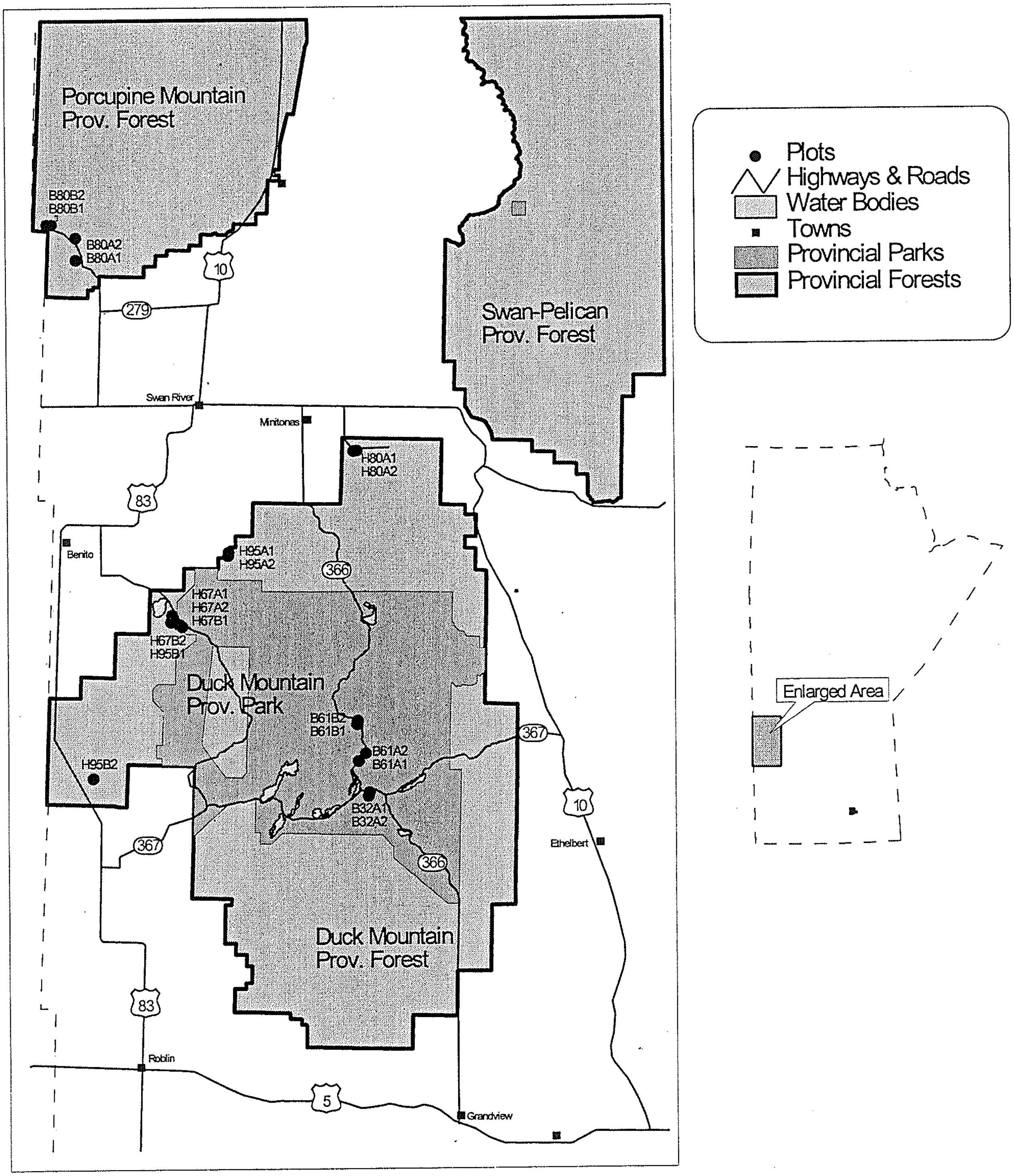
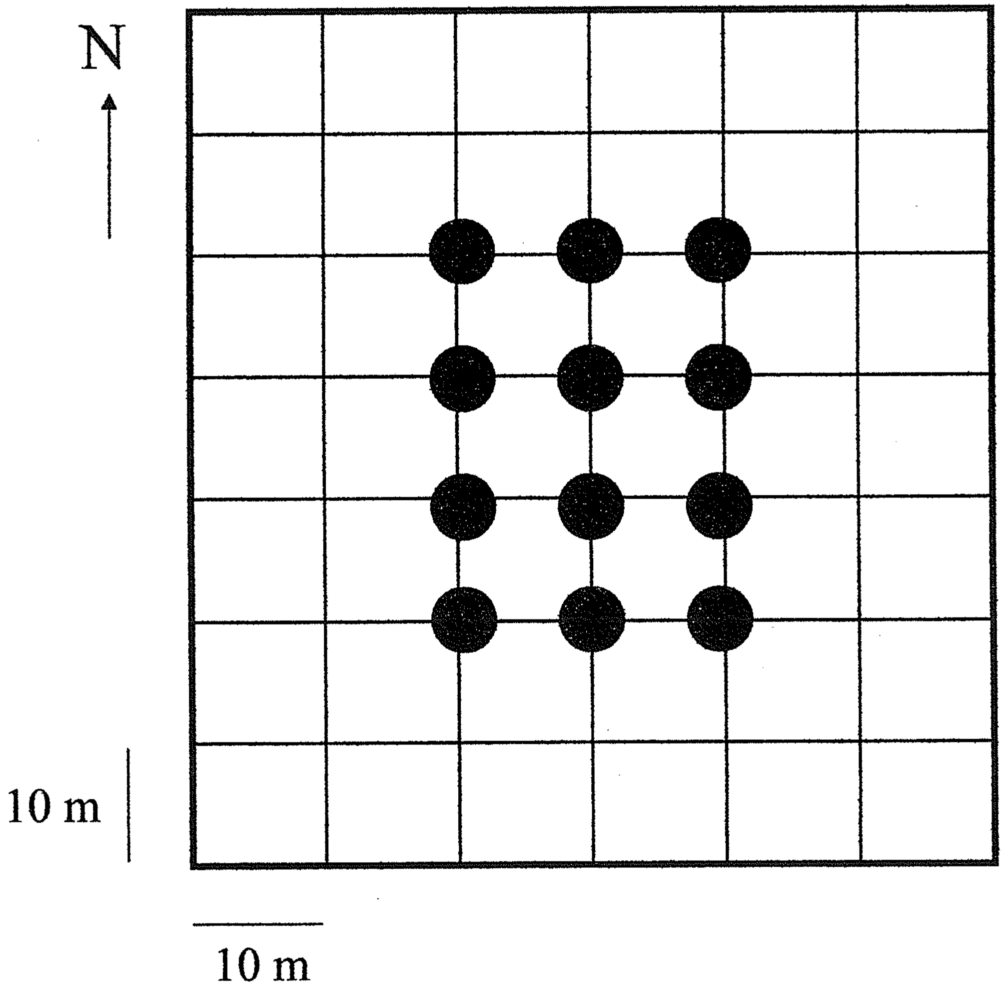


Figure 2: Plot layout

- 70 m x 60 m
- Pitfall traps ●



Results

Vegetation

A list of all species from the tree, shrub and herb/moss strata sampled in this study is provided in Appendix II, which also shows the density of each species in the tree stratum and the percent cover of all plants in the shrub and herb/moss strata. Appendices III, IV and V present details of vegetation measurements for burn and harvest plots, and means for each site respectively. Stem counts and mean percent cover for all species from the tree and shrub strata for each plot are shown in Appendix VI.

Vegetation types

Table 2 shows the vegetation types (v-types) from all plots (Zoladeski et al. 1995). Appendix VII, based on Zoladeski et al. (1995), summarizes v-type characteristics. The most common v-type was 'Aspen hardwood' (V5), which was characteristic of all plots except B32A2 and four quadrats each in B61B2 and B80A1 (Table 2). 'Aspen hardwood' sites are characterized by an overstory that is dominated by *Populus tremuloides*, a shrub layer of *Amelanchier* spp. and an herbaceous layer of *Aralia nudicaulis* (Appendix VII). The occurrence of *Pinus banksiana* and *Picea glauca* in plot B32A2 resulted in v-types that differed from those that occurred in the rest of the plots (Table 2). Plot B80A1 had a high abundance of *Betula papyrifera* (Appendix VI), resulting in four of five quadrats being classified as 'White birch hardwood and mixedwood' (V4) (Table 2). All v-types identified in this study fall within a moisture regime of 'moist' to 'fresh' and are considered nutrient rich (Zoladeski et al. 1995).

Tree stratum

In 19 of 20 plots, *Populus tremuloides* was the most common species in the tree stratum, and in B80A1 it was the second most common tree stratum species (Appendix II). In 10 plots, *Populus balsamifera* was the second most common tree stratum species. Three plots, B61A1, B61B2 and B32A2, had either *Pinus banksiana* or *Picea glauca* as the second most common tree stratum species. Relative to all other plots, B80A1 had a high abundance of *Betula papyrifera*.

Six tree stratum variables were statistically compared (Table 3). Three of these variables were significantly affected by time since disturbance: stem density and light intensity were higher in the 1980 plots; while canopy cover was higher in the 1961/67 plots (Table 3). Stem density was higher in the burn plots and was the only variable that showed a disturbance effect (Table 3). Stem density, the number of tree species, and log-series α each showed a significant interaction between disturbance type and time since disturbance (Table 3).

In the 1961/67 plots, stem density was higher in the burn plots and was the only variable that was significantly affected by disturbance type (Table 3). In the 1980 plots, disturbance type significantly affected five of the six variables: stem density and canopy cover were higher in the burn plots; more species were found in the harvest plots; and the log-series α and light intensity were higher in the harvest plots (Table 3).

In the H95 plots, the trees were shorter and more densely spaced than in other plots (Table 3; Appendix IV). Although the tree stratum in the H95 plots was made up exclusively of sapling *Populus tremuloides* and *Populus balsamifera*, each site did include one to five mature residual trees that were left following the timber harvests.

In principal component analysis (PCA) of the tree stratum, the first two axes explained 55.0% of the variation in the species data (Figure 3). *Populus tremuloides* was very dense in the H95 plots, and this strongly influenced the analysis. The densities of *Betula papyrifera* and *Salix* spp. were negatively correlated with *P. tremuloides*, as were coniferous species *Abies balsamea*, *Picea glauca* and *Picea mariana*. *Betula papyrifera* was quite dense in plot B80A1, and was strongly associated with this plot. The second axis separated plots based on *Corylus cornuta* Marsh. and *Prunus* spp, which were positively correlated with each other. The H80 and B80 plots were widely separated along the second axis, due to the presence of these species in the tree stratum of the H80 plots and their absence from the B80 plots. *Alunus crispa* (Ait.) Pursh was also much more abundant in the H80 plots than the B80 plots. The tree stratum of the B80 plots had a greater density of *Populus balsamifera* and *Salix* spp. than the H80 plots.

To reduce the influence of the H95 plots, the second and third axes of the PCA from Figure 3 were plotted (Figure 4); these two axes explained 35.0% of the variation in the species data. Species such as *Abies balsamea*, *Betula papyrifera* and *Picea glauca* were strongly associated with the third axis. Older burn plots, such as those in the B61 site and plot B32A2, were positively associated with these three species, while the H67 plots, H80 plots and B80 plots were negatively associated with these three species.

Shrub stratum

Appendix II shows all species from the shrub stratum and their mean percent cover in all study plots. *Rosa acicularis* Lindl. was the only species that occurred in the shrub stratum of all 20 plots, and was one of the three most abundant species in the shrub stratum in 17 plots. The next two most commonly occurring species, *Rubus idaeus* L. and *Symphiocarpos albus* (L.) Blake, were found in 19 and 16 plots respectively.

Table 4 shows the four shrub stratum variables that were statistically compared. None of the variables were significantly affected by time since disturbance. Disturbance type significantly affected two variables: stem density was higher in burn plots and the Shannon-Weiner Index was higher in harvest plots (Table 4). In the 1961/67 plots, stem density was significantly higher in the burn plots than the harvest plots (Table 4). None of the variables differed in the 1980 plots.

Of the 27 plant species that were recorded in the shrub stratum, *Disporum trachycarpum* (Wats.) B. & H. was significantly more dense in the 1961/67 plots than the 1980 plots, and was the only species that was significantly affected by time since disturbance (Table 5). Two species were affected by disturbance type: *Rosa acicularis* was significantly more dense in the shrub stratum of burn plots, while *Ribes oxyacanthoides* L. was significantly more dense in the shrub stratum of harvest plots (Table 5). *Rosa acicularis* was more dense in the B80 plots than in the H80 plots, and in the B61 plots than in H67 plots (Table 5).

Corylus cornuta was abundant in the shrub stratum of all the H95 plots, as well as in plots B32A1, B61A1, H67B1 and H67B2 (Appendix II). *Populus tremuloides* was abundant in the shrub stratum in all H95 plots, and virtually absent from the shrub stratum of all other plots (Appendix II).

In PCA of the shrub stratum, the first two axes explained 46.4% of the variation (Figure 5). The first axis separated plots based on *C. cornuta*, *Populus balsamifera*, *Populus tremuloides*, *Prunus pensylvanica* L.f. and *Prunus virginiana* L., all of which were abundant in the H95 plots. Plots were separated along the second axis based on two species groups: *Apocynum androsaemifolium* L., *Picea glauca*, *Shepherdia canadensis* and *Viburnum edule* (Michx.) Raf. were associated with the B80 plots; while *Alnus crispa*, *Ribes oxyacanthoides*, *Rubus acaulis* Michx. and *Ribes triste* Pall. were associated with the H80, H67 plots, and three of the B61 plots. The B61 and H67 plots showed significant overlap, while the B80 and H80 plots were separated by the second axis.

Herb/moss stratum

Appendix II shows the mean percent cover of the two most common species in the herb/moss stratum all plots. Appendices III and IV show the mean total percent cover of the herb/moss stratum and the percentage of bare ground in all burn and harvest plots respectively; Appendix V shows site means for these variables. *Aralia nudicaulis* and unidentified grass species were the two most common taxa in the herb/moss stratum, occurring as one of the most common plants in 11 and 10 plots respectively (Appendix II). *Aralia nudicaulis* occurred in all sites, and grass was very abundant in all sites except the H80 site. *Rubus pubescens* Raf. And *Viola pubescens* Ait. were each among the two most common plants in the herb/moss stratum in four plots (Appendix II).

The total percent cover in the herb/moss stratum was significantly affected by time since disturbance, and was higher in the 1961/67 plots than the 1980 plots (Table 4). Disturbance type did not affect percent cover and there were no significant differences within either the 1961/67 or 1980 age classes. The interaction between time since disturbance and disturbance type was not significant.

Carabid beetles

Number of carabid beetles

A total of 13873 carabid beetles representing 51 species were caught over the three years of this study. In 2000, 1061 carabid beetles were caught, representing 34 species; in 2001, 9224 carabid beetles were caught, representing 36 species; and in 2002, 3588 carabid beetles were caught, representing 28 species. These differences reflect variations in the length of the trapping period and the number of plots sampled in each of the three sampling years (Table 1). The 10 most frequently caught species accounted for 95.9% of the total catch. *Platynus decentis* was the most frequently caught species, accounting for 52.5% of the total catch. The next nine species in order of catch frequency were *Pterostichus pensylvanicus*, *Calathus ingratus*, *Pterostichus adstrictus*, *Agonum retractum* LeConte, *Carabus taedatus* LeConte, *Synuchus impunctatus* (Say), *Calosoma frigidum* Kirby, *Sphaeroderus nitidicollis* LeConte and *Stereocercus haematopus* Dejean. The most frequently caught species in each plot by trapping year are shown in Appendix VIII. Appendices IX, X and XI show the number of individuals of all species of carabid beetles caught in 2000, 2001 and 2002 respectively.

In 2001, significantly more carabid beetles were caught in burned plots than in harvested plots (Table 7). In 2000 and 2001, significantly more carabid beetles were caught in the B61 plots than in the H67 plots (Tables 6 & 7). In 2001 and 2002, the 1980 plots did not show a significant difference in the number of carabid beetles caught (Tables 7 & 8). In 2001, time since disturbance significantly affected the number of carabid beetles caught;

significantly more carabid beetles were caught in the 1961/67 plots than in the 1980 plots (Table 7). No significant differences were detected in the number of species of carabid beetles caught in 2000, 2001 or 2002.

In 2001, burn plots had much higher catch frequencies of carabid beetles in both the overall disturbance comparison, and the comparison of the plots disturbed in 1980. Despite these large disparities, ANOVA did not detect significant differences (Table 7). The primary reason was a lack of consistency among plots within sites, which resulted in large variances.

Log-series α, evenness and the Jaccard index

Appendices IX, X and XI show the log-series α and evenness values for individual plots for 2000, 2001 and 2002 respectively. No significant differences were detected in the log-series α in any of the sampling years (Tables 6, 7 & 8). Although no significant differences were observed, plots that were more recently disturbed had consistently higher log-series α values than older plots (Tables 6, 7 & 8). There were no significant differences in evenness in any of the sampling years, but more recently disturbed plots had consistently lower values (i.e. were more even) than older plots (Tables 6, 7 & 8). There were no significant differences in the Berger-Parker index, but more recently disturbed plots had consistently lower values (i.e. showed less dominance) than older plots (Tables 6, 7 & 8).

The Jaccard index of similarity for site to site comparisons for 2000, 2001 and 2002 are shown in Tables 9, 10 & 11 respectively. Of all sites, the B61 plots were the most similar within a site in 2000 and 2001 (Tables 9 & 10). There was a general trend of decreasing similarity between sites as the time since disturbance between them increased (i.e. the B32 and B61 plots were more similar than the B32 and B80 plots) (Tables 9 & 10). In 2001, the mean Jaccard index value between the B61 plots and the H67 plots was higher than between the B80 plots and the H80 plots (Table 10). The mean Jaccard index value between B80 plots and H80 plots was higher in 2002 (Table 11) than in 2001 (Table 10).

Figure 6 shows the results of hierarchical cluster analysis of carabid beetles caught in 2000. The plots in the H95 site and plot H67A2 were grouped together, away from all other plots. Despite being clustered together, the distances between these plots were still relatively high. The two B32 plots were grouped closely together, as were the B61 plots and the remaining three H67 plots. Six of eight 1961/67 plots were placed in the same cluster within a distance of 0.5. This indicated a relatively high degree of similarity between the harvest and burn plots in this age class. Plots B80B1 and B80B2, grouped together and away from most other plots; while B80A1 and B80A2 were clustered more closely with the H67 and B61 plots. This seemed to indicate that there was more heterogeneity within more recently disturbed plots.

Figure 7 shows the results of hierarchical cluster analysis of carabid beetles caught in 2001. The analysis showed plot H95A2 to be the most different, relative to all other plots.

The remaining H95 plots clustered together with plot H80A1. The two H80 plots were widely separated, although three of the B80 plots clustered together. All B61 plots were placed on the same cluster within a distance of 0.4. Overall, this analysis showed a lack of consistency among plots within sites, although overall distances were smaller than in figure 6.

Figure 8 shows the results of hierarchical cluster analysis of carabid beetles caught in 2002. The six plots did not cluster according to disturbance type. Plots B80A2 and B80B1 were clustered together, away from the remaining plots. Plots B80A1 and H80A1 had the highest degree of similarity.

Most frequently caught species

Appendices IX, X, and XI show the total number of species caught in each plot in 2000, 2001 and 2002 respectively. In 2000, a total of 34 species were caught, but no single species was caught in all 17 plots. In 2001, a total of 36 species were caught. Three species, *Agonum retractum*, *Platynus decentis* and *Pterostichus pensylvanicus* were caught in all 20 study plots (Appendix VIII). In 2002, of 28 species were caught, seven species, *Agonum retractum*, *Calathus ingratus*, *Platynus decentis*, *Pterostichus adstrictus*, *Pterostichus pensylvanicus*, *Sphaeroderus nitidicollis* and *Synuchus impunctatus*, were caught in all 6 study plots.

In 2000, nine species had a catch frequency greater than one percent of the total catch for that year (Table 12). Two of these species, *Carabus taedatus* and *Pterostichus adstrictus* were caught with significantly greater frequency in the B61 plots than in the H67 plots (Table 12). A paired t-test on the number of beetles caught for the nine most frequently caught species that compared the B61 plots with the H67 plots showed that the B61 plots had a significantly higher number of beetles caught ($t_8 = 2.5$, $p = 0.038$).

In 2001, ten species each had a catch frequency greater than one percent of the total catch (Table 13). Two of these species, *Carabus taedatus* and *Pterostichus adstrictus* were caught with significantly greater frequency in the 1961/67 plots than the 1980 plots. *Pterostichus pensylvanicus* was the only species that was caught with significantly greater frequency in the burn plots than the harvest plots (Table 13). Three species were significantly affected by disturbance in the 1961/67 plots: *C. taedatus*, *P. adstrictus* and *P. pensylvanicus* were all caught with greater frequency in the B61 plots than the H67 plots (Table 13). Three of the ten species had higher, but non-significant, catch frequencies in the H67 plots than in the B61 plots; these were *Calosoma frigidum*, *Sphaeroderus nitidicollis* and *Synuchus impunctatus* and. A paired t-test on the ten most frequently caught species comparing the B61 plots with the H67 plots showed no significant difference ($t_9 = 2.1$, $p = 0.067$). None of the ten species were significantly affected by disturbance type in the 1980 sites (Table 13). The only species that was caught more frequently in the H80 plots than the B80 plots was *S. nitidicollis* (Table 13).

A paired t-test on the ten most frequently caught species comparing the B80 plots with the H80 plots showed no significant difference ($t_9 = 1.4, p = 0.183$).

In 2002, six species each had a catch frequency of greater than one percent of the total catch (Table 14). *Calosoma frigidum* was caught with significantly greater frequency in the H80 plots than the B80 plots (Table 14). *Agonum retractum* was the only species that was caught more frequently in the B80 plots than the H80 plots. A paired t-test on the catch frequency of the six species comparing the B80 plots with the H80 plots showed no significant difference ($t_5 = -1.1, p = 0.329$).

Seasonal variations in catch frequency

Two of the three years showed a trend of decreasing catch frequency as the season progressed (Figure 9). The only exception was in 2002, where there was an increase in catch frequency in early July in the B80 plots. This same trend was also observed in the B80 plots in 2001. Note that in the number of plots sampled each year was not consistent, and that 2001 was the only year in which all plots were sampled.

In 2001, the ten most frequently caught species showed a variety of seasonal occurrence patterns (Figure 10). *Calosoma frigidum*, *Carabus chamissonis* Fischer von Wadlheim, *Platynus decentis*, *Pterostichus adstrictus*, *Pterostichus pensylvanicus* and *Stereocercus haematopus* were all most caught most frequently in June and declined as the summer progressed. The catch frequency of *Agonum retractum* and *Calathus ingratus* peaked in early July. *Carabus taedatus* seemed to have a bimodal seasonal distribution, being most frequently caught in early June and again in mid-August. *Synuchus impunctatus* was most frequently caught in early August.

Rare and unique species

In 2000, 18 species were caught predominantly or exclusively within one site. Of these, the occurrences of two species were considered to be non-random using the Poisson distribution: *Agonum simile* Kirby and *Stereocercus haematopus* (Table 15).

In 2001, 15 species were caught predominantly or exclusively within one site. Of these, the occurrences of four species were considered to be non-random using the Poisson distribution: *Agonum trigeminum* Lindroth, *Dicaelus sculptilis* Say (Randall), *Pterostichus punctatissimus* and *Stereocercus haematopus* (Table 15).

In 2002, 11 species were caught exclusively in the H80 site or the B80 site. *Carabus chamissonis* was the only species whose occurrence was considered non-random using the Poisson distribution (Table 15).

Relative to all other species that were unique to a site or disturbance type, *Stereocercus haematopus* had a very high catch frequency in 2000 and 2001 (Appendices IX & X). It was caught in three plots (B32A1, B32A2 and B61A2); of those plots, B32A2 had the highest catch frequency in both years.

Bradycellus semipubescens Lindroth was the only new provincial record among all species caught. It had previously been recorded in New Brunswick, Quebec, Ontario and Alberta (Natural Resources, Canada 2004). No species that are considered non-native or invasive were caught during this study.

Principle component analysis

2000

In PCA of the carabid beetle data from 2000, the first two axes explained 61.2% of the species variation (Figure 11). The first axis separated plots based on catch frequency of *Calathus ingratus*, *Carabus taedatus*, *Pterostichus adstrictus* and *Pterostichus pensylvanicus*. Plots in the B61 and B32 sites were positively associated with these species. At the opposite end of the first axis, were *Agonum cupreum* Dejean, *Agonum gratiosum* (Mannerheim), *Carabus maeander* Fischer von Wadlheim and *Patrobus septentrionis* Dejean. These species were associated with plots in the H95 site and with H67A1 and H67A2.

The second axis was associated with *Synuchus impunctatus*. Plots in the B80 site, as well as H67B1 and H67B2 were associated with this species. With the exception of H67B2, the first axis separated plots based on disturbance type and some separation of plots based on time since disturbance.

2001

In PCA of the carabid beetle species from 2001, the first two axes explained 61.0% of the variation in the species data (Figure 12). Separation among plots along the first axis was based on *Calathus ingratus*, *Carabus chamissonis*, *Carabus taedatus*, *Platynus decentis* and *Pterostichus adstrictus*. Plots in the B32 and B61 sites were associated with these species. *Agonum cupreum*, *Agonum gratiosum*, *Carabus maeander* and *Synuchus impunctatus* were negatively correlated with these species along the first axis; as were the H95 plots, the H80 plots and plot H67A1. The first axis separated the plots based on time since disturbance.

The second axis separated plots based on *Agonum retractum* and *Agonum simile*. Plots which were associated with these species included H67A2, H67B2 and B80B1. Both plots in the B32 site were strongly associated with *Stereocercus haematopus*.

Figure 13 shows the separation of burn and harvest plots based on the first axis PCA scores taken from Figure 12. Based on first axis separation, plots H67B1 and H67B2 were more closely associated with burn plots than with harvest plots (Figures 12 and 13). These two plots had higher catch frequencies of *Calathus ingratus*, *Pterostichus adstrictus* and *Platynus decentis*, and a lower catch frequency of *Synuchus impunctatus* relative to the other two H67 plots.

Based on first axis separation, plots B80A1 and B80B2 were more closely associated with harvest plots than with burn plots (Figures 12 and 13). When compared to B80A2 and B80B1, the other two plots in the site, these plots had lower catch frequencies of *Calathus ingratus*, *Carabus chamissonis* and *Platynus decentis*. Plot B80B2 was devoid of *P. adstrictus*, a species strongly correlated with the negative end of the first axis. Plot B80A1 had a higher catch frequency of *Synuchus impunctatus* than any of the other B80 plots.

2002

In PCA of the carabid beetle data from 2002, the first two axes explained 64.0% of the variation (Figure 14). The first axis separated plots based primarily on *Agonum retractum*, *Carabus chamissonis* and *Poecilus lucublandus*. Plots B80A2 and B80B1 had a high catch frequency of these species. *Calosoma frigidum* and *Synuchus impunctatus* and were strongly associated with the H80 plots. *Carabus maeander*, *Pterostichus adstrictus*, *Pterostichus pensylvanicus* and *Sphaeroderus nitidicollis* were associated with the second axis; plots B80A2, H80A1 and H80A2 were associated with these species. *Platynus decentis* was strongly associated with plot B80A2. Neither axis separated the plots based on disturbance type, although the analysis was heavily influenced by plot B80A2, which had an overall catch frequency that was much higher than any of the other plots.

Redundancy analysis

Carabid beetle species and treatment variables

2000

In redundancy analysis (RDA) of all carabid beetles caught in the 1961/67 plots in 2000 with disturbance type as the environmental variable, the first two axes explained 68.1% of the variation in the species data (Figure 15). Monte Carlo tests indicated that the disturbance type variable was significant ($p \leq 0.05$). *Agonum retractum*, *Carabus taedatus*, *Pterostichus pensylvanicus* and *Sphaeroderus nitidicollis* were positively correlated with the burn variable. These species were more frequently caught in plots B61A2 and B61B1, but all were frequently caught in the B61 plots. Positive associations between species and the harvest variable were not as strong as those for the burn variable. Species that were positively associated with the harvest variable included *Agonum gratiosum*, *Agonum superioris* Lindroth and *Synuchus impunctatus*. *Platynus decentis* was the only species that was strongly associated with the second axis. The catch frequency of this species varied considerably between plots in each site, and was responsible for the wide separation of plots along the second axis.

2001

In RDA of all carabid beetles caught in the 1961/67 and 1980 plots in 2001 with disturbance type and time since disturbance as the environmental variables, the first two axes explained 42.8% of the variation in the species data (Figure 16). Monte Carlo tests indicated that both disturbance type and time since disturbance were significant ($p \leq 0.05$). A group of species including *Calathus ingratus*, *Carabus chamissonis*, *Carabus taedatus*, *Platynus decentis Pterostichus adstrictus* and *Pterostichus pensylvanicus* were strongly positively associated with the B61 plots. Species associations with the H67 plots were not as strong, although *Carabus maeander* and *Sphaeroderus nitidicollis* did show positive associations. *Calosoma frigidum* was strongly correlated with the thirty-five-years-since-disturbance variable, and was caught in all but one of the 1961/67 plots. No species were strongly associated with the twenty-years-since-disturbance variable, but rather were associated with either the B80 or H80 plots. *Agonum gratiosum* was positively associated with the H80 plots, while *Agonum cupreum* was positively associated with the B80 plots.

Carabid beetle species and environmental variables

2000

In RDA of all carabid beetles caught in 2000 with significant environmental variables, the first two axes explained 37.1% of the variation in the species data (Figure 17). Monte Carlo tests indicated that canopy cover and tree age were significant ($p \leq 0.05$). Both canopy cover and tree age are related to time since disturbance, and this resulted in a separation of plots on this basis. *Carabus taedatus*, *Pterostichus adstrictus* and *Pterostichus pensylvanicus* were strongly associated with tree age, and were caught predominately in older plots (e.g. B32). *Calathus ingratus*, *Platynus decentis* and *Sphaeroderus nitidicollis* were strongly positively associated with canopy cover, and were caught with high frequency in the H67 and B61 plots, where canopy cover was greatest. Several species were strongly negatively correlated with canopy cover, including *Agonum cupreum*, *Agonum gratiosum*, *Carabus maeander* and *Patrobus septentrionis*. These species were all caught most frequently in the H95 plots, where a tree canopy was virtually absent. *Agonum simile* and *Agonum superioris* were closely associated with the B80 plots.

2001

In RDA of all carabid beetles caught in 2001 with significant environmental variables, the first two axes explained 39.7% of the variation in the species data (Figure 18). Monte Carlo tests on the environmental variables indicated that tree age and canopy cover were significant ($p \leq 0.05$). These two variables are related to time since disturbance, and this resulted in a separation of plots on this basis. Species that were positively correlated with tree age included *Carabus taedatus*, *Pterostichus adstrictus* and *Carabus chamissonis*. *Synuchus impunctatus* was negatively correlated with tree age. Canopy cover was greatest in the H67 and B61 plots. Species that were positively correlated with canopy cover included *Calathus ingratus*, *Calosoma frigidum* and *Sphaeroderus nitidicollis*. The H95 plots, which lacked a canopy, and a number of species, were strongly negatively correlated with canopy cover. These species included *Agonum cupreum*, *Agonum gratiosum* and *Carabus maeander*. *Stereocercus haematopus* was strongly associated with the B32 plots. *Platynus decentis* seemed to be equally positively correlated with tree age and canopy cover. Both sets of paired sites were closely associated, indicating similarities in canopy cover and tree age.

Carabid beetle species and shrub stratum

2000

In RDA of all carabid beetles caught in 2000 with shrub stratum species as environmental variables the first two axes explained 48.1% of the variation in the species data (Figure 19). Monte Carlo tests on all shrub stratum species indicated that *Amelanchier alnifolia* Nutt., *Apocynum androsaemifolium*, *Disporum trachycarpum*, *Populus balsamifera* and *Symphiocarpus albus* were significant ($p \leq 0.05$). This analysis resulted in a wide separation of plots within sites. *D. trachycarpum* and *P. balsamifera* were correlated with the first axis, and negatively with each other. There was some separation of plots along the first axis based on time since disturbance; older plots were associated with *D. trachycarpum*, while more recently disturbed plots were associated with *P. balsamifera*. *Calathus ingratus* and *Carabus taedatus* were associated with *D. trachycarpum*, as were plots B61B1 and B61B2. The H95 plots had a high density of shrub stratum *P. balsamifera*; carabid beetle species associated with *P. balsamifera* included *Agonum gratiosum* and *Carabus maeander*. The shrub stratum species *A. androsaemifolium* was correlated with the second axis. Plots B80B1 and B80B2, and carabid beetle species *Agonum simile* were positively correlated with *A. androsaemifolium*.

Shrub stratum species *Amelanchier alnifolia* and *Symphiocarpus albus* were negatively correlated with *Apocynum androsaemifolium* along the second axis. *Carabus chamissonis* and *Stereocercus haematopus*, and the B32 plots were associated with these two shrub species.

2001

In RDA of all carabid beetles caught in 2001 with shrub stratum species as environmental variables, the first two axes explained 43.3% of the variation in the species data (Figure 20). Monte Carlo tests on all shrub stratum species indicated that *Apocynum androsaemifolium*, *Cornus stolonifera* Michx., *Disporum trachycarpum* and *Shepherdia canadensis* (L.) Nutt. were significant ($p \leq 0.05$). There was some separation of plots along the first axis based on time since disturbance; older plots were positively correlated with *D. trachycarpum*. Carabid beetle species associated with *D. trachycarpum* included *Calathus ingratus*, *Carabus taedatus*, *Platynus decentis* and *Pterostichus adstrictus*. Carabid beetle species *Agonum cupreum* and *Synuchus impunctatus* were negatively correlated with *D. trachycarpum*. The second axis separated *A. androsaemifolium* and *S. canadensis*, which were negatively correlated with one another. *Shepherdia canadensis* was associated with the B32 plots and *Stereocercus haematopus*. *Apocynum androsaemifolium* was positively associated with *Agonum retractum*. *Cornus stolonifera* was strongly associated with plot H95A2 and *Agonum gratiosum* and *Carabus maeander*.

The large group of plots located near the centre of the diagram did not have any occurrence of these plant species in the shrub stratum.

Table 2a: Vegetation types (v-types) from the 5 tree-stratum sampling areas in each plot.

Plot	V-Types
B32A1	V5 V5 V5 V5 V8
B32A2	V8 V8 V8 V10 V13
B61A1	V5 V5 V5 V8 V9
B61A2	V5 V5 V5 V5 V9
B61B1	V5 V5 V5 V5 V5
B61B2	V5 V8 V9 V9 V9
B80A1	V4 V4 V4 V4 V5
B80A2	V5 V5 V5 V5 V5
B80B1	V5 V5 V5 V5 V5
B80B2	V5 V5 V5 V5 V5
H67A1	V5 V5 V5 V5 V5
H67A2	V5 V5 V5 V5 V5
H67B1	V5 V5 V5 V5 V5
H67B2	V5 V5 V5 V5 V5
H80A1	V5 V5 V5 V8 V8
H80A2	V5 V5 V5 V8 V8
H95A1	V5 V5 V5 V5 V5
H95A2	V5 V5 V5 V5 V5
H95B1	V5 V5 V5 V5 V5
H95B2	V5 V5 V5 V5 V5

Table 2b: V-types names listed in table 2a[1].

V-Type	V4	V5	V8	V9	V10	V13
Type Name	White birch hardwood and mixedwood	Aspen hardwood	Trembling aspen mixedwood/tall shrub	Trembling aspen mixedwood/low shrub	Trembling aspen mixedwood/ feather moss	White spruce mixedwood

[1] See appendix VII for more detailed descriptions and characteristics of the v-types listed

Table 3: Effects of time since disturbance, disturbance type and the interaction between time since disturbance and disturbance type on tree stratum variables (mean ± SEM). Bolded p-values indicate significant differences, $p \leq 0.05$.

Treatment (n)		**Stem density (/m^2)**	**Number of species**	**Log-series α**	**% Canopy closure**	**% Light intensity**	**% Stems *Populus***
1932	Burn (2)	0.13 ± 0.02	7.0 ± 1.00	1.95 ± 0.57	84 ± 3.1	21.4 ± 2.20	61.5 ± 18.47
1961/67	Burn (4)	0.49 ± 0.04	6.8 ± 0.63	1.19 ± 0.13	92 ± 0.5	17.3 ± 0.97	72.6 ± 3.39
	Harvest (4)	0.37 ± 0.01	6.0 ± 0.71	1.17 ± 0.20	90 ± 1.7	10.3 ± 3.93	77.0 ± 8.18
	$F_{1,10}$	3.0	0.6	<0.1	3.3	1.1	0.1
	P	0.116	0.448	0.896	0.100	0.315	0.782
1980	Burn (4)	1.26 ± 0.06	4.8 ± 0.75	0.62 ± 0.10	83 ± 1.4	21.60 ± 4.10	74.7 ± 18.00
	Harvest (2)	0.55 ± 0.15	8.5 ± 0.50	1.45 ± 0.02	77 ± 2.0	30.80 ± 8.72	55.3 ± 0.57
	$F_{1,10}$	63.3	10.4	11.4	9.1	1.3	1.0
	P	**<0.001**	**0.009**	**0.007**	**0.013**	0.284	0.333
1995	Harvest (4)	10.27 ± 0.81	2.0 ± 0.00	NA	NA	58.15 ± 7.92	100.0 ± 0.00
Age Class	1961/67 (8)	0.43 ± 0.03	6.4 ± 0.46	1.18 ± 0.11	91 ± 0.9	13.8 ± 2.08	74.8 ± 4.18
	1980 (6)	1.02 ± 0.16	6.0 ± 0.93	0.90 ± 0.19	81 ± 1.2	24.7 ± 3.98	68.2 ± 12.09
	$F_{1,10}$	68.9	0.1	0.8	76.5	5.7	0.6
	P	**<0.001**	0.746	0.377	**<0.001**	**0.039**	0.444
Disturbance	Burn (8)	0.87 ± 0.149	5.8 ± 0.59	0.91 ± 0.13	88 ± 1.0	19.4 ± 2.11	73.6 ± 8.49
	Harvest (6)	0.43 ± 0.055	6.8 ± 0.70	1.26 ± 0.14	85 ± 1.7	17.1 ± 4.23	69.8 ± 6.90
	$F_{1,10}$	52.6	4.0	6.4	12.1	<0.1	0.4
	P	**<0.001**	0.073	**0.030**	**0.006**	0.840	0.557
Interaction Age x Disturb.	$F_{1,10}$	25.8	9.0	7.3	1.4	2.4	0.9
	P	**<0.001**	**0.013**	**0.022**	0.262	0.154	.356

NA: Not applicable

Table 4: Effects of time since disturbance, disturbance type and the interaction between time since disturbance and disturbance type on shrub and herb/moss strata variables (mean ± SEM). Bold p-values indicate significant differences, $p \leq 0.05$.

Treatment (n)		Shrub Stratum				Herb/Moss Stratum
		Stem density (/m^2)	**Number of species**	**Shannon-Weiner Index**	**% Cover**	**% Cover**
1932	Burn (2)	18.9 ± 4.75	12.0 ± 0.00	2.1 ± 0.07	30.5 ± 8.98	62.0 ± 5.24
1961/67	Burn (4)	17.4 ± 2.78	9.8 ± 0.48	1.6 ± 0.05	26.3 ± 2.44	58.6 ± 3.09
	Harvest (4)	8.6 ± 1.41	12.0 ± 2.35	1.9 ± 0.22	27.9 ± 6.28	63.3 ± 2.02
	$F_{1,10}$	9.5	1.2	2.4	0.1	0.6
	P	**0.012**	0.293	0.156	0.809	0.446
1980	Burn (4)	12.1 ± 1.92	7.5 ± 1.04	1.4 ± 0.18	19.7 ± 4.67	54.6 ± 2.86
	Harvest (2)	11.5 ± 0.50	8.5 ± 0.50	1.8 ± 0.19	32.8 ± 4.04	47.8 ± 4.51
	$F_{1,10}$	<0.1	0.2	1.8	2.7	0.8
	P	0.850	0.696	0.215	0.192	0.390
1995	Harvest (4)	29.7 ± 9.24	10.5 ± 0.87	1.7 ± 0.10	53.8 ± 10.73	72.3 ± 2.61
Age Class	1961/67 (8)	13.0 ± 2.20	8.6 ± 0.68	1.7 ± 0.12	27.1 ± 3.14	60.9 ± 1.85
	1980 (6)	11.9 ± 1.22	10.8 ± 1.66	1.5 ± 0.15	24.1 ± 4.18	52.3 ± 2.44
	$F_{1,10}$	0.3	3.2	0.4	<0.1	6.9
	P	0.600	0.103	0.524	0.881	**0.034**
Disturbance	Burn (8)	14.8 ± 1.85	8.6 ± 0.68	1.5 ± 0.09	23.0 ± 2.74	56.6 ± 2.52
	Harvest (6)	9.6 ± 1.07	10.8 ± 1.66	1.8 ± 0.15	29.5 ± 4.24	58.1 ± 3.70
	$F_{1,10}$	4.4	1.0	4.0	2.1	<0.1
	P	0.062	0.335	0.074	0.181	0.850
Interaction Age x Disturb.	$F_{1,10}$	3.2	0.2	<0.1	1.3	1.4
	P	0.102	0.705	0.957	0.287	0.259

Table 5: The three shrub-stratum species that were significantly affected by time since disturbance and/or disturbance type. Mean number of stems per plot per m^2 (mean ± SEM). Bold p-values indicate significant differences, $p \leq 0.05$.

Treatment (n)		*Disporum trachycarpum*	*Ribes oxyacanthoides*	*Rosa acicularis*
1932	Burn (2)	0.00 ± 0.00	0.00 ± 0.00	1.03 ± 0.22
1961/67	Burn (4)	0.08 ± 0.01	0.00 ± 0.00	1.40 ± 0.22
	Harvest (4)	0.03 ± 0.01	0.04 ± 0.02	0.43 ± 0.14
	$F_{1,10}$	8.7	2.5	14.5
	P	**0.025**	0.168	**0.009**
1980	Burn (4)	0.00 ± 0.00	0.00 ± 0.00	1.13 ± 0.18
	Harvest (2)	0.00 ± 0.00	0.07 ± 0.07	0.39 ± 0.01
	$F_{1,10}$	NA	2.7	7.8
	P	NA	0.178	**0.049**
1995	Harvest (4)	0.00 ± 0.00	0.0 ± 0.00	1.62 ± 0.54
Age Class	1961/67 (8)	0.05 ± 0.01	0.02 ± 0.01	0.92 ± 0.22
	1980 (6)	0.00 ± 0.00	0.02 ± 0.02	0.88 ± 0.19
	$F_{1,10}$	11.6	0.1	0.1
	P	**0.005**	0.905	0.907
Disturbance	Burn (8)	0.04 ± 0.02	0.00 ± 0.00	1.26 ± 0.14
	Harvest (6)	0.02 ± 0.01	0.05 ± 0.02	0.42 ± 0.09
	$F_{1,10}$	1.2	5.5	22.6
	P	0.293	**0.037**	**0.001**
Interaction	$F_{1,10}$	5.8	0.4	0.4
Age x Disturb.	*P*	**0.036**	0.544	0.546

NA: Not applicable

Table 6: Effects of disturbance type on carabid beetles caught in 2000 (mean per plot ± SEM). Bolded p-values indicate significant differences, $p \le 0.05$.

Treatment (n)		Individuals per plot	Species per plot	Log-series α	Evenness[1]	Berger-Parker Index
1932	Burn (2)	87.0 ± 1.00	10.5 ± 0.50	3.13 ± 0.22	0.16 ± 0.02	0.36 ± 0.01
1961/67	Burn (4)	131.8 ± 24.99	9.3 ± 0.48	2.38 ± 0.29	0.20 ± 0.02	0.36 ± 0.02
	Harvest (4)	46.5 ± 7.07	8.5 ± 0.96	3.37 ± 0.80	0.14 ± 0.03	0.33 ± 0.04
	$F_{1,6}$	14.0	0.6	1.7	1.8	0.5
	P	**0.010**	0.477	0.242	0.230	0.516
1980	Burn (4)	32.8 ± 8.61	8.5 ± 0.87	5.65 ± 2.51	0.17 ± 0.03	0.42 ± 0.09
1995	Harvest (3)	14.3 ± 4.48	6.3 ± 0.33	6.68 ± 2.39	0.12 ± 0.03	0.34 ± 0.05

[1] Evenness values are negative values with minus signs removed.

Table 7: Effects of time since disturbance, disturbance type, and the interaction between time since disturbance and disturbance type on carabid beetles caught in 2001 (mean per plot ± SEM). Bolded p-values indicate significant differences, $p \leq 0.05$.

Treatment (n)		Individuals per plot	Species per plot	Log-series α	Evenness[1]	Berger-Parker Index
1932	Burn (2)	828.5 ± 67.50	13.5 ± 0.50	2.3 ± 0.14	0.22 ± 0.00	0.55 ± 0.08
1961/67	Burn (4)	841.5 ± 59.98	13.0 ± 1.47	2.2 ± 0.29	0.23 ± 0.03	0.48 ± 0.03
	Harvest (4)	431.5 ± 105.46	12.8 ± 1.11	2.6 ± 0.34	0.18 ± 0.02	0.56 ± 0.04
	$F_{1,10}$	7.2	<0.1	0.3	1.3	4.1
	P	**0.023**	0.892	0.595	0.289	0.071
1980	Burn (4)	387.0 ± 153.91	14.8 ± 0.95	3.3 ± 0.33	0.15 ± 0.01	0.49 ± 0.09
	Harvest (2)	109.0 ± 46.00	10.5 ± 2.50	3.4 ± 1.60	0.19 ± 0.09	0.28 ± 0.07
	$F_{1,10}$	2.2	3.8	<0.1	0.4	2.1
	P	0.167	0.081	0.906	0.521	0.221
1995	Harvest (4)	177.8 ± 41.79	14.00 ± 0.707	3.7 ± 0.12	0.14 ± 0.01	0.36 ± 0.07
Age Class	1961/67 (8)	636.3 ± 95.77	12.9 ± 0.85	2.4 ± 0.22	0.21 ± 0.02	0.52 ± 0.03
	1980 (6)	127.2 ± 41.67	13.3 ± 1.26	3.3 ± 0.46	0.17 ± 0.03	0.42 ± 0.08
	$F_{1,10}$	10.4	<0.1	3.3	1.0	4.0
	P	**0.009**	0.863	0.098	0.340	0.073
Disturbance	Burn (8)	614.3 ± 115.00	13.9 ± 0.88	2.7 ± 0.29	0.19 ± 0.02	0.49 ± 0.05
	Harvest (6)	323.7 ± 95.91	12.0 ± 1.06	2.8 ± 0.49	0.19 ± 0.03	0.47 ± 0.07
	$F_{1,10}$	8.2	2.5	0.2	<0.1	1.0
	P	**0.017**	0.143	0.668	0.851	0.343
Interaction	$F_{1,10}$	0.3	2.0	0.1	1.5	4.6
Age x Disturb	*P*	0.595	0.188	0.806	0.249	0.058

[1] Evenness values are negative values with minus signs removed.

Table 8: Effects of disturbance type on carabid beetles caught in 2002 (mean per plot ± SEM). Bolded p-values indicate significant differences, $p \leq 0.05$.

Treatment (n)		**Individuals per plot**	**Species per plot**	**Log-series α**	**Evenness**[1]	**Berger-Parker Index**
1980	Burn (4)	580.5 ± 233.75	14.0 ± 1.58	2.7 ± 0.27	0.43 ± 0.06	0.63 ± 0.08
	Harvest (2)	633.0 ± 153.00	14.5 ± 2.50	2.7 ± 0.72	0.43 ± 0.12	0.66 ± 0.02
	$F_{1,4}$	<0.1	<0.1	<0.1	<0.1	0.1
	P	0.892	0.868	0.994	0.986	0.809

[1] Evenness values are negative values with minus signs removed.

Table 9: Jaccard's index of similarity for all site-to-site comparisons among carabid beetle catches in 2000. (mean, minimum/maximum index values, number of values incorporated in mean)

		Site				
		B32	**B61**	**B80**	**H67**	**H95**
Site	**B32**	0.500 (NA[1]) (1)				
	B61	0.459 (0.333/0.615) (8)	0.578 (0.357/0.800)(6)			
	B80	0.309 (0.214/0.462) (8)	0.442 (0.230/0.778) (16)	0.476 (0.270/0.640) (6)		
	H67	0.365 (0.231/0.538) (8)	0.479 (0.230/0.889) (16)	0.438 (0.200/0.730) (16)	0.440 (0.230/0.580) (6)	
	H95	0.138 (0.000/0.333) (6)	0.203 (0.000/0.400) (12)	0.199 (0.000/0.400) (12)	0.288 (0.000/0.460) (12)	0.191 (0.090/0.300) (3)

[1] NA: Not applicable (only two plots, therefore no min/max values).

Table 10: Jaccard's index of similarity for all site-to-site comparisons among carabid beetle catches in 2001. (mean, minimum/maximum index values, number of values incorporated in mean)

		Site					
		B32	**B61**	**B80**	**H67**	**H80**	**H95**
Site	**B32**	0.588 (NA[1]) (1)					
	B61	0.638 (0.471/0.812) (8)	0.657 (0.588/0.824) (6)				
	B80	0.495 (0.368/0.667) (8)	0.543 (0.438/0.684) (16)	0.515 (0.330/0.630) (6)			
	H67	0.540 (0.318/0.800) (8)	0.611 (0.471/0.692) (16)	0.574 (0.440/0.690) (16)	0.614 (0.530/0.710) (6)		
	H80	0.387 (0.227/0.500) (4)	0.438 (0.353/0.500) (8)	0.405 (0.320/0.470) (8)	0.519 (0.420/0.650) (8)	0.400 (NA) (1)	
	H95	0.332 (0.130/0.474) (8)	0.416 (0.158/0.529) (16)	0.420 (0.170/0.690) (16)	0.466 (0.240/0.760) (16)	0.450 (0.250/0.590) (8)	0.579 (0.420/0.670) (6)

[1] NA: Not applicable (only two plots, therefore no min/max values).

Table 11: Jaccard's index of similarity for all site-to-site comparisons among carabid beetle catches in 2002. (mean, minimum/maximum index values, number of values incorporated in mean)

		Site	
		B80	**H80**
Site	**B80**	0.531 (0.444/0.650) (6)	
	H80	0.549 (0.435/0.786) (8)	0.450 (NA[1]) (1)

[1] NA: Not applicable (only two plots, therefore no min/max values).

Table 12: Effects of disturbance type on the nine[1] most frequently caught species of carabid beetles in 2000 (mean number of individuals per plot ± SEM). Bolded p-values indicate significant differences, $p \le 0.05$.

Treatment (n)		*Calathus ingratus*	*Carabus taedatus*	*Sphaeroderus nitidicollis*	*Agonum retractum*	*Platynus decentis*	*Pterostichus pensylvanicus*	*Pterostichus adstrictus*	*Synuchus impunctatus*	*Stereocercus haematopus*
1932	Burn (2)	21.0 ± 9.0	18.5 ± 13.5	4.0 ± 2.0	0.0 ± 0.0	3.5 ± 2.5	10.0 ± 3.0	12.0 ± 5.0	1.0 ± 1.0	12.5 ± 6.5
1961/67	Burn (4)	41.8 ± 14.0	30.5 ± 7.0	7.8 ± 1.4	18.0 ± 7.8	10.0 ± 6.0	11.0 ± 2.3	8.3 ± 4.5	1.3 ± 0.5	1.3 ± 1.3
	Harvest (4)	8.0 ± 3.6	0.5 ± 0.3	4.0 ± 1.5	1.0 ± 0.6	3.0 ± 1.3	2.0 ± 0.7	2.3 ± 1.1	9.0 ± 4.3	0.0 ± 0.0
	$F_{1,6}$	5.4	18.1	3.5	4.7	1.3	13.5	1.7	3.2	1.0
	P	0.059	**0.005**	0.112	0.074	0.300	**0.010**	0.243	0.126	0.356
1980	Burn (4)	13.8 ± 3.0	1.3 ± 0.8	8.5 ± 1.2	5.3 ± 2.6	7.3 ± 3.9	0.3 ± 0.3	1.3 ± 0.6	5.5 ± 3.4	0.0 ± 0.0
1995	Harvest (4)	1.7 ± 1.7	1.0 ± 1.0	3.3 ± 3.3	0.3 ± 0.3	0.0 ± 0.0	1.0 ± 0.6	0.0 ± 0.0	0.3 ± 0.3	0.0 ± 0.0

[1] Species whose catch frequency represented ≥ 1% of the total catch from all paired sites.

Table 13: Effects of time since disturbance and disturbance type on the ten[1] most frequently caught species of carabid beetles in 2001 (mean number of individuals per plot ± SEM). Bolded p-values indicate significant differences, $p \le 0.05$.

Treatment (n)		*Platynus decentis*	*Pterostichus pensylvanicus*	*Calathus ingratus*	*Pterostichus adstrictus*	*Agonum retractum*	*Carabus taedatus*	*Calosoma frigidum*	*Synuchus impunctatus*	*Carabus chamissonis*	*Sphaeroderus nitidicollis*
1932	Burn (2)	457.0 ± 101.0	5.5 ± 3.5	47.0 ± 23.0	187.5 ± 15.5	4.5 ± 3.5	32.0 ± 24.0	3.0 ± 3.0	0.5 ± 0.5	19.5 ± 4.5	2.5 ± 0.5
1961/67	Burn (4)	412.3 ± 57.7	122.5 ± 18.8	71.5 ± 17.4	119.0 ± 17.6	18.5 ± 5.7	52.8 ± 8.5	10.5 ± 4.3	1.0 ± 0.6	17.3 ± 9.3	6.0 ± 2.2
	Harvest (4)	234.0 ± 50.5	28.8 ± 19.2	52.3 ± 19.2	35.3 ± 17.5	16.5 ± 5.7	2.3 ± 1.6	30.3 ± 18.7	14.5 ± 6.2	1.5 ± 1.0	7.3 ± 1.1
	$F_{1,10}$	2.4	22.7	0.8	18.6	<0.1	55.8	1.7	4.9	4.2	0.2
	P	0.154	**0.001**	0.387	**0.002**	0.852	**<0.001**	0.228	0.051	0.068	0.629
1980	Burn (4)	230.3 ± 127.5	49.8 ± 12.0	35.8 ± 8.1	6.8 ± 3.2	27.5 ± 10.8	1.8 ± 1.1	8.5 ± 5.2	5.8 ± 4.5	5.0 ± 3.4	4.8 ± 2.0
	Harvest (2)	31.5 ± 23.5	25.0 ± 21.0	24.5 ± 11.5	3.5 ± 3.5	3.0 ± 2.0	0.0 ± 0.0	0.5 ± 0.5	5.0 ± 4.0	0.0 ± 0.0	5.5 ± 1.5
	$F_{1,10}$	2.0	1.1	0.2	<0.1	3.6	<0.1	0.2	<0.1	0.3	0.1
	P	0.190	0.329	0.675	0.894	0.085	0.837	0.680	0.922	0.608	0.812
1995	Harvest (4)	60.0 ± 28.6	20.3 ± 7.6	14.3 ± 7.7	3.5 ± 1.8	11.8 ± 4.6	2.0 ± 1.4	0.0 ± 0.0	23.0 ± 16.4	0.0 ± 0.0	2.3 ± 1.9
Age Class	1961/67 (8)	323.1 ± 48.9	75.6 ± 20.1	61.9 ± 12.5	77.1 ± 19.6	17.5 ± 3.8	27.5 ± 10.4	20.4 ± 9.6	7.8 ± 3.9	9.4 ± 5.3	6.6 ± 1.2
	1980 (6)	164.0 ± 91.1	41.5 ± 10.7	32.0 ± 6.4	5.7 ± 2.3	19.3 ± 8.6	1.2 ± 0.8	5.8 ± 3.7	5.5 ± 3.0	3.3 ± 2.4	5.0 ± 1.3
	$F_{1,10}$	4.4	6.0	3.5	8.0	0.1	24.8	1.7	0.2	1.3	0.6
	P	0.061	**0.034**	0.089	**0.018**	0.791	**0.001**	0.221	0.632	0.286	0.467
Disturbance	Burn (8)	321.3 ± 73.3	86.1 ± 17.2	53.6 ± 11.2	62.9 ± 23.0	23.0 ± 5.9	27.3 ± 10.4	9.5 ± 3.2	3.4 ± 2.3	11.1 ± 5.1	5.4 ± 1.4
	Harvest (6)	166.5 ± 53.7	27.5 ± 7.7	43.0 ± 13.8	24.7 ± 13.0	12.0 ± 4.6	1.5 ± 1.1	20.3 ± 13.4	11.3 ± 4.5	1.0 ± 0.7	6.7 ± 0.9
	$F_{1,10}$	4.3	14.5	0.8	21.9	2.6	23.9	0.2	1.8	2.9	0.3
	P	0.066	**0.003**	0.387	**0.001**	0.141	**0.001**	0.639	0.215	0.120	0.625
Interaction Age x Disturb	$F_{1,10}$	<0.1	4.9	0.1	6.9	1.8	20.8	1.3	2.2	0.8	<0.1
	P	0.913	0.051	0.817	**0.026**	0.204	**0.001**	0.280	0.170	0.399	0.902

---

[1] Species whose catch frequency represented ≥ 1% of the total catch from all paired sites.

Table 14: Effects of disturbance type on the six[1] most abundant species of carabid beetles caught in 2002 (mean number of individuals per plot ± SEM). Bolded p-values indicate significant differences, $p \leq 0.05$.

Treatment (n)		*Platynus decentis*	*Pterostichus pensylvanicus*	*Calathus ingratus*	*Agonum retractum*	*Synuchus impunctatus*	*Calosoma frigidum*
1980	Burn (4)	407.3 ± 203.22	62.5 ± 17.48	47.5 ± 11.06	30.3 ± 8.26	8.3 ± 4.61	4.5 ± 1.04
	Harvest (2)	418.5 ± 113.50	95.5 ± 25.50	64.0 ± 25.00	5.5 ± 3.50	10.5 ± 4.50	17.0 ± 1.00
	$F_{1,4}$	<0.1	1.2	0.5	3.9	0.1	55.6
	P	0.973	0.340	0.505	0.120	0.777	**0.002**

[1] Species whose catch frequency represented ≥ 1% of the total catch from all paired sites.

Table 15: Carabid beetle species where the pattern of catch frequency in a single plot differs significantly from that expected by random chance in each sampling year, with number of individuals caught per plot by site and Poisson probability, $p \leq 0.05$. (Some sites contain multiple plots where catch frequency differed significantly from expected.)

Sampling Year	Species	Site containing plot						P_p[1]
		B32	B61	B80	H67	H80	H95	
2000	*Agonum simile*	0	0	3	0	NA[2]	0	0.02
	Stereocercus haematopus	19	0	0	0	NA	0	<0.01
2001	*Agonum trigeminum*	0	0	0	0	0	3	0.01
	Dicaelus sculptilis	0	0	0	0	0	3	0.01
	Pterostichus punctatissimus	4	0	0	0	0	0	<0.01
	Stereocercus haematopus	101/23	14	0	0	0	0	<0.01
2002	*Carabus chamissonis*	NA	NA	8/8	NA	0	NA	<0.01

[1] P_p – Poisson probability; the probability that the species would be randomly caught in its actual catch frequency.
[2] NA – Not applicable (site was not sampled that year).

Figure 3: Principle component analysis (PCA) of the tree stratum species in all plots with species scores (→) and plot scores (○). Species data log transformed.

Plot labels are described in Table 1.

Key to tree stratum species: Abi bal = *Abies balsamea*, Ace spi = *Acer spicatum*, Aln cri = *Alnus crispa*, Ame aln = *Amelanchier alnifolia*, Bet pap = *Betula papyrifera*, Cor cor = *Corylus cornuta*, Pic ban = *Pinus banksiana*, Pic gla = *Picea glauca*, Pic mar = *Picea mariana*, Pop bal = *Populus balsamifera*, Pop del = *Populus deltoides*, Pop tre = *Populus tremuloides*, Pru spp = *Prunus* species, Sal spp = *Salix* species.

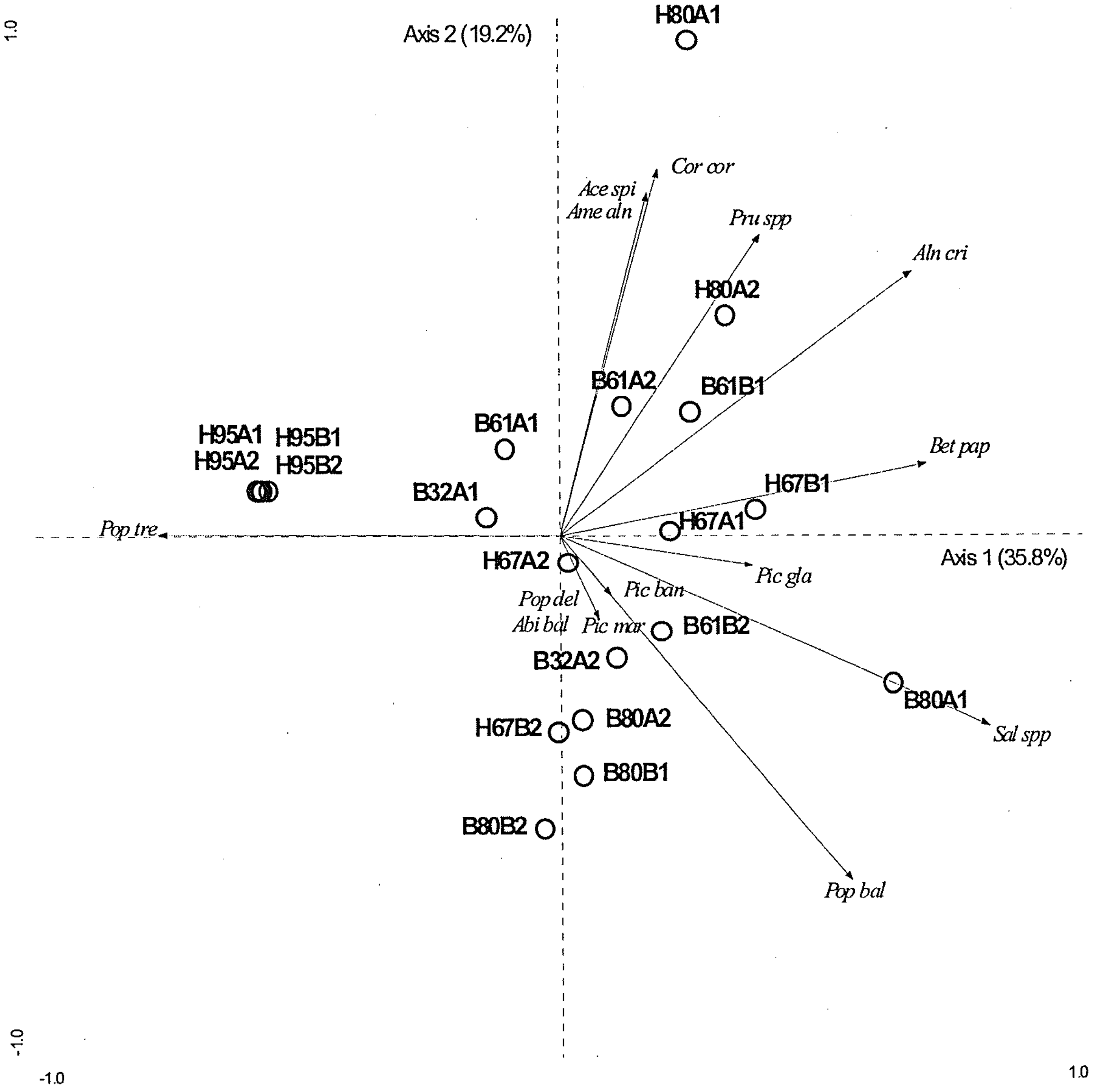

H80A1
Axis 2 (19.2%)
1.0
Cor cor
Ace spi
Ame aln
Pru spp
Aln cri
H80A2
B61A2
B61B1
B61A1
H95A1
H95B1
H95A2
H95B2
Bet pap
H67B1
B32A1
H67A1
Pop tre
Axis 1 (35.8%)
H67A2
Pic gla
Pic ban
Pop del
Abi bal
Pic mar
B61B2
B32A2
B80A1
Sal spp
H67B2
B80A2
B80B1
B80B2
Pop bal
-1.0
-1.0
1.0

Figure 4: PCA (axes 2 & 3) of the tree stratum species in all plots with species scores (→) and plot scores (○). Species data log transformed.

Plot labels are described in Table 1.

Key to tree stratum species: Abi bal = *Abies balsamea*, Ace spi = *Acer spicatum*, Aln cri = *Alnus crispa*, Ame aln = *Amelanchier alnifolia*, Bet pap = *Betula papyrifera*, Cor cor = *Corylus cornuta*, Pic ban = *Pinus banksiana*, Pic gla = *Picea glauca*, Pic mar = *Picea mariana*, Pop bal = *Populus balsamifera*, Pop del = *Populus deltoides*, Pop tre = *Populus tremuloides*, Pru spp = *Prunus* species, Sal spp = *Salix* species.

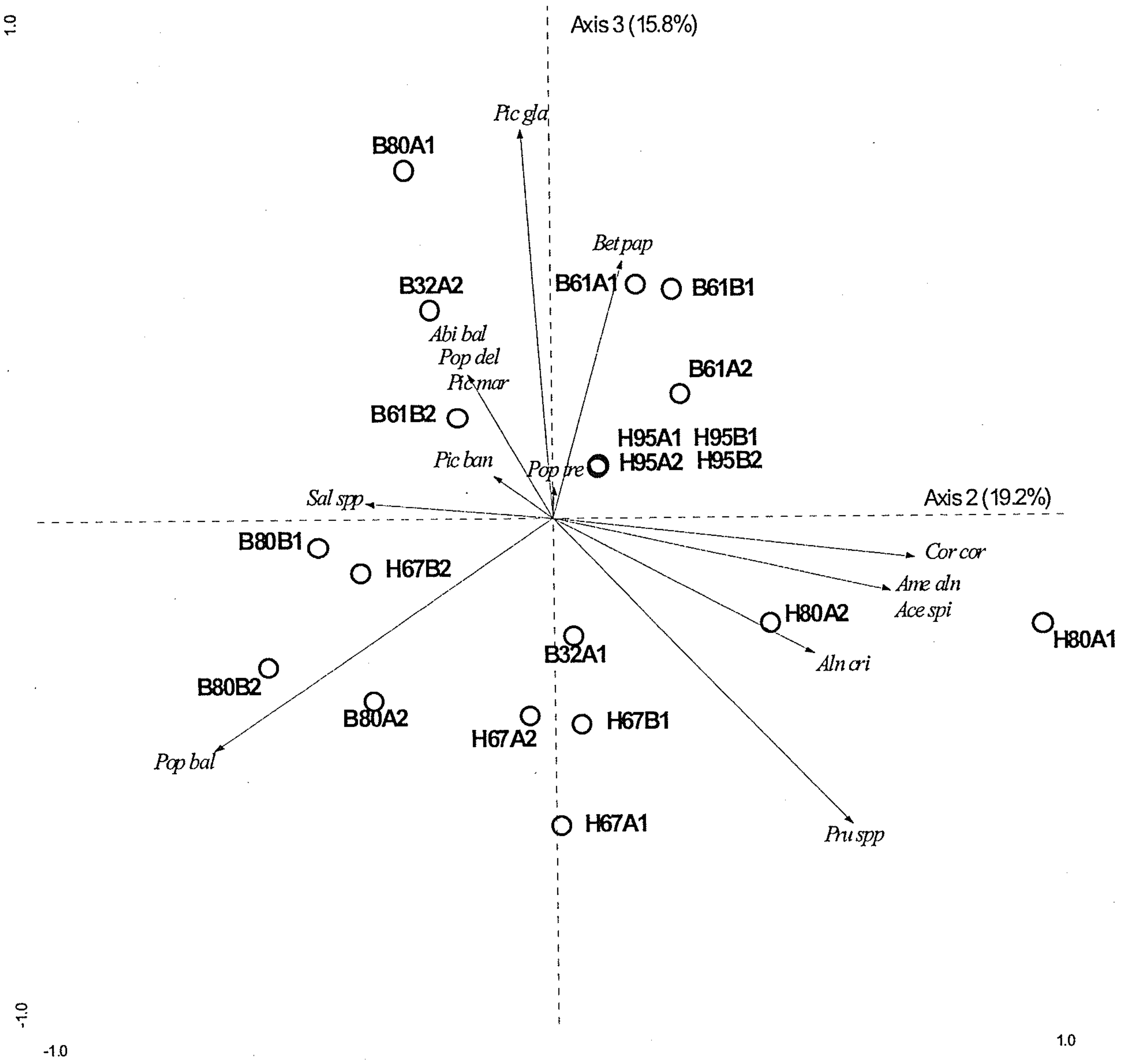

1.0
Axis 3 (15.8%)
Pic gla
B80A1
Bet pap
B32A2
B61A1
B61B1
Abi bal
Pop del
Pic mar
B61A2
B61B2
H95A1
H95B1
H95A2
H95B2
Pic ban
Pop tre
Axis 2 (19.2%)
Sal spp
B80B1
H67B2
Cor cor
Ame aln
Ace spi
H80A2
H80A1
B32A1
Aln cri
B80B2
B80A2
H67A2
H67B1
Pop bal
H67A1
Pru spp
-1.0
-1.0
1.0

Figure 5: PCA ordination diagram of the shrub stratum species in all plots with species scores (→) and plot scores (○). Species data log transformed.

Plot labels are described in Table 1.

Key to shrub stratum species: Abi bal = *Abies balsamea*, Aln cri = *Alnus crispa*, Ame aln = *Amelanchier alnifolia*, Apo and = *Apocynum androsaemifolium*, Cor cor = *Corylus cornuta*, Cor sto = *Cornus stolonifera*, Die lon = *Diervilla lonicera*, Dis tra = *Disporum trachycarpum*, Lon dio = *Lonicera dioica*, Pic gla = *Picea glauca*, Pop bal = *Populus balsamifera*, Pop tre = *Populus tremuloides*, Pru pen = *Prunus pensylvanica*, Pru vir = *Prunus virginiana*, Rha aln = *Rhamnus alnifolia*, Rib lac = *Ribes lacustre*, Rib oxy = *Ribes oxyacanthoides*, Rib tri = *Ribes triste*, Ros aci = *Rosa acicularis*, Rub aca = *Rubus acaulis*, Rub ida = *Rubus idaeus*, Sal spp = *Salix* species, She can = *Shepherdia canadensis*, Str ros = *Streptopus roseus*, Sym alb = *Symphoricarpos albus*, Vib edu = *Viburnum edule*, Vib opu = *Viburnum opulus*.

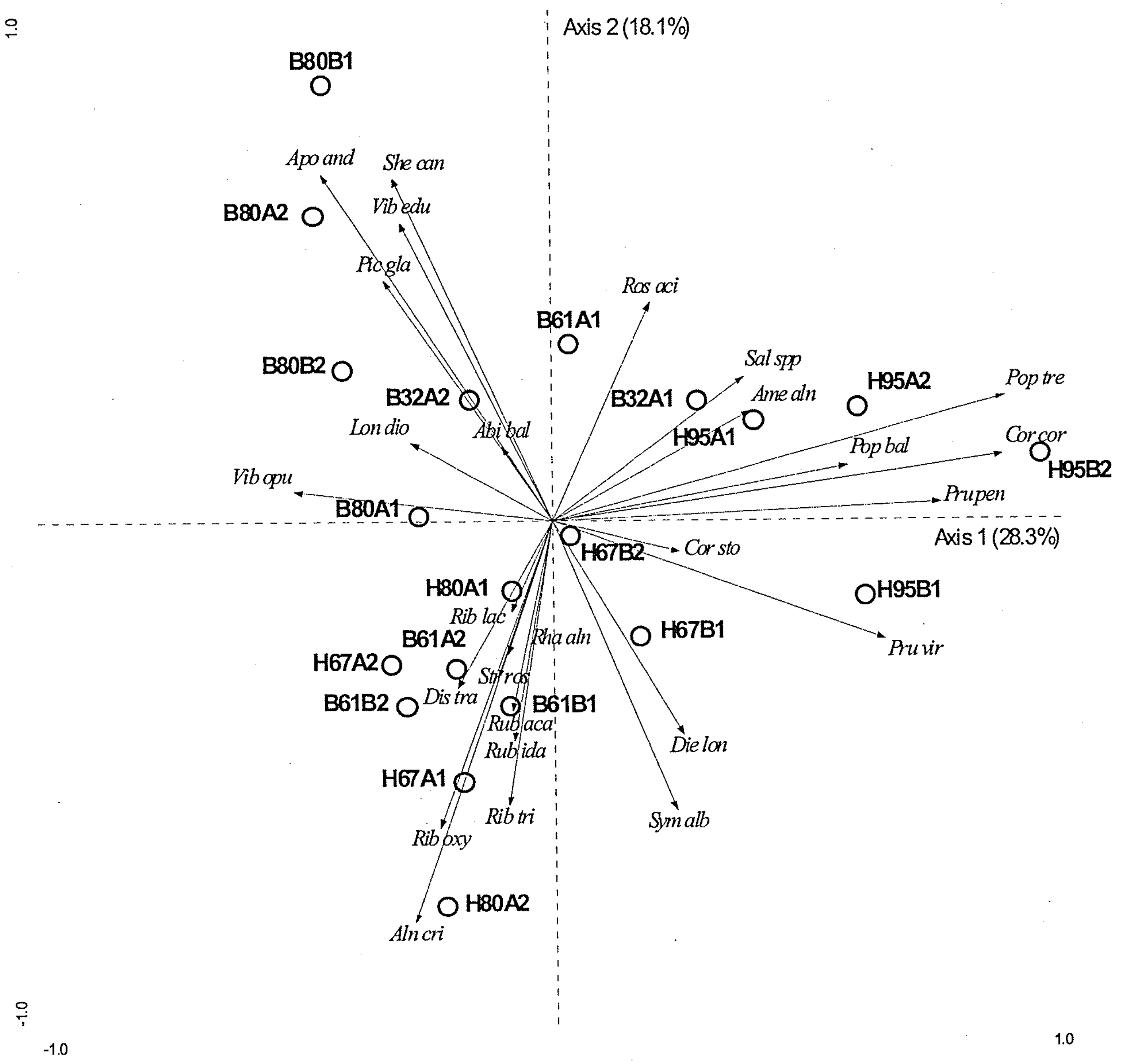

Axis 2 (18.1%)
Axis 1 (28.3%)
1.0
-1.0
-1.0
1.0
B80B1
Apo and
She can
Vib edu
B80A2
Pic gla
Ras aci
B61A1
Sal spp
B80B2
B32A2
B32A1
Ame aln
H95A2
Pop tre
Lon dio
Abi bal
H95A1
Pop bal
Cor cor
H95B2
Vib opu
Pru pen
B80A1
H67B2
Cor sto
H80A1
H95B1
Rib lac
Rha aln
H67B1
B61A2
Pru vir
H67A2
Str ros
Dis tra
B61B2
B61B1
Rub aca
Rub ida
Die lon
H67A1
Rib tri
Sym alb
Rib oxy
H80A2
Aln cri

Figure 6: Hierarchical cluster analysis of plots sampled in 2000 based on Jaccard's index of similarity using carabid beetles.

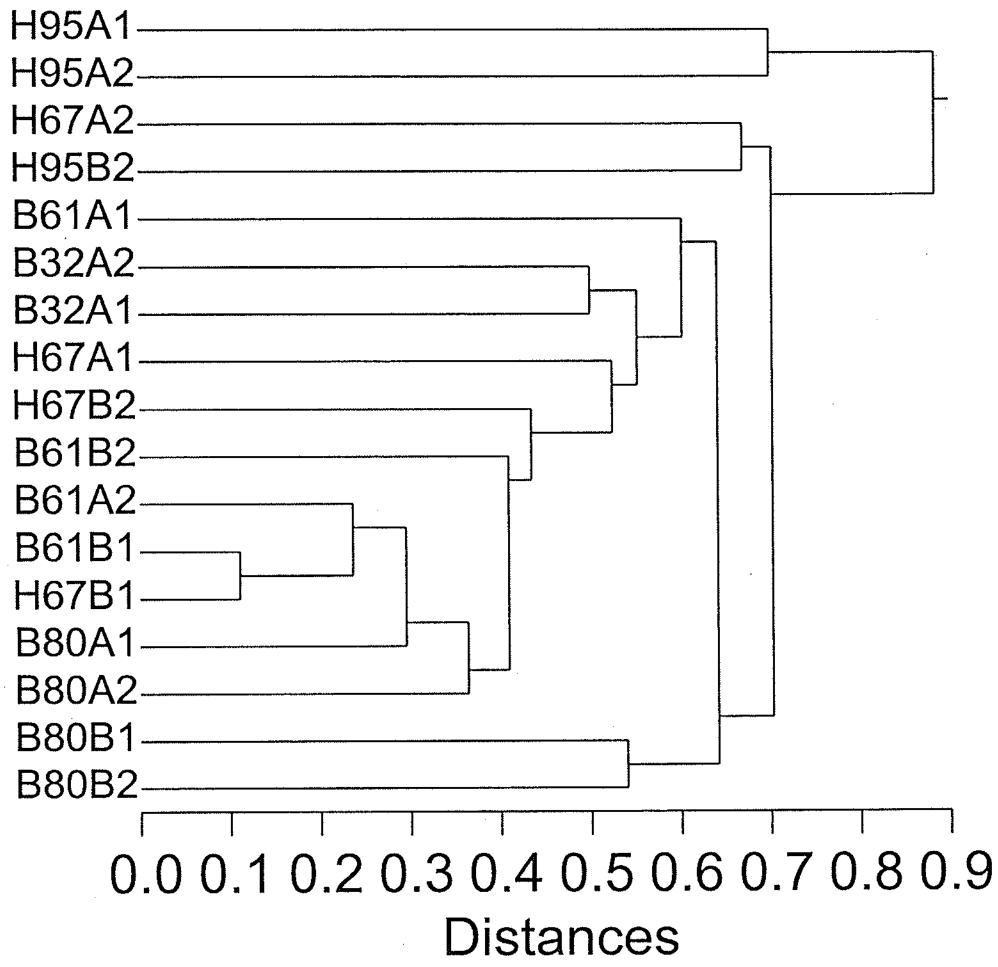


Figure 7: Hierarchical cluster analysis of plots sampled in 2001 based on Jaccard's index of similarity using carabid beetles

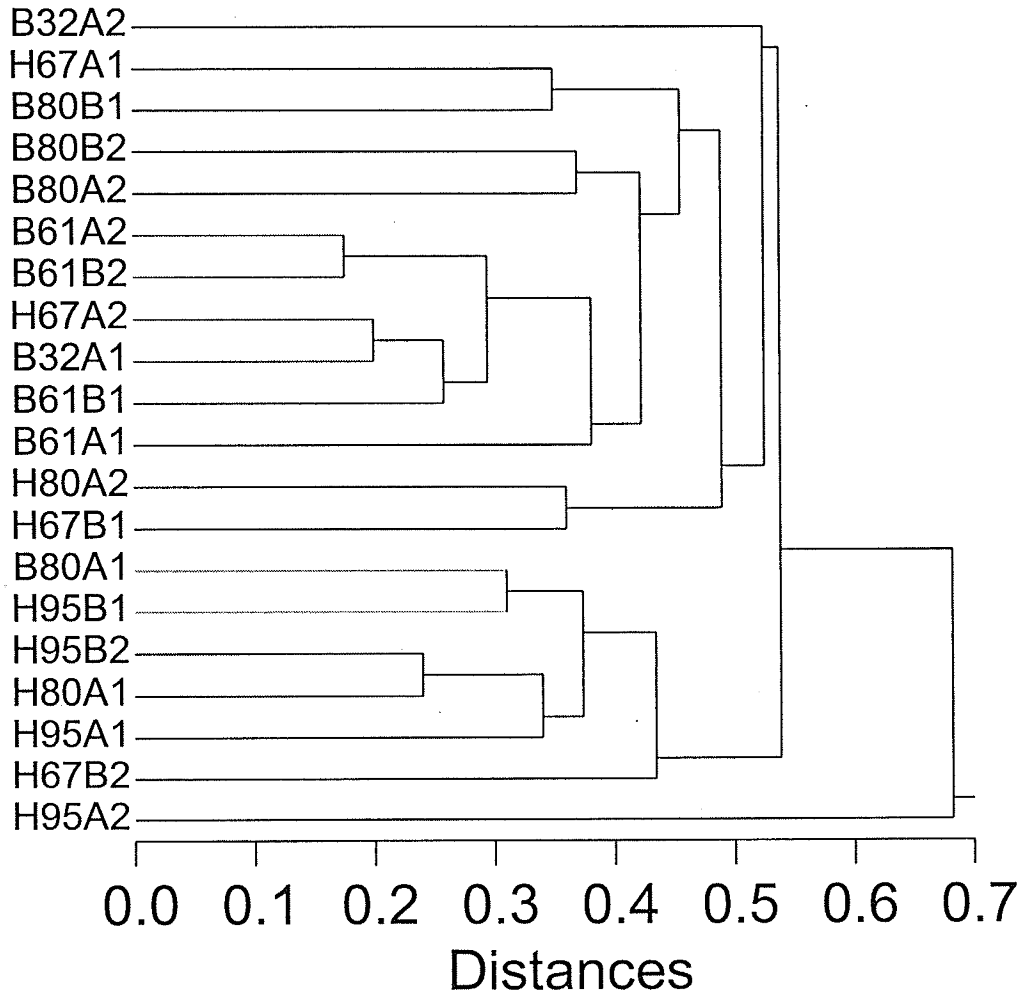


Figure 8: Hierarchical cluster analysis of plots sampled in 2002 based on Jaccard's index of similarity using carabid beetles.

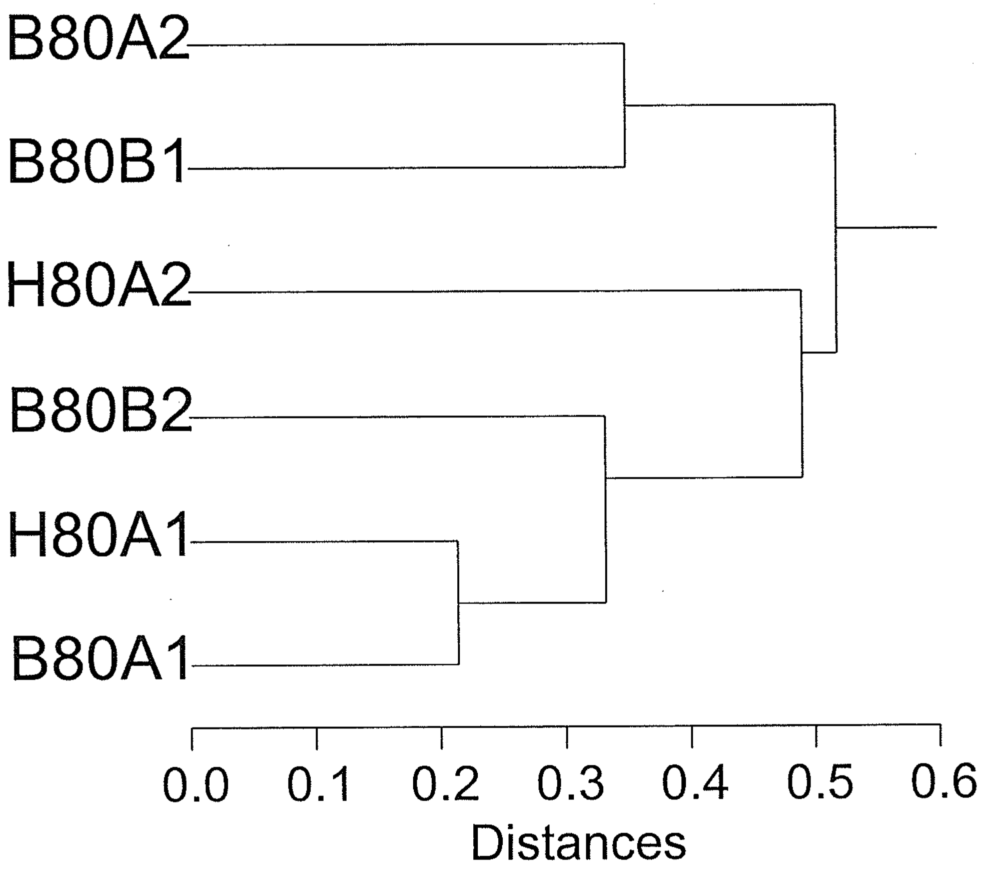


Figure 9: The number of carabid beetles caught during each trapping period in 2000, 2001 and 2002.

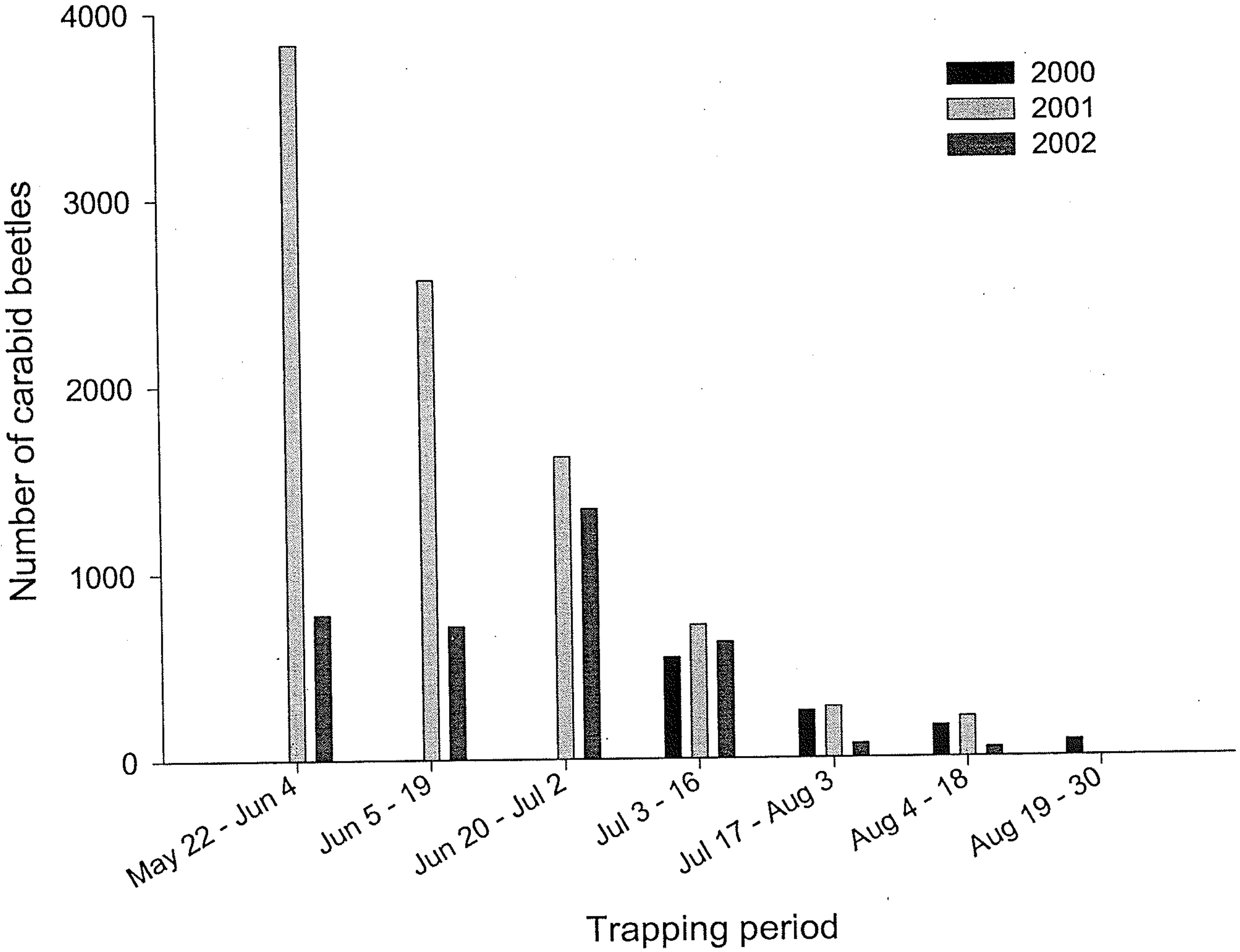


Figure 10: Seasonal variation in catch ferquency among the ten most ferquently caught carabid beetle species collected in 2001 (note that the y-axis varies with each species).

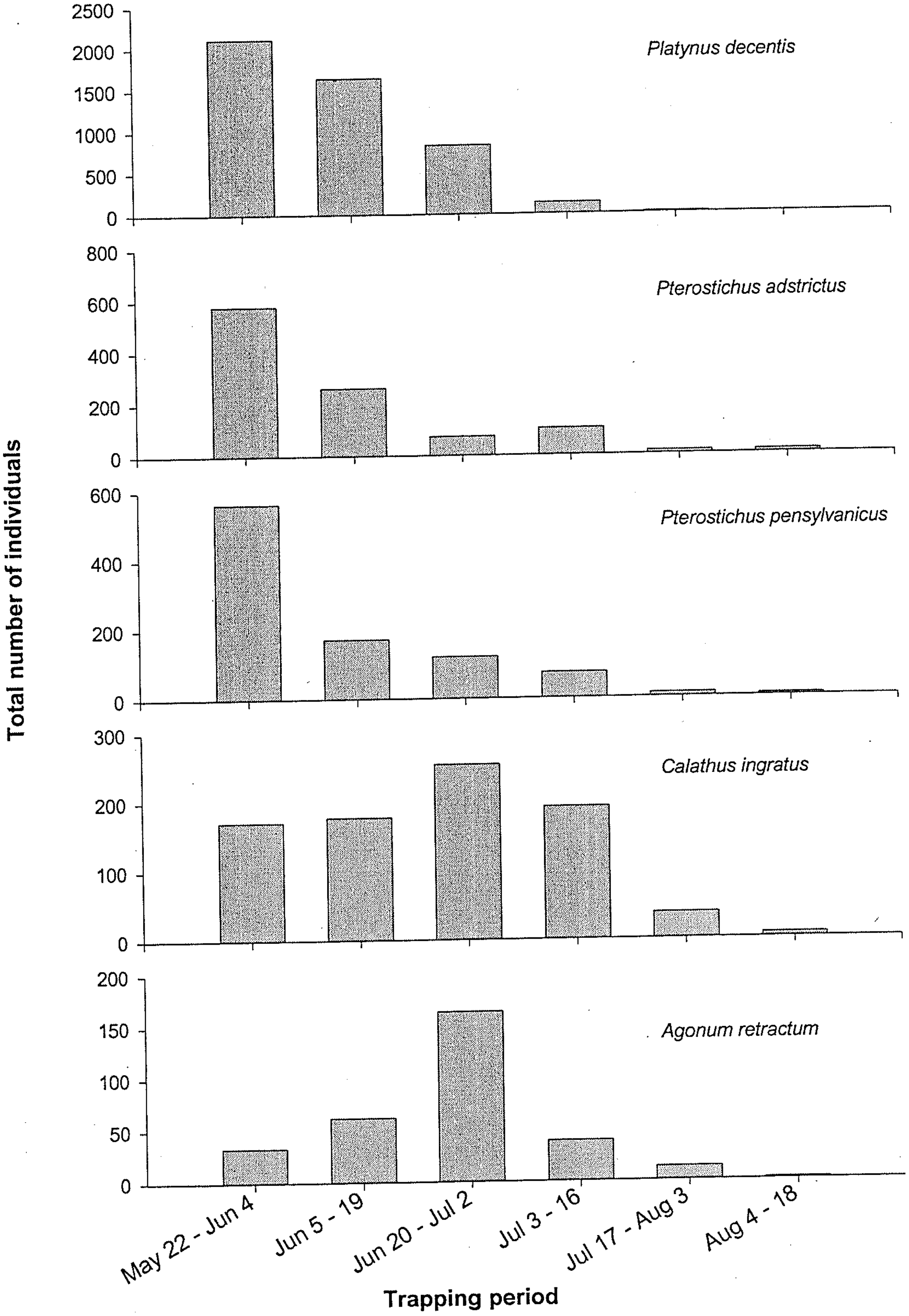


Figure 10: cont.

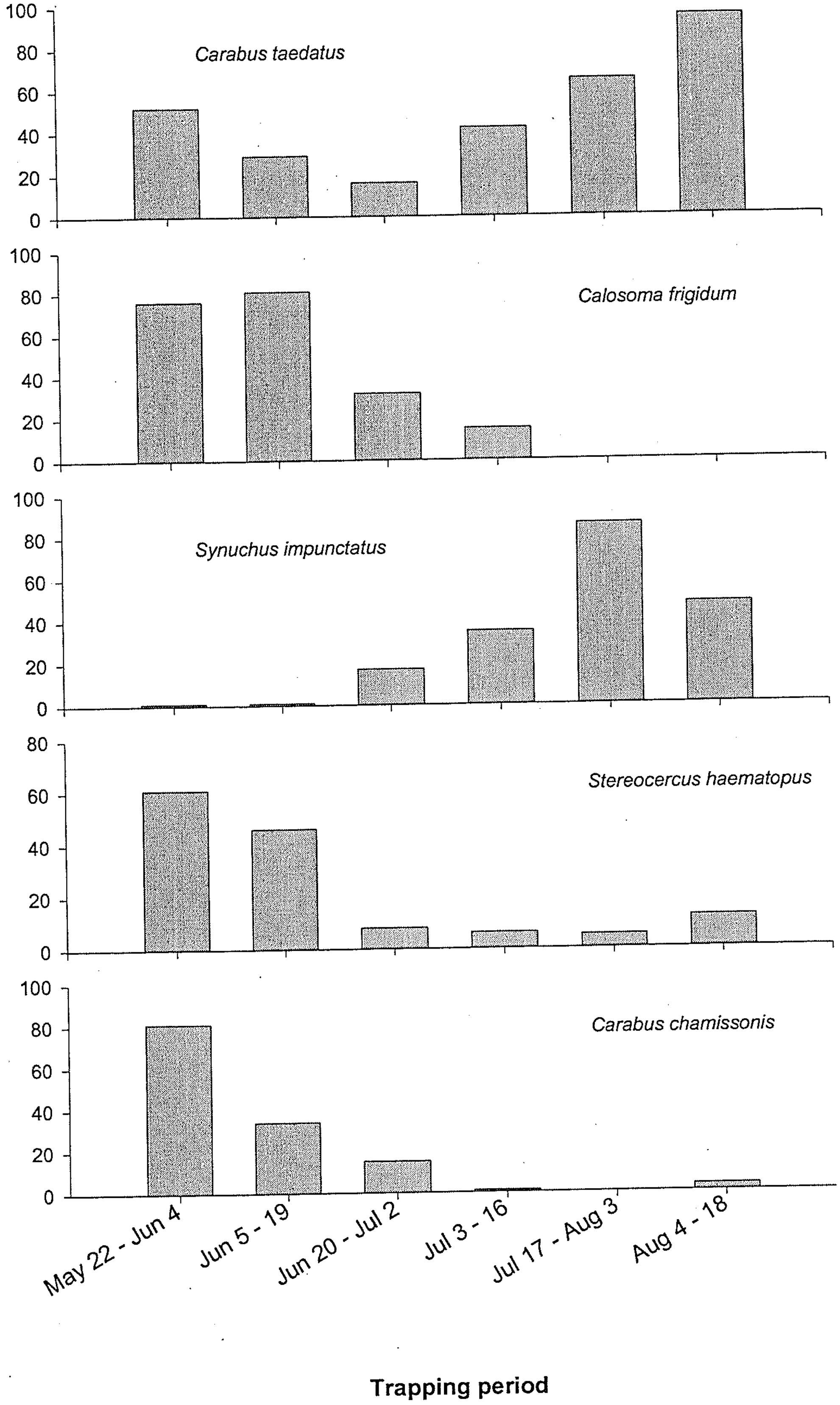
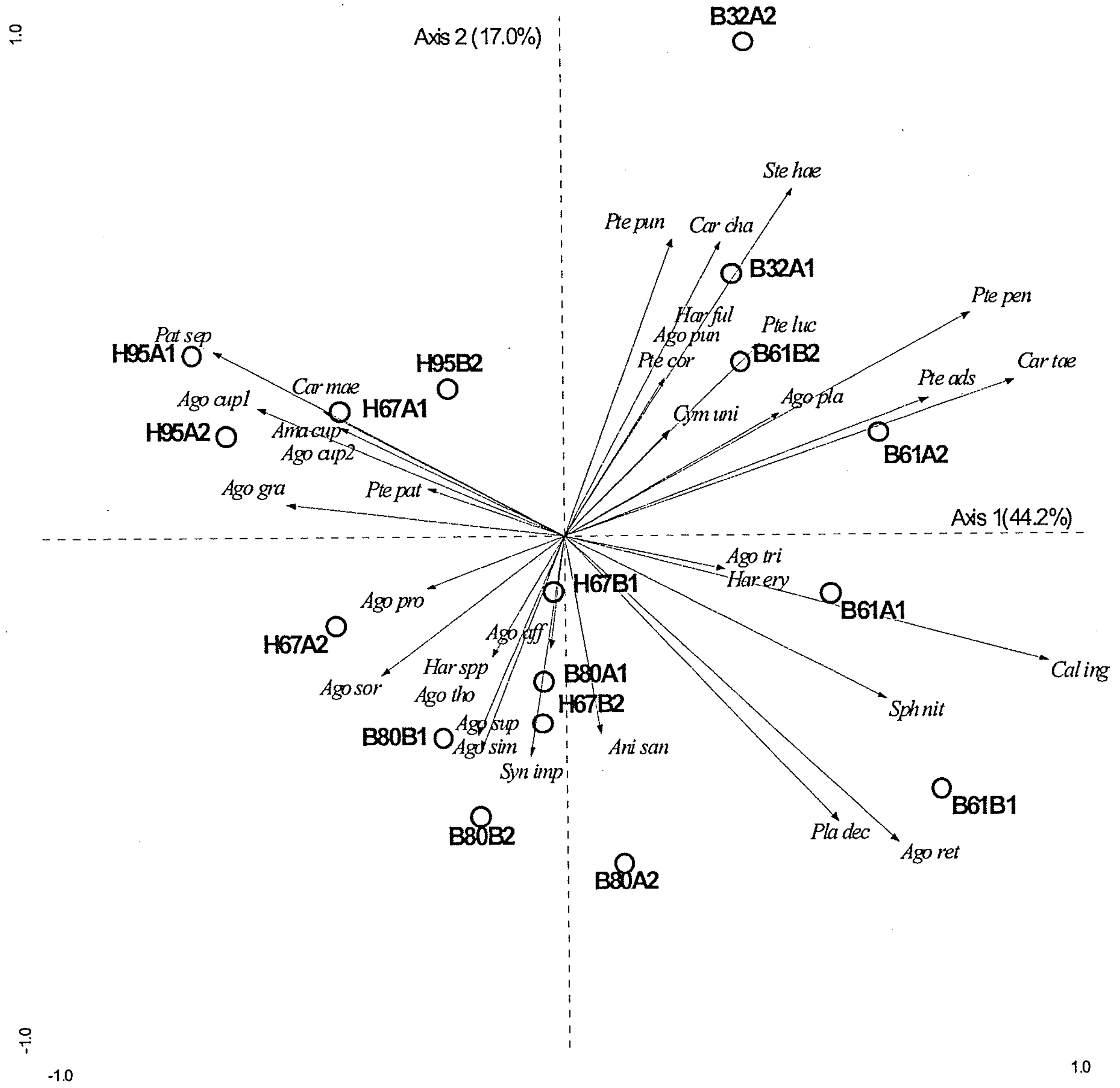


Figure 11: PCA of all carabid beetle species caught in 2000 in all plots with species scores (→) and plot scores (○). Species data log transformed.

Plot labels are described in Table 1.

Key to carabid beetle species: Ago aff = *Agonum affine,* Ago cup1 = *Agonum cupreum*, Ago cup2 = *Agonum cupripenne*, Ago gra = *Agonum gratiosum*, Ago pla = *Agonum placidum*, Ago pro = *Agonum propinquum*, Ago pun = *Agonum puncticeps*, Ago ret = *Agonum retractum*, Ago sim = *Agonum simile*, Ago sor = *Agonum sordens*, Ago sup = *Agonum superioris*, Ago tho = *Agonum thoreyi*, Ago tri = *Agonum trigeminum*, Ama cup = *Amara cupreolata*, Ani san = *Anisodactylus sanctaecrucis*, Cal ing = *Calathus ingratus*, Car cha = *Carabus chamissonis*, Car mae = *Carabus maeander*, Car tae = *Carabus taedatus*, Cym uni = *Cymindis unicolor*, Har ery = *Harpalus erythropus*, Har ful = *Harpalus fulvilabris*, Har spp = *Harpalus* species, Pat sep = *Patrobus septentrionis*, Pla dec = *Platynus decentis*, Pte ads = *Pterostichus adstrictus*, Pte luc = *Pterostichus luctuosis*, Pte pat = *Pterostichus patruelis*, Pte pen = *Pterostichus pensylvanicus*, Pte pun = *Pterostichus punctatissimus*, Sph nit = *Sphaeroderus nitidicollis*, Ste hae = *Stereocercus haematopus*, Syn imp = *Synuchus impunctatus*.

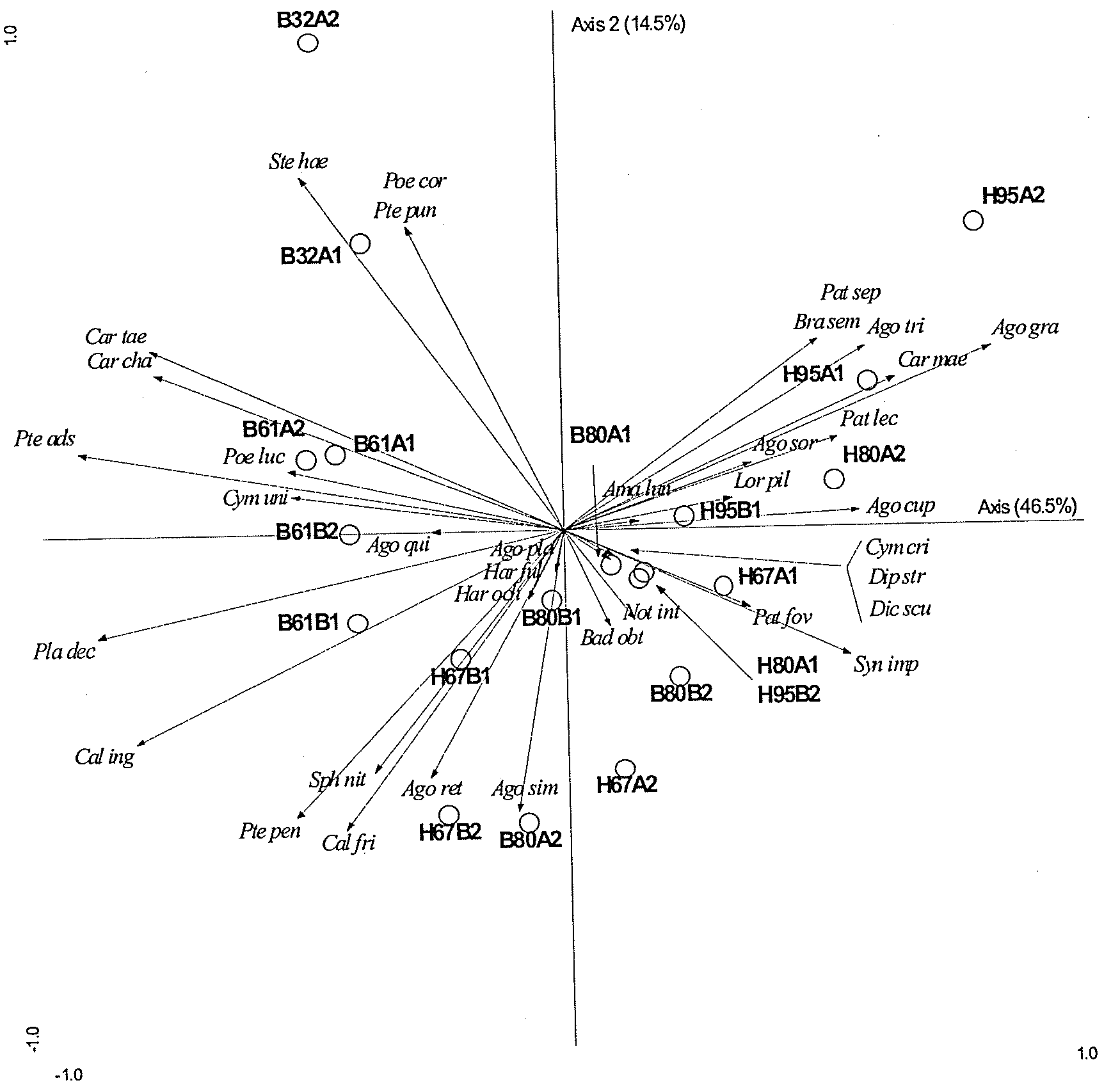


Axis 2 (17.0%)
Axis 1(44.2%)
1.0
-1.0
-1.0
1.0
B32A2
B32A1
B61B2
B61A2
B61A1
B61B1
H95A1
H95A2
H95B2
H67A1
H67A2
H67B1
H67B2
B80A1
B80A2
B80B1
B80B2
Ste hae
Pte pun
Car cha
Har ful
Ago pun
Pte cor
Pte luc
Pte pen
Car tae
Pte ads
Ago pla
Cym uni
Pat sep
Car mae
Ago cup1
Ama cup
Ago cup2
Ago gra
Pte pat
Ago tri
Har ery
Cal ing
Sph nit
Ago ret
Pla dec
Ani san
Syn imp
Ago sim
Ago sup
Ago tho
Har spp
Ago aff
Ago sor
Ago pro

Figure 12: PCA of all carabid beetle species caught in 2001 in all plots with species scores (→) and plot scores (○). Species data log transformed.

Plot labels are described in Table 1.

Key to carabid beetle species: Ago cup = *Agonum cupreum*, Ago gra = *Agonum gratiosum*, Ago pla = *Agonum placidum*, Ago qui = *Agonum quiquepunctatum*, Ago ret = *Agonum retractum*, Ago sim = *Agonum simile*, Ago sor = *Agonum sordens*, Ago tri = *Agonum trigeminum*, Ama lun = *Amara lunicolis*, Bad obt = *Badister obtusus*, Bra sem = *Bradycellus semipubescens*, Cal ing = *Calathus ingratus*, Cal fri = *Calosoma frigidum*, Car cha = *Carabus chamissonis*, Car mae = *Carabus maeander*, Car tae = *Carabus taedatus*, Cym cri = *Cymindis cribricollis*, Cym uni = *Cymindis unicolor*, Dic scu = *Dicaelus sculptilis*, Dip str = *Diplocheila striatopunctata*, Har ful = *Harpalus fulvilabris*, Har och = *Harpalus ochropus*, Lor pil = *Loricera pilicornis*, Not int = *Notiophilus intermedius*, Pat fov = *Patrobus fovecollis*, Pat lec = *Patrobus lecontei*, Pat sep = *Patrobus septentrionis*, Pla dec = *Platynus decentis*, Poe cor = *Poecilus corvus*, Poe luc = *Poecilus lucublandus*, Pte ads = *Pterostichus adstrictus*, Pte pen = *Pterostichus pensylvanicus*, Pte pun = *Pterostichus punctatissimus*, Sph nit = *Sphaeroderus nitidicollis*, Ste hae = *Stereocercus haematopus*, Syn imp = *Synuchus impunctatus*.



Axis 2 (14.5%)
Axis (46.5%)
1.0
-1.0
1.0
-1.0
B32A2
B32A1
Ste hae
Poe cor
Pte pun
H95A2
Pat sep
Bra sem
Ago tri
Ago gra
Car mae
H95A1
Car tae
Car cha
Pat lec
Ago sor
H80A2
Lor pil
B61A2
B61A1
Poe luc
Pte ads
B80A1
Ama lun
H95B1
Ago cup
Cym uni
B61B2
Ago qui
Ago pla
Har fu
Har ob
Cym cri
Dip str
Dic scu
H67A1
B80B1
Not int
Pat fov
Bad obt
B61B1
Pla dec
H67B1
H80A1
H95B2
Syn imp
B80B2
Cal ing
H67A2
Sph nit
Ago ret
Ago sim
H67B2
B80A2
Pte pen
Cal fri

Figure 13a: Site scores from the first axis of figure 12, showing the separation of burn (gray bars) and harvest (white bars) plots. (2001 carabid beetles)

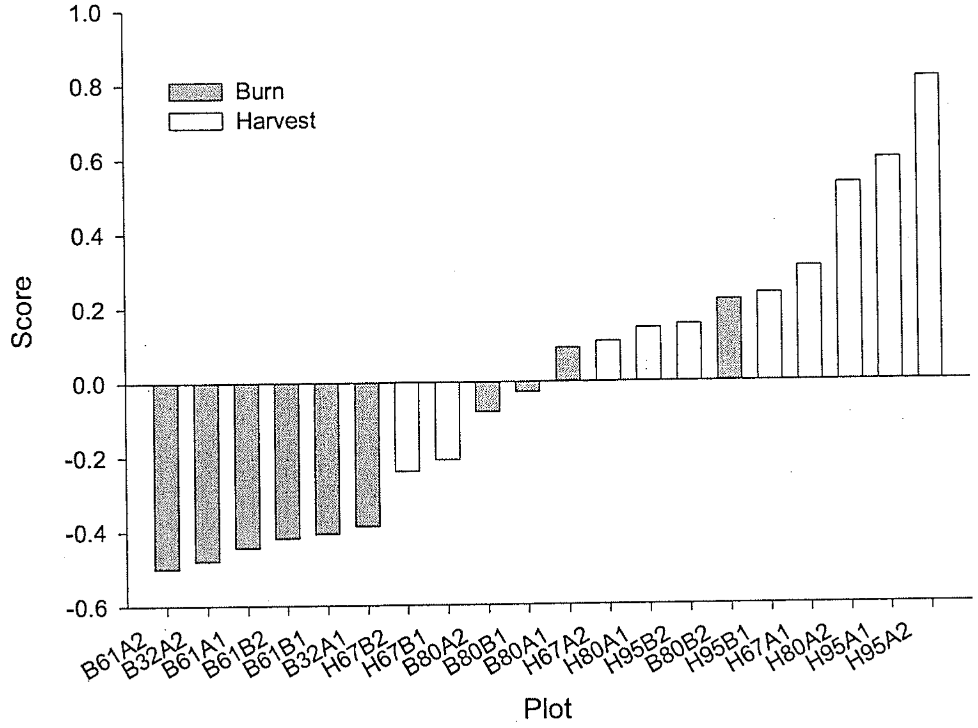


Figure 13b: Site scores from the first axis of figure 12, showing the separation of plots by year of disturbance. (2001 carabid beetles)

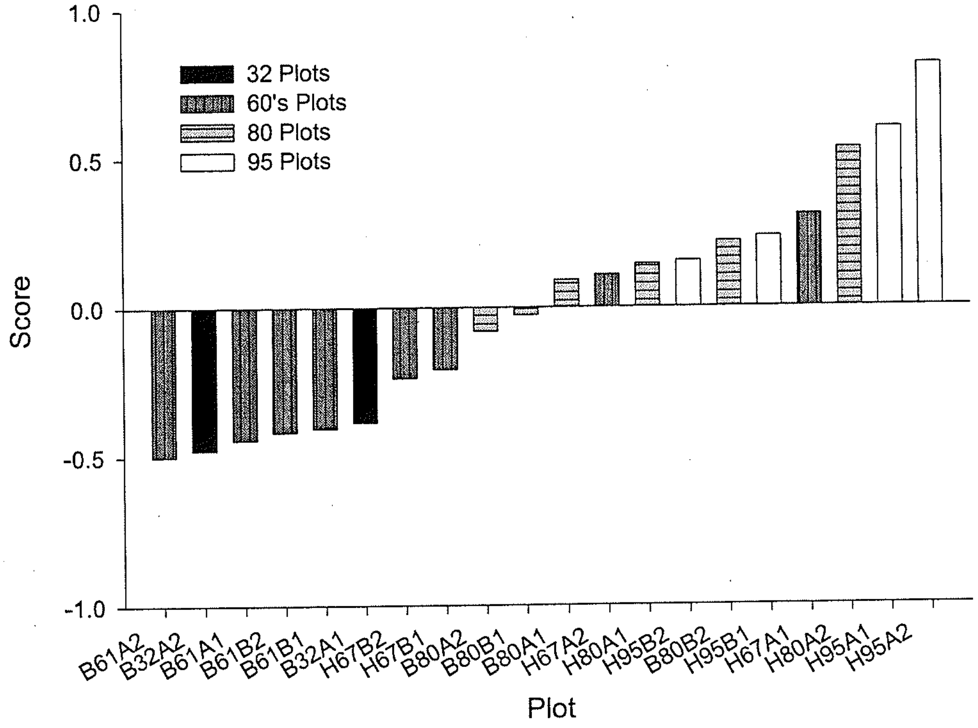


Figure 14: PCA ordination diagram of all carabid beetle species caught in 2002 in all plots with species scores (→) and plot scores (○). Species data log transformed.

Plot labels are described in Table 1.

Key to carabid beetle species: Ago cup1 = *Agonum cupreum*, Ago cup2 = *Agonum cupripenne*, Ago gra = *Agonum gratiosum*, Ago pla = *Agonum placidum*, Ago ret = *Agonum retractum*, Ago sor = *Agonum sordens*, Ago tri = *Agonum trigeminum*, Ama cup = *Amara cupreolata*, Ama imp = *Amara impuncticollis*, Bad obt = *Badister obtusus*, Bra sem = *Bradycellus semipubescens*, Cal ing = *Calathus ingratus*, Cal fri = *Calosoma frigidum*, Car cha = *Carabus chamissonis*, Car mae = *Carabus maeander*, Car tae = *Carabus taedatus*, Cym uni = *Cymindis unicolor*, Dic scu = *Dicaelus sculptilis*, Har ful = *Harpalus fulvilabris*, Pat fov = *Patrobus fovecollis*, Pat lon = *Patrobus longicornus*, Pat sep = *Patrobus septentrionis*, Pla dec = *Platynus decentis*, Poe luc = *Poecilus lucublandus*, Pte ads = *Pterostichus adstrictus*, Pte pen = *Pterostichus pensylvanicus*, Sph nit = *Sphaeroderus nitidicollis*, Syn imp = *Synuchus impunctatus*.

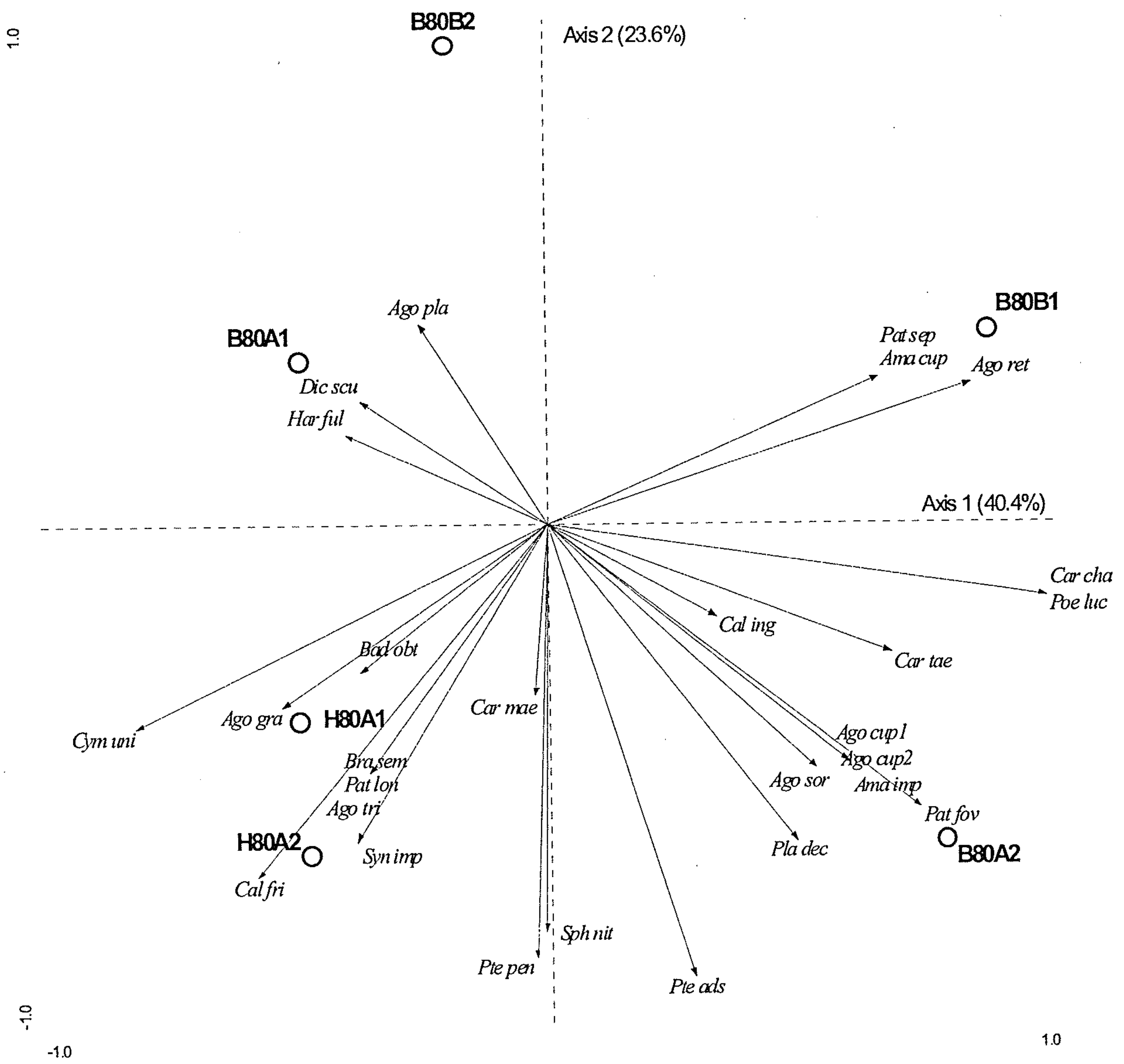
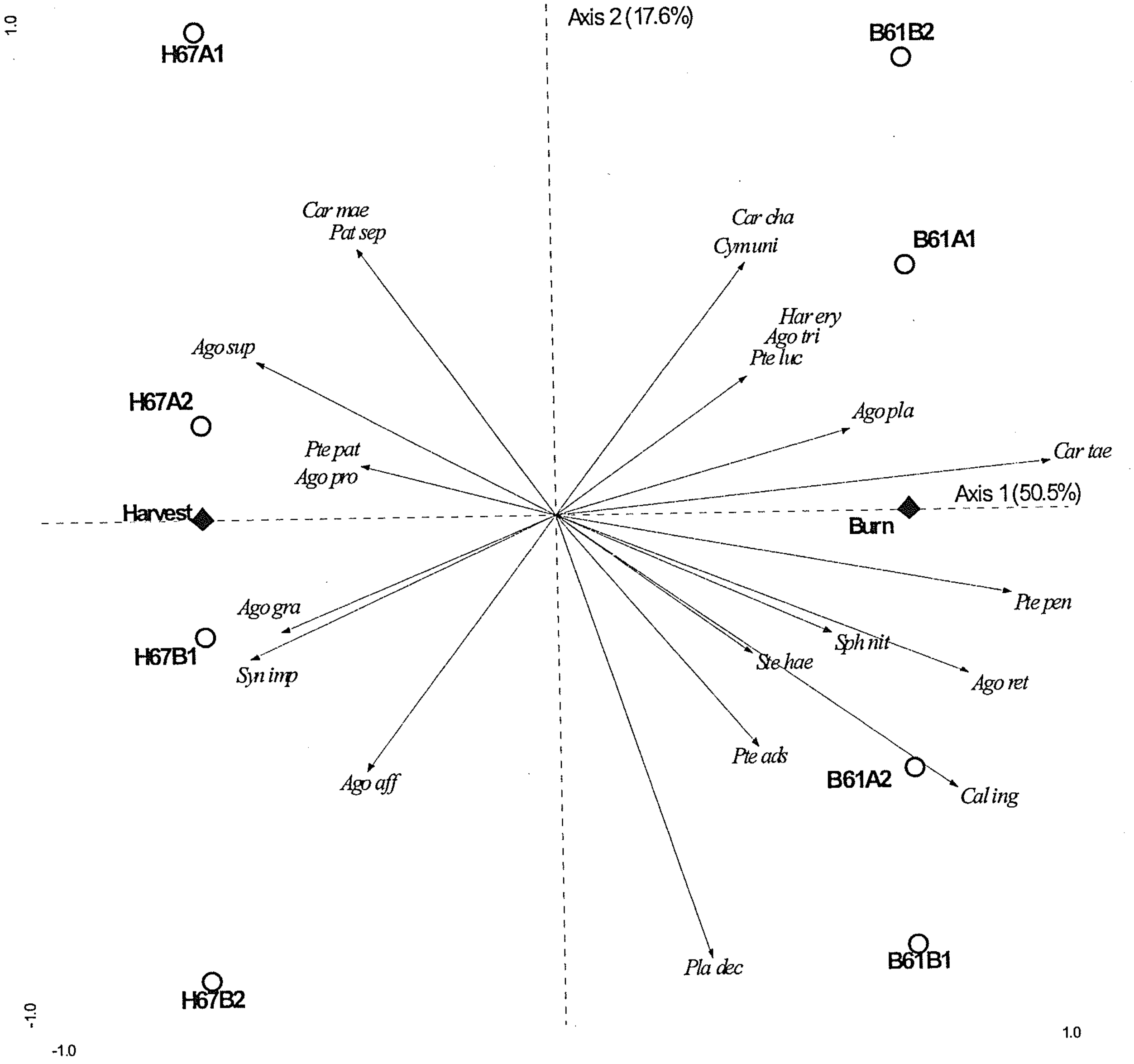

Axis 2 (23.6%)
Axis 1 (40.4%)
1.0
-1.0
-1.0
1.0
B80B2
B80B1
B80A1
B80A2
H80A1
H80A2
Ago pla
Dic scu
Har ful
Pat sep
Ama cup
Ago ret
Car cha
Poe luc
Cal ing
Car tae
Bad obt
Ago gra
Cym uni
Car mae
Bra sem
Pat lon
Ago tri
Syn imp
Cal fri
Ago cup1
Ago cup2
Ama imp
Ago sor
Pat fov
Pla dec
Sph nit
Pte pen
Pte ads

Figure 15: Redundancy analysis (RDA) of the carabid beetle species caught in 2000 from plots in sites B61 and H67 and disturbance type, with species scores (→), plot scores (○) and treatment variables (♦). Species data log transformed.

Key to carabid beetle species: Ago aff = *Agonum affine,* Ago gra = *Agonum gratiosum*, Ago pla = *Agonum placidum*, Ago pro = *Agonum propinquum*, Ago ret = *Agonum retractum*, Ago sup = *Agonum superioris*, Ago tri = *Agonum trigeminum*, Cal ing = *Calathus ingratus*, Car cha = *Carabus chamissonis*, Car mae = *Carabus maeander*, Car tae = *Carabus taedatus*, Cym cri = *Cymindis cribricollis*, Har ery = *Harpalus erythropus*, Pat sep = *Patrobus septentrionis*, Pla dec = *Platynus decentis*, Pte ads = *Pterostichus adstrictus*, Pte luc = *Pterostichus luctuosis*, Pte pat = *Pterostichus patruelis*, Pte pen = *Pterostichus pensylvanicus*, Sph nit = *Sphaeroderus nitidicollis*, Ste hae = *Stereocercus haematopus*, Syn imp = *Synuchus impunctatus*.

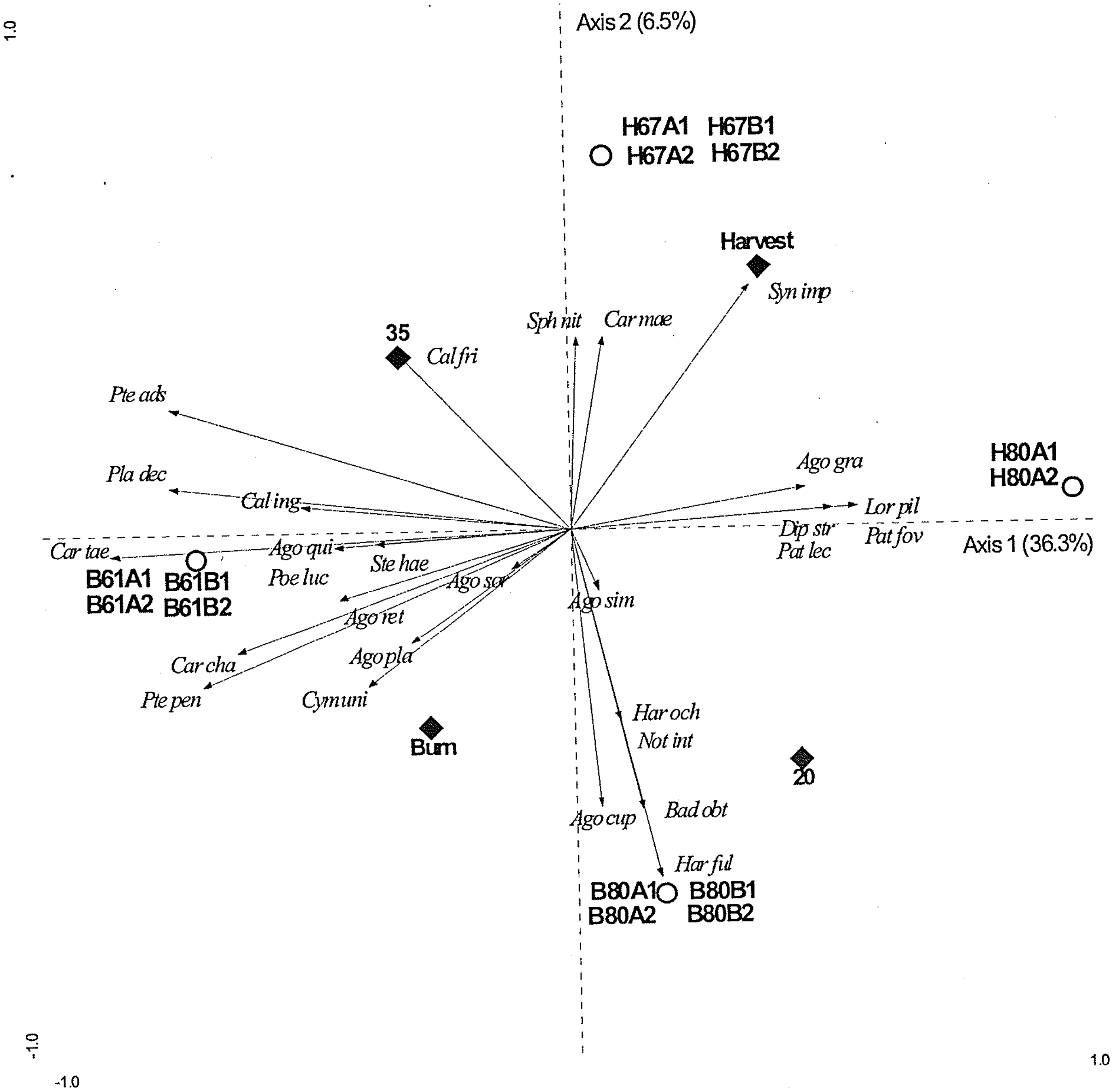


Axis 2 (17.6%)
Axis 1 (50.5%)
1.0
-1.0
-1.0
1.0
H67A1
H67A2
H67B1
H67B2
B61B2
B61A1
B61A2
B61B1
Harvest
Burn
Car mae
Pat sep
Ago sup
Pte pat
Ago pro
Ago gra
Syn imp
Ago aff
Car cha
Cym uni
Har ery
Ago tri
Pte luc
Ago pla
Car tae
Pte pen
Sph nit
Ste hae
Ago ret
Pte ads
Cal ing
Pla dec

Figure 16: RDA of the carabid beetle species caught in 2001 from plots in sites B80, H80, B61 and H67 and treatment variables (time since disturbance and disturbance type) with species scores (→), plot scores (○) and treatment variables (♦). Species data log transformed.

Key to carabid beetle species: Ago cup = *Agonum cupreum*, Ago gra = *Agonum gratiosum*, Ago pla = *Agonum placidum*, Ago qui = *Agonum quiquepunctatum*, Ago ret = *Agonum retractum*, Ago sim = *Agonum simile*, Ago sor = *Agonum sordens*, Bad obt = *Badister obtusus*, Cal ing = *Calathus ingratus*, Cal fri = *Calosoma frigidum*, Car cha = *Carabus chamissonis*, Car mae = *Carabus maeander*, Car tae = *Carabus taedatus*, Cym uni = *Cymindis unicolor*, Dip str = *Diplocheila striatopunctata*, Har ful = *Harpalus fulvilabris*, Har och = *Harpalus ochropus*, Lor pil = *Loricera pilicornis*, Not int = *Notiophilus intermedius*, Pat fov = *Patrobus fovecollis*, Pat lec = *Patrobus lecontei*, Pla dec = *Platynus decentis*, Poe luc = *Poecilus lucublandus*, Pte ads = *Pterostichus adstrictus*, Pte pen = *Pterostichus pensylvanicus*, Sph nit = *Sphaeroderus nitidicollis*, Ste hae = *Stereocercus haematopus*, Syn imp = *Synuchus impunctatus*.

Key to treatment variables: 20 = twenty years since disturbance, 35 = thirty-five years since disturbance.



Axis 2 (6.5%)
Axis 1 (36.3%)
1.0
-1.0
-1.0
1.0
H67A1 H67B1
H67A2 H67B2
Harvest
Syn imp
35
Cal fri
Sph nit
Car mae
Pte ads
Pla dec
Cal ing
Car tae
B61A1 B61B1
B61A2 B61B2
Ago qui
Poe luc
Ste hae
Ago sor
Ago ret
Ago pla
Car cha
Pte pen
Cym uni
Burn
Ago gra
Lor pil
Dip str
Pat lec
Pat fov
H80A1
H80A2
Ago sim
Har och
Not int
20
Ago cup
Bad obt
Har ful
B80A1 B80B1
B80A2 B80B2

Figure 17: RDA of the carabid beetle species caught in 2000 in all plots and significant environmental variables with species scores (→), plot scores (○) and environmental variables (- - - ▶). Species data log transformed.

Plot labels are described in Table 1.

Key to carabid beetle species: Ago aff = *Agonum affine,* Ago cup1 = *Agonum cupreum*, Ago cup2 = *Agonum cupripenne*, Ago gra = *Agonum gratiosum*, Ago pla = *Agonum placidum*, Ago pro = *Agonum propinquum*, Ago pun = *Agonum puncticeps*, Ago ret = *Agonum retractum*, Ago sim = *Agonum simile*, Ago sor = *Agonum sordens*, Ago sup = *Agonum superioris*, Ago tho = *Agonum thoreyi*, Ago tri = *Agonum trigeminum*, Ama cup = *Amara cupreolata*, Ani san = *Anisodactylus sanctaecrucis*, Cal ing = *Calathus ingratus*, Car cha = *Carabus chamissonis*, Car mae = *Carabus maeander*, Car tae = *Carabus taedatus*, Cym uni = *Cymindis unicolor*, Har ery = *Harpalus erythropus*, Har ful = *Harpalus fulvilabris*, Har spp = *Harpalus* species, Pat sep = *Patrobus septentrionis*, Pla dec = *Platynus decentis*, Pte ads = *Pterostichus adstrictus*, Pte cor = *Pterostichus corvinus*, Pte luc = *Pterostichus luctuosis*, Pte pat = *Pterostichus patruelis*, Pte pen = *Pterostichus pensylvanicus*, Pte pun = *Pterostichus punctatissimus*, Sph nit = *Sphaeroderus nitidicollis*, Ste hae = *Stereocercus haematopus*, Syn imp = *Synuchus impunctatus*.

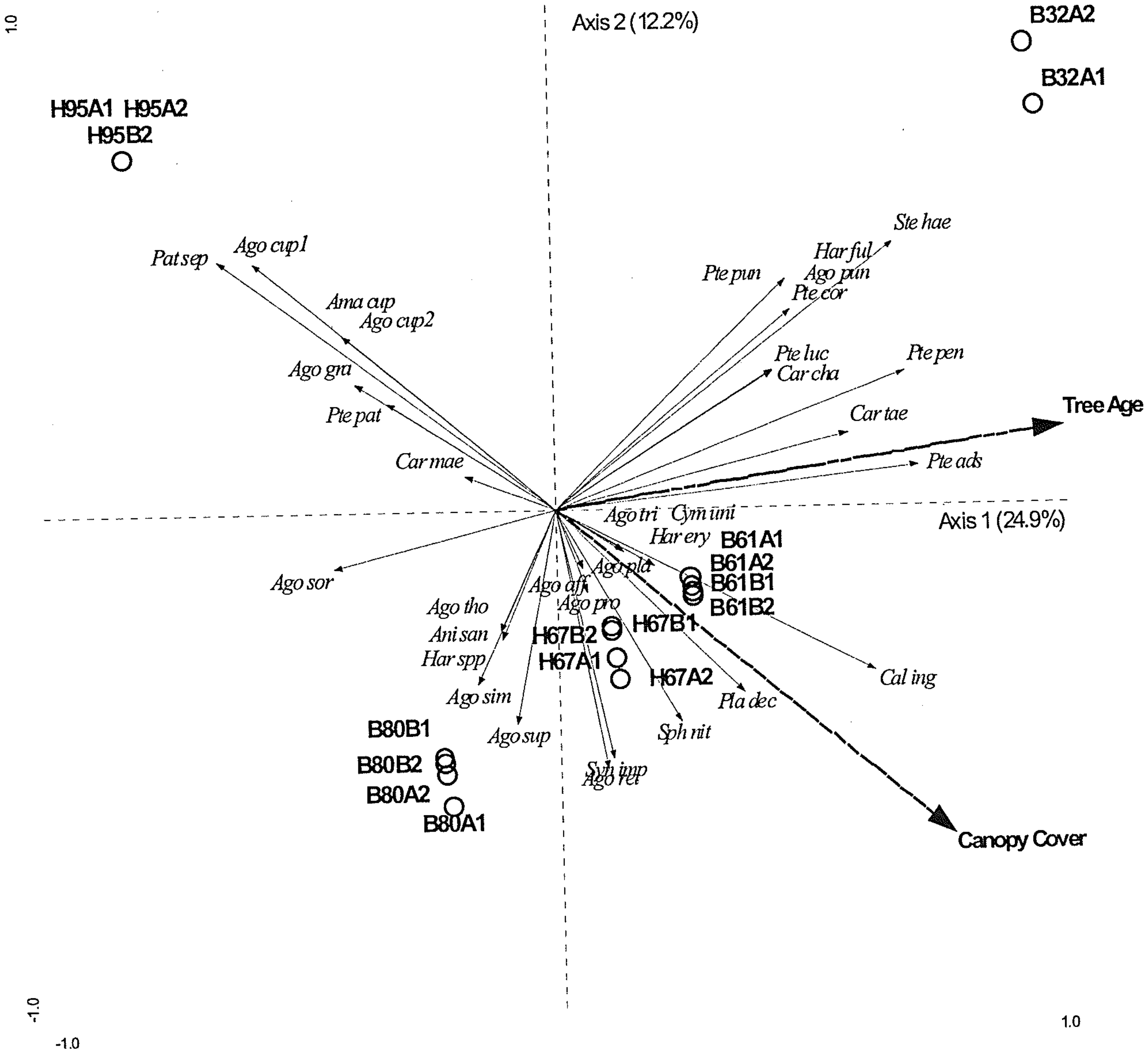

Axis 2 (12.2%)
Axis 1 (24.9%)
1.0
-1.0
-1.0
1.0
B32A2
B32A1
H95A1 H95A2
H95B2
Pat sep
Ago cup1
Ama cup
Ago cup2
Ago gra
Pte pat
Car mae
Ago sor
Ste hae
Har ful
Ago pun
Pte pun
Pte cor
Pte luc
Car cha
Pte pen
Tree Age
Car tae
Pte ads
Ago tri
Cym uni
Har ery
B61A1
B61A2
B61B1
B61B2
Ago pla
Ago aff
Ago pro
H67B1
H67B2
H67A1
H67A2
Cal ing
Pla dec
Sph nit
Ago tho
Ani san
Har spp
Ago sim
Ago sup
Syh imp
Ago ret
B80B1
B80B2
B80A2
B80A1
Canopy Cover

Figure 18: RDA of the carabid beetle species caught in 2001 in all plots and significant environmental variables with species scores (→), plot scores (○) and environmental variables (- - - ▶). Species data log transformed.

Plot labels are described in Table 1.

Key to carabid beetle species: Ago cup = *Agonum cupreum*, Ago gra = *Agonum gratiosum*, Ago pla = *Agonum placidum*, Ago qui = *Agonum quiquepunctatum*, Ago ret = *Agonum retractum*, Ago sim = *Agonum simile*, Ago sor = *Agonum sordens*, Ago tri = *Agonum trigeminum*, Ama lun = *Amara lunicolis*, Bad obt = *Badister obtusus*, Bra sem = *Bradycellus semipubescens*, Cal ing = *Calathus ingratus*, Cal fri = *Calosoma frigidum*, Car cha = *Carabus chamissonis*, Car mae = *Carabus maeander*, Car tae = *Carabus taedatus*, Cym cri = *Cymindis cribricollis*, Cym uni = *Cymindis unicolor*, Dic scu = *Dicaelus sculptilis*, Dip str = *Diplocheila striatopunctata*, Har ful = *Harpalus fulvilabris*, Har och = *Harpalus ochropus*, Lor pil = *Loricera pilicomis*, Not int = *Notiophilus intermedius*, Pat fov = *Patrobus fovecollis*, Pat sep = *Patrobus septentrionis*, Pla dec = *Platynus decentis*, Poe cor = *Poecilus corvus*, Poe luc = *Poecilus lucublandus*, Pte ads = *Pterostichus adstrictus*, Pte pen = *Pterostichus pensylvanicus*, Pte pun = *Pterostichus punctatissimus*, Sph nit = *Sphaeroderus nitidicollis*, Ste hae = *Stereocercus haematopus*, Syn imp = *Synuchus impunctatus.*

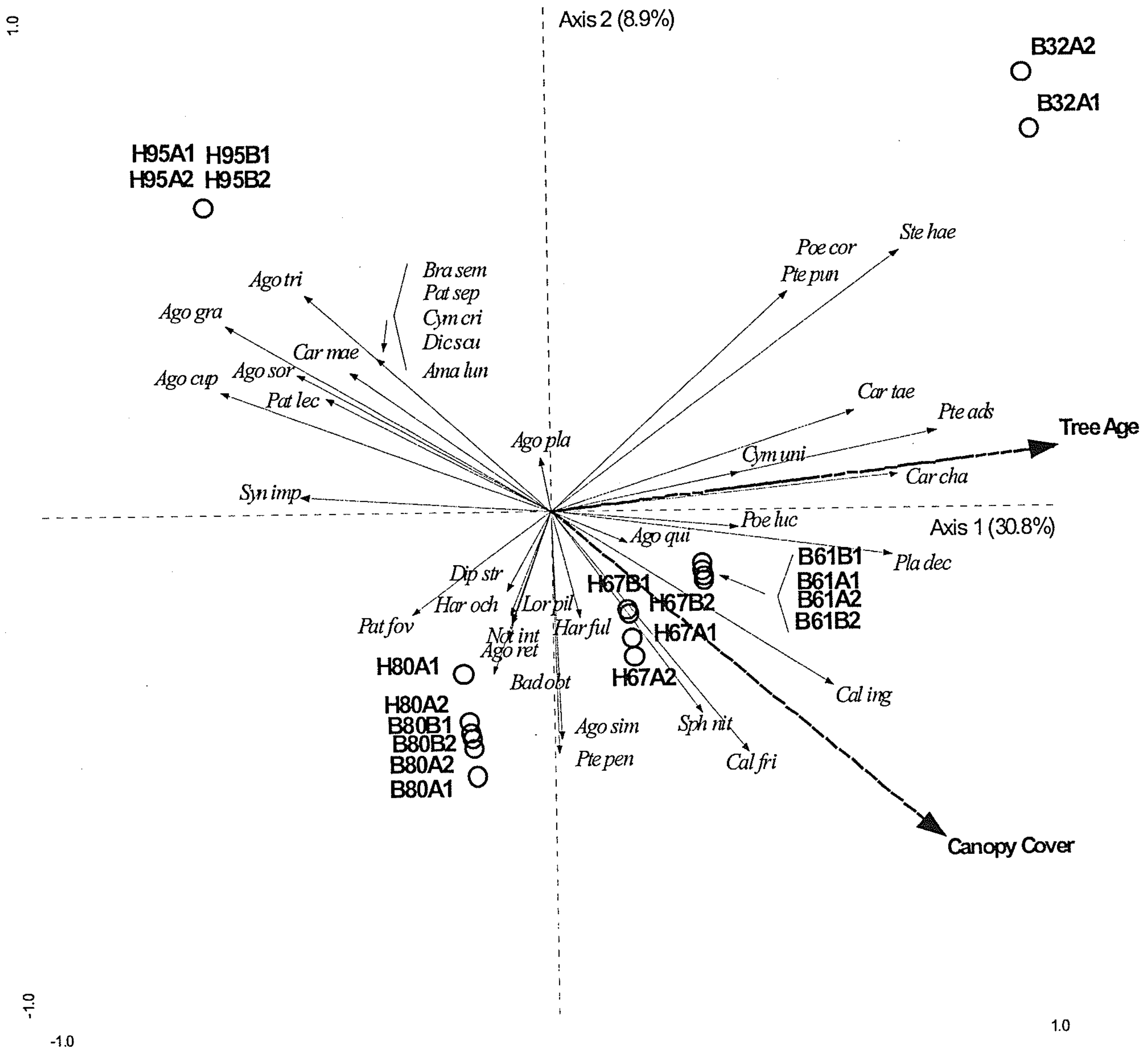

Axis 2 (8.9%)
Axis 1 (30.8%)
1.0
-1.0
-1.0
1.0
B32A2
B32A1
H95A1 H95B1
H95A2 H95B2
Ste hae
Poe cor
Pte pun
Bra sem
Pat sep
Cym cri
Dic sau
Ama lun
Ago tri
Ago gra
Car mae
Ago sor
Ago cup
Pat lec
Car tae
Pte ads
Tree Age
Cym uni
Car cha
Ago pla
Syn imp
Poe luc
Ago qui
Pla dec
B61B1
B61A1
B61A2
B61B2
H67B1
H67B2
H67A1
H67A2
Dip str
Har och
Lor pil
Pat fov
Not int
Har ful
Ago ret
H80A1
Bad obt
Cal ing
H80A2
B80B1
B80B2
B80A2
B80A1
Ago sim
Sph nit
Pte pen
Cal fri
Canopy Cover

Figure 19: RDA of the carabid beetle species caught in 2000 in all plots and significant shrub stratum species with carabid beetle species scores (→), plot scores (○) and shrub stratum species (♦). Species data log transformed.

Plot labels are described in Table 1.

Key to carabid beetle species: Ago aff = *Agonum affine,* Ago cup1 = *Agonum cupreum*, Ago cup2 = *Agonum cupripenne*, Ago gra = *Agonum gratiosum*, Ago pla = *Agonum placidum*, Ago pro = *Agonum propinquum*, Ago pun = *Agonum puncticeps*, Ago ret = *Agonum retractum*, Ago sim = *Agonum simile*, Ago sor = *Agonum sordens*, Ago sup = *Agonum superioris*, Ago tho = *Agonum thoreyi*, Ago tri = *Agonum trigeminum*, Ama cup = *Amara cupreolata*, Ani san = *Anisodactylus sanctaecrucis*, Cal ing = *Calathus ingratus*, Car cha = *Carabus chamissonis*, Car mae = *Carabus maeander*, Car tae = *Carabus taedatus*, Cym uni = *Cymindis unicolor*, Har ery = *Harpalus erythropus*, Har ful = *Harpalus fulvilabris*, Har spp = *Harpalus* species, Pat sep = *Patrobus septentrionis*, Pla dec = *Platynus decentis*, Pte ads = *Pterostichus adstrictus*, Pte cor = *Pterostichus corvinus*, Pte luc = *Pterostichus luctuosis*, Pte pat = *Pterostichus patruelis*, Pte pen = *Pterostichus pensylvanicus*, Pte pun = *Pterostichus punctatissimus*, Sph nit = *Sphaeroderus nitidicollis*, Ste hae = *Stereocercus haematopus*, Syn imp = *Synuchus impunctatus.*

Key to shrub species: Ame aln = *Amelanchier alnifolia*, Apo and = *Apocynum androsaemifolium*, Cor cor = *Corylus cornuta*, Dis tra = *Disporum trachycarpum*, Pop bal = *Populus balsamifera*, Sym alb = *Symphoricarpos albus*, Vib edu = *Viburnum edule.*

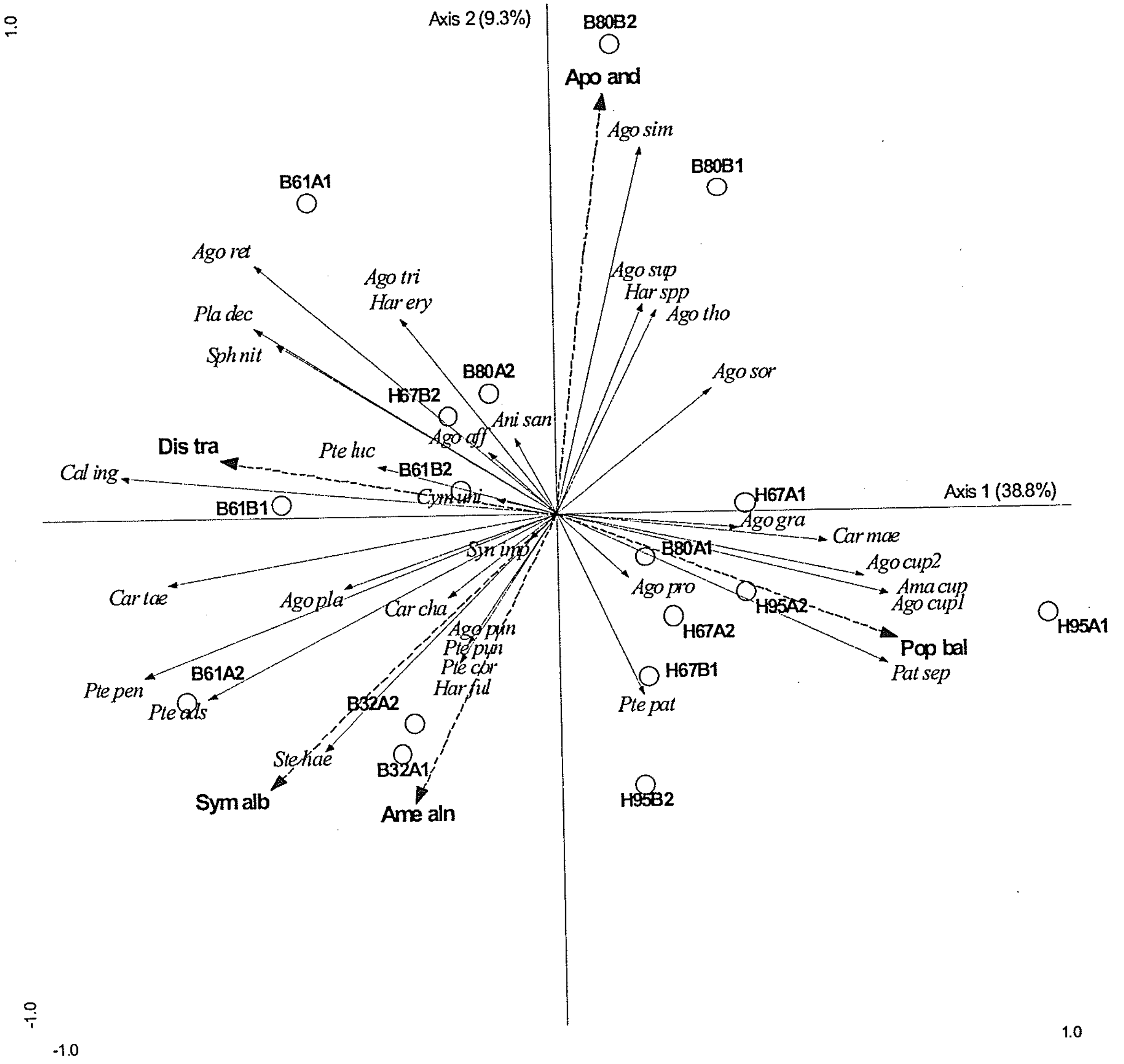
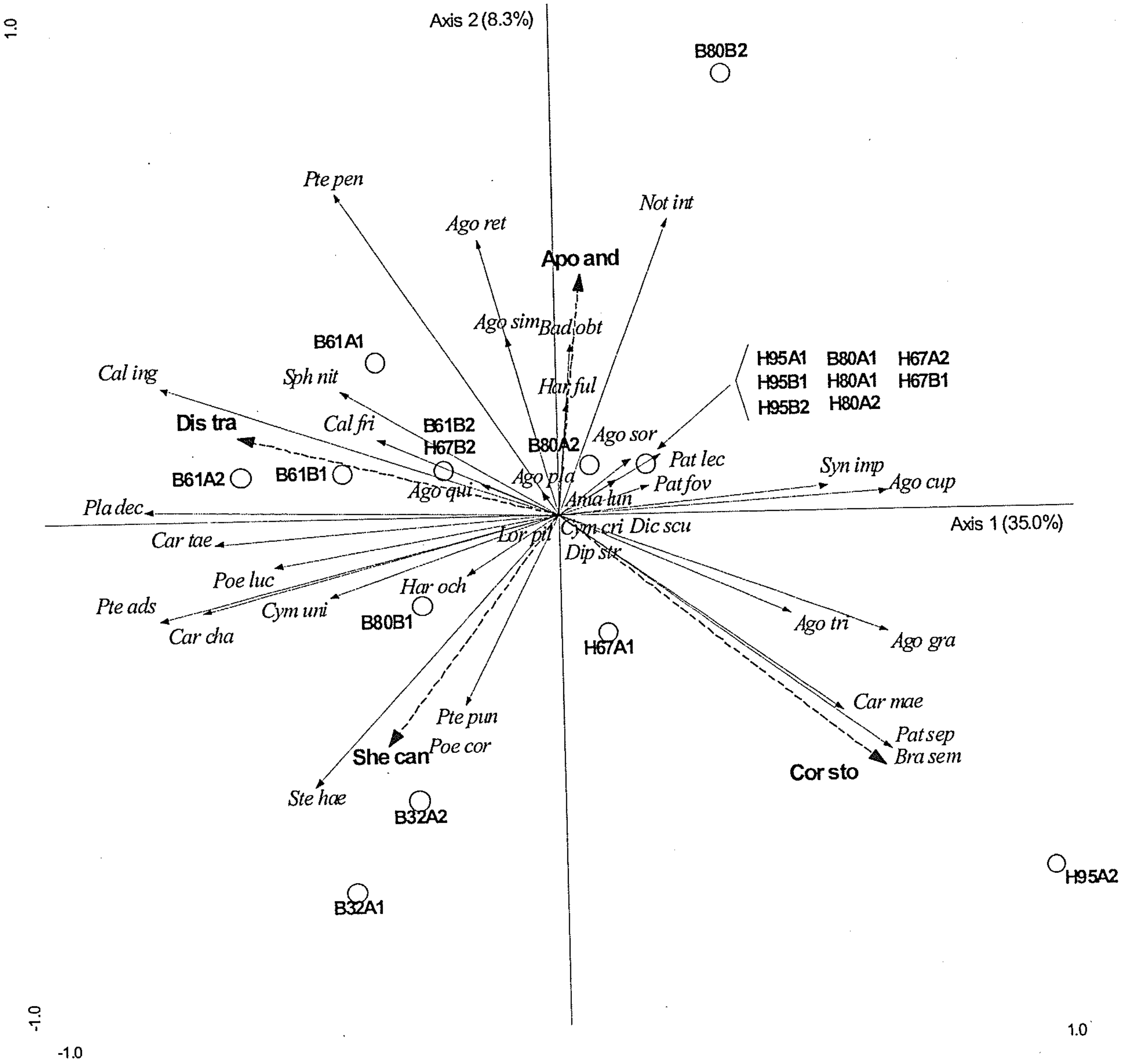

1.0
-1.0
-1.0
1.0
Axis 2 (9.3%)
Axis 1 (38.8%)
B80B2
Apo and
Ago sim
B80B1
B61A1
Ago ret
Ago tri
Har ery
Pla dec
Sph nit
Ago sup
Har spp
Ago tho
Ago sor
B80A2
H67B2
Ani san
Ago aff
Dis tra
Pte luc
B61B2
Cal ing
Cym uni
B61B1
H67A1
Ago gra
Car mae
B80A1
Syn imp
Ago cup2
Car tae
Ago pro
Ama cup
Ago cup1
Ago pla
Car cha
H95A2
H95A1
H67A2
Ago pun
Pte pun
Pop bal
Pat sep
Pte cor
H67B1
B61A2
Pte pen
Har ful
Pte ads
B32A2
Pte pat
Ste hae
B32A1
H95B2
Sym alb
Ame aln

Figure 20: RDA ordination diagram of the carabid beetle species caught in 2001 in all plots and shrub stratum species with carabid beetle species scores (→), plot scores (○) and shrub stratum species (♦). Species data log transformed.

Plot labels are described in Table 1.

Key to carabid beetle species: Ago cup = *Agonum cupreum*, Ago gra = *Agonum gratiosum*, Ago pla = *Agonum placidum*, Ago qui = *Agonum quiquepunctatum*, Ago ret = *Agonum retractum*, Ago sim = *Agonum simile*, Ago sor = *Agonum sordens*, Ago tri = *Agonum trigeminum*, Ama lun = *Amara lunicolis*, Bad obt = *Badister obtusus*, Bra sem = *Bradycellus semipubescens*, Cal ing = *Calathus ingratus*, Cal fri = *Calosoma frigidum*, Car cha = *Carabus chamissonis*, Car mae = *Carabus maeander*, Car tae = *Carabus taedatus*, Cym cri = *Cymindis cribricollis*, Cym uni = *Cymindis unicolor*, Dic scu = *Dicaelus sculptilis*, Dip str = *Diplocheila striatopunctata*, Har ful = *Harpalus fulvilabris*, Har och = *Harpalus ochropus*, Lor pil = *Loricera pilicornis*, Not int = *Notiophilus intermedius*, Pat fov = *Patrobus fovecollis*, Pat sep = *Patrobus septentrionis*, Pla dec = *Platynus decentis*, Poe cor = *Poecilus corvus*, Poe luc = *Poecilus lucublandus*, Pte ads = *Pterostichus adstrictus*, Pte pen = *Pterostichus pensylvanicus*, Pte pun = *Pterostichus punctatissimus*, Sph nit = *Sphaeroderus nitidicollis*, Ste hae = *Stereocercus haematopus*, Syn imp = *Synuchus impunctatus*.

Key to shrub stratum species: Apo and = *Apocynum androsaemifolium*, Cor sto = *Cornus stolonifera*, Dis tra = *Disporum trachycarpum*, She can = *Shepherdia canadensis*.


1.0
Axis 2 (8.3%)
B80B2
Pte pen
Ago ret
Not int
Apo and
Ago sim
Bad obt
B61A1
Cal ing
Sph nit
Har ful
H95A1
B80A1
H67A2
H95B1
H80A1
H67B1
H95B2
H80A2
Dis tra
Cal fri
B61B2
H67B2
B80A2
Ago sor
Pat lec
Syn imp
Pat fov
Ago cup
B61A2
B61B1
Ago qui
Ago pla
Ama lun
Pla dec
Axis 1 (35.0%)
Car tae
Lor pil
Cym cri
Dic scu
Dip str
Poe luc
Har och
Pte ads
Cym uni
B80B1
Car cha
Ago tri
Ago gra
H67A1
Car mae
Pte pun
Pat sep
Poe cor
She can
Bra sem
Cor sto
Ste hae
B32A2
H95A2
B32A1
-1.0
-1.0
1.0

Discussion

Implications and limitations of the methodology

Many techniques exist to sample insect populations, each with associated advantages and disadvantages (Southwood 1978; Triplehorn and Johnson 2004). The method employed in this study, pitfall trapping, has been used extensively to collect carabid beetles (e.g. Barlow 1970; Loreau 1985; Niemelä et al. 1992; Werner and Raffa 2003). Pitfall trap catches are influenced by factors that may bias the catch, consequently, results obtained from pitfall trapping must be interpreted with caution (Spence and Niemelä 1994). It should also be noted that pitfall trapping does not provide a measure, or even an estimate of absolute abundance (Desender and Maelfait 1986). Pitfall trap catches are capable of providing estimates of relative abundance (Spence and Niemelä 1994), and that is how they were used in the current study.

In this study there was a tendency for the traps to be dug up by animals such as moose (which was once observed digging up a trap) and porcupines, often resulting in a partial or complete loss of two weeks trapping data for that particular trap. Occasionally the traps would collect large numbers of carrion beetles (Coleoptera: Silphidae), which were probably attracted to the traps by the scent of decaying organic matter. The carrion beetles themselves seemed to produce an odor, which may have played a role in attracting the animals that subsequently dug up the trap. Comparable studies have reported similar problems (Wytrykush 2001; Capar 2003), and they would seem to be common to this type of research. A way of minimizing the impact of disturbed traps and carrion beetles would have been to empty the traps more frequently, however in this study, accessibility and distance constraints necessitated a two week interval between collections. Snails, which are an important prey item for many carabid species such as *Sphearoderus nitidicollis* (Digweed 1993), were often found on the underside of pitfall trap lids. These snails may have served as an attractant to some carabid beetle species, resulting in an over-representation of species which prey on snails.

As with all natural populations, those sampled in this study were subject to fluctuations due to factors beyond the scope of this study. These fluctuations are evident when the catch frequency of carabid beetles between sampling years are compared. The seasonal occurrence patterns of individual species also impacted the results. In this study, carabid beetles were caught most frequently at the beginning of the sampling seasons (late May) and decreased as the season progressed. A longer sampling period beginning earlier in the season and continuing into September would have yielded more results, however pitfall traps were set as soon as spring conditions permitted access to all plots.

Unfortunately, in only two age classes were both burn and harvest sites established (1980 and 1961/67). It would have been preferable to sample from a site in a recently burned forest to pair with the site that was harvested in 1995. This possibility was explored, but forest fire suppression in the Duck and Porcupine Mountains has limited the number of large fires since the early 1980s (Manitoba Natural Resources 1997).

Another factor to be considered is the harvesting practices of the forest industry, and how they have evolved over the period in question. The techniques used to harvest in 1967 may have been different than those used to harvest in 1995. The differences in harvest techniques between 1961/67 and 1980 may include reduced soil compaction, which may improve conditions for re-growth of vegetation, and an increase in the amount of coarse woody debris left on the site (Conway 1992).

Caution should be used when applying the results and recommendations non-aspen-spruce mixedwood forests. The carabid beetle communities examined in this study differ considerably from those found in other Manitoba forest types including white spruce-balsam fir (Wytrykush 2001) and black spruce (Capar 2003), although the carabid beetle communities found in this study are consistent with those found in similar forests in Alberta (Niemelä et al. 1992) and northern Wisconsin (Werner and Raffa 2000).

Replication accuracy and vegetation structure

It is important to be confident that the plots within sites were similar enough to pool the results obtained from those plots. Holliday (1991), Niemelä et al. (1992) and Pearce et al. (2003) have each reported that micro-habitat factors are among the most important determinants affecting the small-scale distribution of carabid beetles. Accurate plot replication is important as a means of minimizing the influence of local habitat variations.

From a vegetation structure and species perspective, similarity within sites generally increased with plot age, so that plots within recently disturbed sites were less similar than plots within older forest stands. The overall trend in the vegetation structure was an initial, dense stand of young *Populus balsamifera* and *Populus tremuloides* in recently disturbed sites. These had self-thinned by 20 years after the disturbance, and other species such as *Betula papyrifera*, *Picea glauca* and *Salix* spp., were present in the understory of the 1980 sites. Canopy closure occurred approximately 30-40 years after the disturbance, in the 1961/67 sites. Patches in the canopy, caused by dying, mature aspen, resulted in gaps where *P. glauca* and *Salix* spp. were found.

A very high density of shrubs and short sapling 'trees', primarily *Populus balsamifera* and *Populus tremuloides* characterized all H95 plots. These plots also showed the highest percent cover in the herb/moss stratum. The absence of a tree canopy over 2 m tall and a high degree of local patchiness resulted in high light levels reaching the ground. All H95 plots had live, mature aspen trees that were left following the harvest (as patch tree retention) and an often dense, highly variable layer of coarse woody debris. This coarse woody debris was of recent origin and showed little signs of decay. Relative to other sites, these plots showed the most variability in vegetation structure. This variation was due to the interactions between the unique topography of each plot and the differences between individual harvests. These differences included where machinery operated, where the residual trees were left, and the distribution of coarse woody debris. Aside from the effects of heavy machinery, the variations observed in individual timber harvests are similar to those reported for forest fires (Haeussler and Bergeron 2004).

The 1980 plots had a tree canopy that was higher off the ground, and shrub and herb/moss strata that were less dense than the H95 plots. The reduction of the shrub and herb/moss layers was due to the higher tree canopy that reduced the amount of available light nearer the forest floor. The tree canopy was still dominated by *Populus balsamifera* and *Populus tremuloides*. The B80 site showed some differences between plots. Plot B80A1 had a high density of *Betula papyrifera* in the tree stratum, although this difference in the tree canopy did not seem to influence the composition of the understory vegetation or the carabid beetle community. Plot B80A2 had a much higher catch frequency of *Platynus decentis* than all other B80 plots. The cause of this difference is unknown and may be due to an environmental factor that was not measured during this study. Coarse woody debris was abundant in all the B80 plots, and was often present in large piles of burned tree trunks. Within the H80 site, the two plots showed little difference in the vegetation or carabid beetle communities. The H80 plots had a lower percentage of trees that were *Populus* spp. and less coarse woody debris than the B80 plots. The shrub stratum of the B80 plots had more occurrences of coniferous species such as *Abies balsamea* and *Picea glauca*.

The 1961/67 plots were characterized by a further thinning of the tree stratum, and a higher, denser tree canopy. This age class showed the highest levels of canopy cover and a corresponding low level of light reaching the forest floor. Johnstone et al. (2004) found that canopy cover in aspen stands in British Columbia was highest approximately 30-40 years after the disturbance, the same stand age where canopy cover was greatest in this study. The vegetation in the shrub and herb/moss strata varied little between the 1961/67 sites and the 1980 sites, and it appeared that many shade-tolerant species had established themselves by 20 years after the disturbance. The tree canopy was still dominated by *Populus tremuloides*, but an increasing number of coniferous species had become established. Within the B61 site, plots were very similar in all vegetation and environmental factors that were measured. The H67 site also showed little variation among plots. Additionally, the tree and shrub strata of the B61 and H67 sites were very similar.

In the 1932 plots, the death of some mature *Populus tremuloides* created a more open canopy with large gaps. These gaps resulted in large areas with increased light levels at the forest floor, allowing for a 'sub-canopy' of coniferous trees and high shrubs, primarily *Alnus crispa* and *Corylus cornuta*. Light penetration was greater than in the 1961/67 sites and comparable to levels observed in the 1980 sites. The two 1932 plots showed little variation, although B32A2 had a higher percentage of coniferous trees and a shrub layer that was more dense than B32A1. Coarse woody debris was minimal in these sites, and consisted primarily of mature trees that had recently died. Virtually all recognizable remnants of the forest fire were gone.

Carabid beetle responses

The responses of carabid beetles observed in this study can be grouped into three categories: (1) responses related to the time of year (seasonal responses); (2) responses related to the time since the disturbance (stand age responses); and (3) differences and similarities between responses to forest fire and timber harvesting (disturbance type responses).

Seasonal responses

The time of year is an important factor in determining carabid beetle occurrence (Werner and Raffa 2003). Some researchers have reported that the overall abundance of carabid beetles remains constant throughout the season (e.g. Werner and Raffa 2003). Most studies however, have found that catch frequency varies with the season (e.g. Niemelä et al. 1992; Lafrenière 1994; Wytrykush 2001; Capar 2003). At latitudes similar to the present study, the greatest number of carabid beetles occur in May-June, as this is the primary activity period for many of the most frequently caught species. Studies which have used similar sampling methods to the present study have reported seasonal variations in the appearance and catch frequency of individual species (e.g. Niemelä et al. 1992; Werner and Raffa 2003).

In this study, carabid beetle catch frequency and community composition changed throughout the sampling period. In all three sampling years, carabid beetle catch frequency was highest early in the season, and then declined as the season progressed.

The earliest samples from this study were removed from the pitfall traps in early June, and may have been caught as early as May 22. The high catch frequencies observed early in the sampling period are due primarily to one species: *Platynus decentis*. This species is a forest generalist often associated with "mesic to hydric" deciduous forests (Epstein and Kulman 1990), although Holliday (1991) reported much higher catches of *P. decentis* in coniferous forests than aspen forests in the Interlake Region of Manitoba. The catch frequency of this species was very high in all plots over the first few weeks of sampling, and then declined steeply, findings consistent with those of Werner and Raffa (2003). *Platynus decentis* is known to have two activity periods: one in the spring and early summer when reproduction occurs, and a second in the fall (Bousquet and Pilon 1977) (Table 16). The sampling period of this study did not extend into the second activity period, and therefore *P. decentis* appeared to have only one activity period.

The occurrence patterns of species that were among the most frequently caught early in the season, including *Platynus decentis*, *Pterostichus adstrictus* and *Pterostichus pensylvanicus* were nearly identical to those reported in other studies and were in accordance with known activity periods (Barlow 1970; Epstein and Kulman 1990; Holliday 1991) (Table 16). Occurrence patterns of *Calosoma frigidum*, which was caught most frequently in early-June, and *Agonum retractum*, which was caught most frequently in July were also very similar to those reported by Werner and Raffa (2003). Other species that had high mid-season catch frequencies, included *Calathus ingratus* and *Agonum placidum* Say. The catch frequency of *Synuchus impunctatus* was highest late in the season (August), findings similar to Bousquet and Pilon (1977) and Moore et al. (2004).

These variations in seasonal occurrence and the resulting changes in carabid beetle communities indicated that the ecological requirements of carabid beetles may have depended on season as much as they did on other factors. Different emergence strategies (i.e. some species over-winter as adults, while others over-winter as larvae) (Table 16) result in dynamic communities where one ecological niche may have been occupied by several species, each at a different time of the season. Activity cycles of carabid beetles have also been shown to follow fluctuations in their prey (Hengeveld 1981; Loreau 1988). *Calosoma frigidum* preys mainly on caterpillars, particularly the forest tent caterpillar (*Malacosoma disstria* Hubner) (Crins 1980). The adults of this species are active early in the summer and may enter hibernation mid-summer, coinciding with the pupation of their prey (Lindroth 1961-1969) (Table 16). There was little evidence of major infestation by the forest tent caterpillar in any of the study sites, although the southern portion of Duck Mountain Provincial Park did experience a significant outbreak in the summer of 2001.

These changes in community composition necessitate an understanding of how communities are structured at different times of the season. Possible future monitoring surveys by forestry companies or government monitoring programs that use this study as baseline information will need to consider the time of season when to best conduct their surveys. (i.e. sampling would have to be conducted over the same sampling period as the current study, or during a small window when the composition of the expected community is well understood).

Stand age responses

As stand age increased, carabid beetle catch frequency also increased. The B32 and B61 plots consistently had the highest number of carabid beetles caught. These plots had high catch frequencies of *Platynus decentis* and *Pterostichus adstrictus*. Werner and Raffa (2000) reported that *P. decentis* was a forest generalist associated with old growth forests in the Great Lakes Region. *Platynus decentis* has also been negatively associated with coarse woody debris (Pearce et al. 2003), which would have been less abundant in older forests due to decay. *Pterostichus adstrictus* has also been reported to be a habitat generalist, but is one of the most common insects in the boreal forest (Lindroth 1961-1969; Digweed 1993) (Table 16). Pearce et al. (2003) found that *P. adstrictus* to be positively correlated with the volume of moderately-decayed woody debris. Both species were caught in all sites, but were caught much less frequently in more recently disturbed plots. These findings are consistent with those of other studies which found timber harvesting results in an initial decrease of forest generalist species, which then tend to recover with succession (e.g. Lenski 1982; Niemelä et al. 1993; Butterfield 1997).

The number of species of carabid beetles caught varied little from the most-recently disturbed sites to the oldest sites, and was not affected by time since disturbance. Werner and Raffa (2000; 2003) have reported similar findings in hemlock and hardwood dominated stands.

Although the number of species did not vary considerably with time since disturbance, the diversity of carabid beetle communities did. Alpha diversity (as measured by the log-series α), was highest in recently disturbed plots, and then steadily declined as stand age increased. Carabid beetles in the 1995 site were the most even, and the level of evenness decreased as stand age increased. These findings are supported by levels of species dominance (Berger-Parker index), which were lowest in the 1995 site, increased in the 1980 sites, and again in the 1961/67 and 1932 sites. Dominance levels were influenced by *Platynus decentis*, which was the most frequently caught species in all but two plots in 2001 (H80A2 and H95A2). Increases associated with stands age may be due to increased available habitat in the form of accumulated leaf litter (Pearce et al. 2003).

These findings are consistent with other research that has suggested that the random nature of recently disturbed sites provides more ecological niches and correspondingly higher levels of carabid beetle diversity (Beaudry et al. 1997). The Jaccard index showed that carabid beetle communities change over time and that as forest stands age after a disturbance, the species composition of carabid beetle communities follows a similar path.

The catch frequency of the species that initially colonized the most recently disturbed sites was relatively even. As these forests mature following a disturbance, the relative catch frequency of some species of carabid beetle species seems to becomes very high, but the overall number of species on the site changes very little. The species that seemed to dominate the carabid beetle communities in older plots (in terms of catch frequency) included *Platynus decentis*, *Pterostichus adstrictus*, and to a lesser extent, *Calathus ingratus* and. Both *P. decentis* and *Carabus taedatus* are forest insects, a group which traditionally see their numbers drop following a disturbance, then gradually return as the forest matures (Niemelä et al. 1992). While *Pterostichus adstrictus* is considered a habitat generalist, it is one of the most frequently encountered species of carabid beetles in the boreal forest. *Calathus ingratus* has also been reported to respond in a similar manner to forest disturbances (Beaudry et al. 1997).

A high proportion of the species that colonized the most recently disturbed plots (H95) are associated with meadows and dry, open spaces. These species included *Agonum cupreum*, *Agonum cupripenne* Say, *Agonum placidum*, *Cymindis cribricollis* Dejean and *Cymindis unicolor* Kirby (Lindroth 1961-1969; Runtz and Peck 1994; Addison and Barber 1997; Beaudry et al. 1997; Apigian and Wheelwright 2000) (Table 16). Although forest generalists such as *Platynus decentis* and *Calathus ingratus* were also caught in the H95 site, they were caught with much lower frequency than in older sites and their presence may be attributed to remnant populations which remained from prior to the harvest. Those older sites (H67, B61 and B32) had the highest catch frequencies of forest generalists, indicating that as time since disturbance increased, forest generalist species returned to the sites.

A potential determining factor in differences between the number of beetles caught in older stands and more recently disturbed stands may be the amount of leaf litter. Older stands tend to have a more litter because there has been more time for the litter to accumulate. The depth and complexity of leaf litter is an important habitat component for many carabid beetles, spiders and other arthropods (Uetz 1979; Bultman and Uetz 1984; Koivula et al. 1999) especially in deciduous and mixedwood stands (Pearce et al. 2003). Mixedwood and deciduous leaf litter provides more pathways and niches relative to coniferous litter due to the interstitial spaces between curled leaves. These spaces provide more niches for prey items (Bultman and Uetz 1984; Pearce et al. 2003), greater opportunity for carabid beetles to avoid competitors and predators (Pearce et al. 2003), and greater stability in humidity and temperature conditions (Uetz 1979).

Pteroctichus adstrictus and *Pterostichus pensylvanicus* are generalist predators, consuming both animal and plant material (Larochelle 1990; Digweed 1993). Despite these similarities, *P. adstrictus* showed a clear preference for older stands, while *P. pensylvanicus* showed a preference for younger stands, a trend similar to that described by Capar (2003). Goulet (1974) and Pearce et al. (2003) have reported that *P. pensylvanicus* prefers sites with a deep layer of deciduous leaf litter and loose, moist soil. As more recently disturbed sites had less leaf litter than more mature stands, it did not seem to be a determining factor in its distribution in this study, and the determining factor may have been a variable that was not measured in this study.

Stereocercus haematopus is a holarctic species that is found primarily in the tundra (Lindroth 1961-1969), although it has also been recorded from black spruce stands in western Quebec (Paquin and Dupérré 2001). This species was caught almost exclusively in the B32 site, most frequently in plot B32A2. It was also caught in plot B61A2. Its occurrence in a mature forest at such a relatively low latitude (relative to its normal distribution) is difficult to explain; as is the localized, but high, catch frequency. Within plot B32A2, *S. haematopus* was not caught disproportionately in one part of the plot or another. Its presence may be part of a disjunct population, however further sampling from this area specific area in the Duck Mountain would be required to determine the exact area this species inhabits.

It is probable that through random dispersal, individuals of most local carabid beetle species arrive in recently disturbed sites soon after a disturbance event (Spence et al. 2003; Moore et al. 2004). It can therefore be concluded that the environmental conditions of the forest (as determined largely by time since disturbance and the intensity of the disturbance) determine which species are successful in colonizing this new successional stage of the forest.

Disturbance responses

Harvested sites had consistently lower catches of carabid beetles than forests that burned at approximately the same time. The differences in catch frequency are due primarily to the same forest species that were caught with greatest frequency in older sites: *Calathus ingratus*, *Platynus decentis* and *Pterostichus adstrictus*. Harvested forests did have lower species richness or diversity of carabid beetles than burned or mature forests. These similarities differ from other studies that found clearcutting increases carabid beetle diversity compared to mature forests (Duchesne and McAlpine 1993; Addison and Barber 1997). The differences that do exist between harvested and burned sites in this study are greatest in more recently disturbed forests (i.e. 1980 paired sites) and smaller in older forests (i.e. 1961/67 paired sites). These findings are consistent with other carabid beetle research conducted in Manitoba (Wytrykush 2001; Capar 2003).

The decrease in carabid beetle catch frequency soon after timber harvests differs from the findings of Beaudry et al. (1997), who found that clearcut sites had greater numbers of carabid beetles. Werner and Raffa (2000) found that forest management regimes did not affect species richness or the number of carabid beetles caught, but did have a significant impact on species composition.

The Jaccard index was useful for comparing burn sites with paired harvested sites. The mean Jaccard index of the 1961/67 sites was higher than the value for the 1980 burn/harvest. This indicated that the carabid communities in the two disturbance types became more similar as time since disturbance increased.

The B61 and H67 sites had very similar carabid beetle communities, although the burn site had a higher average catch frequency of most species. In the 1961/67 sites, eight of the ten most frequently caught species were caught more frequently in the burn site; four of those eight were caught at least twice as frequently. The two species that were caught more frequently in the harvested site, *Calosoma frigidum* and *Synuchus impunctatus* both favour dry, upland aspen stands (Niemelä et al. 1992) (Table 16), but this rather general forest type description is insufficient to explain the distribution of these two species in the current study. The increase in these species is encouraging from a conservation perspective, because both have been observed to respond negatively to timber harvesting (Beaudry et al. 1997). The species with the largest disparities in catch frequency between burn and harvest sites were *Carabus taedatus* and *Platynus decentis*.

In the 1980 sites, the burn site had an average catch frequency nearly four times greater than the harvest site in 2001. The difference is largely due to a low catch frequency of *Platynus decentis* in the H80 site, which was more frequently caught in the H67 site. In the 1961/67 stands, the difference had been reduced to an average of twice as many.

Werner and Raffa (2000) summarized the three most common responses of carabid beetles to clearcut timber harvests that have been reported in the literature: (1) an increase in carabid beetle species common to open areas; (2) an initial decrease in forest generalists; and (3) permanent disappearance of species that specialize in a particular forest type (forest specialists). The findings of this study exhibit the first two of these responses, but not the third.

In the most recently disturbed site (H95), an increase in carabid beetle species common to open areas was observed. Species characteristic of meadows and open areas that were collected from the H95 site included *Agonum cupripenne, Agonum cupreum, Agonum placidum, Cymindis cribricollis* and *Cymindis unicolor* (Lindroth 1961-1969; Niemelä et al. 1992; Runtz and Peck 1994; Addison and Barber 1997; Beaudry et al. 1997) (Table 16). Unfortunately because there was no burn replicate for the H95 site, it is impossible to determine whether the presence of these species is due to the harvest itself, or rather to a disturbance that removed the canopy. Many species that inhabit meadows and open areas have also been collected in recently burned forests (Natural Resources Canada 2004 and references therein) (Table 16). It seems likely that some of these meadow-inhabiting species would find the characteristics of both recently burned or harvested forests to be suitable (temporary) habitats.

Timber harvesting decreased the number of forest generalist species and the catch frequency of those that remained. Forest generalist species such as *Calathus ingratus* and *Platynus decentis* were present in the H95 site, but their catch frequencies were much lower than in older sites. Other researchers have observed similar patterns with these species (Jennings et al. 1986; Niemelä et al. 1992; Niemelä et al. 1993). Although *Pterostichus adstrictus* has been described as a habitat generalist (Niemelä et al. 1992), its catch frequency increased in a manner similar to that observed in forest specialist species. A similar pattern of initial decrease in catch frequency followed by a steady increase was observed in the burned sites. The most recently disturbed burn site (B80) had the lowest catch frequency of these species.

Determining whether timber harvesting is responsible for the permanent disappearance of forest specialists is particularly difficult because the harvested sites were not sampled prior to being harvested. It does seem unlikely that any forest specialist species were eliminated by timber harvesting since only three of the 18 species found in the B61 site were not found in the H67 site (Table 17). All three of these species, *Agonum quinquepunctatum* Motschulsky, *Poecilus lucublandus* LeConte and *Stereocercus haematopus*, were caught with low frequency in the B61 site and did not appear to be key components of the carabid beetle community in this forest type. Four other species, *Agonum gratiosum*, *Carabus maeander*, *Patrobus fovecollis* Eschscholtz and *Poecilus corvinus* Dejean, were collected in the H67 site but not the B61 site (Table 17). These species were caught in low frequencies, and have been associated with younger, or more open habitats (Niemelä et al. 1992, 1993).

Stereocercus haematopus was never collected from a harvested site. However, it was caught almost exclusively in the B32 site, for which there was no harvest replicate. This is a species primarily of the tundra (Lindroth 1961-1969) and this population may be an ancient remnant. *Agonum retractum*, *Calosoma frigidum* and *Carabus chamissonis* are aspen forest specialists to varying degrees (Niemelä et al. 1993). These species were absent, or infrequently caught in the H95 site. *Calosoma frigidum* was caught in the B80 site, but virtually absent from both the H95 and H80 sites. It was caught in the B32 and B61 sites and most frequently caught in the H67 site. This seems to indicate that harvested stands eventually reach a condition similar to that of a burned forest, but that it may take more time. *Agonum retractum* was caught in all sites, and its catch frequency was not significantly affected by disturbance type. *Carabus chamissonis* (which has also been described as a spruce-bog specialist (Niemelä et al. 1992)) was caught in all burn sites, but only in the oldest harvest site. Furthermore, its catch frequency in the H67 site was more similar to that observed in the B80 site, not the B61 site. The overall trend appears to be that timber harvesting in aspen stands does not eliminate forest specialists, but delays their return, perhaps by up to 20 years.

If timber harvest design is to successfully emulate forest fire, the same species should be found in burned and harvested sites of comparable ages. Table 17 shows species that were caught in at least three plots each from the B80 and B61 sites. Of the 15 species that meet these criteria from the B80 site, only three were not caught in the H80 site (note that the H80 site had only two plots, compared to four in the B80 site). Of the 12 species that were caught in at least three B61 plots, all were caught in at least one of the H67 plots, and only three species were not caught in at least three plots. The overall representation of these species in harvested sites in encouraging. *Agonum cupreum*, which was caught in the B80 site, but not in the H80 site, did occur in the 5-year old harvest, potentially indicating that changes in harvest techniques may have provided habitat for this species.

Recommendations and future considerations

Continued research is necessary in order to gain a better understanding of the impact of timber harvesting on the arthropod communities of aspen forests. Paramount to this pursuit is an improvement in the knowledge of the biology and preferred habitats of carabid beetles and other arthropods of the boreal forest.

The acquisition of samples from a recently burned forest (i.e. less than 5 years old) should be the priority of further research in this region. This study was unable to draw firm conclusions about the immediate effects of timber harvesting on carabid beetles due to a lack of recently burned forest. The intensive (successful) fire suppression in the Duck and Porcupine Mountains would seem to require a prescribed burn in order to answer these questions. The establishment of burned and harvested permanent sample plots (PSP), similar to those at EMEND (Spence et al. 2003), would facilitate the understanding of some of these questions. PSPs which are sampled one or two years prior to the disturbance, and continuously afterward, would be the ideal method for determining how new species colonize recently disturbed sites. This method would also provide a means of determining whether the old growth carabid beetle species found in younger stands are remnants of the old forest, or whether they have re-colonized the site from surrounding forests.

Table 16: Carabid beetle species that were caught in at least 3 of 4 plots within either the B61 site, or the B80 site. Species that were not caught in harvested sites of the same age class are indicated by $^{\pm}$.

B80	**B61**
Agonum cupreum$^{\pm}$	*Agonum placidum*
Agonum placidum	*Agonum retractum*
Agonum retractum	*Agonum sordens*
Agonum simile$^{\pm}$	*Calathus ingratus*
Agonum sordens	*Calosoma frigidum*
Calathus ingratus	*Carabus chamissonis*
Calosoma frigidum	*Carabus taedatus*
Carabus chamissonis$^{\pm}$	*Platynus decentis*
Carabus taedatus	*Pterostichus adstrictus*
Harpalus fulvilabris	*Pterostichus pensylvanicus*
Platynus decentis	*Sphaeroderus nitidicollis*
Pterostichus adstrictus	*Synuchus impunctatus*
Pterostichus pensylvanicus	
Sphaeroderus nitidicollis	
Synuchus impunctatus	

Table 17: Adult carabid beetle habitat preferences, food preferences, activity cycles and overwintering stage of the 18 most frequently caught species in 2001. "??" denotes that the information could not be located in the literature. A list of references follows the table.

Species	**Adult habitats**	**Food**[1]	**Adult activity / breeding period(s)**	**Overwinter stage**
Agonum cupreum	Open country (Prairie), sandy soil (a) Agricultural Field (b) 15-year old post fire Lodgepole pine (c)	DIpteran eggs Lepidopteran eggs Ladybird beetles	??	??
Agonum gratiosum	Open, moist soil, peat (a) Fens, bogs (d) Burned and mature aspen and spruce (e) Spruce forest (k)	Mealworms (captivity)	Breeds late spring early summer (h); but activity cycle ill-defined (e)	Larva (a)
Agonum placidum	Open sandy soil (a) Clearcut mixedwood (f) Clearcut followed by prescribed burn (g) Agricultural field (b) Mature aspen forest (h)	Lepidopteran eggs and larvae Slug (captivity)	Females gravid late summer (a)	Adult (a)
Agonum retractum	Under bushes and hardwood trees (a) Mixedwood clearcut and mature forest (f) Aspen forest (i; k) Mixedwood forest (j; k)	Mealworms (captivity)	??	Adult (a)
Agonum sordens	Mixedwood forest (l) Clearcut cedar (m) Aspen forest (n)	??	??	Adult (a)
Calathus ingratus	Under brush and deciduous trees (a) Mixedwood forest: mature and clearcut (f; l) Clearcut mixedwood (f) Clearcut Jackpine (g) Burned and control aspen and spruce (e; o)	??	One activity cycle per year which takes most of the summer (dd); Breeds early summer (k)	Adult (e; dd) Larva (e; dd)

---

[1] Unless otherwise noted, information is from Larochelle 1990.

Table 17: (cont.)

Species	Adult habitats	Food	Adult activity / breeding period(s)	Overwinter stage
Calosoma frigidum	Many habitats, especially open woodland (a) Mixedwood forest (f; l)	Lepidopteran larvae and eggs (many species) Locusts	Early summer, beetles enter hibernation mid-summer (a)	Adult (a) Exceptionally larva (a)
Carabus chamissonis	Open dry country, tundra; mixedwood forest (a) Mixedwood forest (l; n; p) Lodgepole pine-spruce (q)	Mealworms (captivity) Spider (captivity)	??	Adult (a)
Carabus maeander	Open moist ground; bogs; high humidity (a) Clearcut (r) Burned spruce; and mature spruce (e) Sedge (s) Aspen forest (e; h)	Spiders Earthworms (captivity)		Adult (a)
Carabus taedatus	Open gravely soil with low vegetation; open coniferous forests (a) Agriculture field (t) Tundra (u) Burned and mature aspen and spruce (e; o)	Lepidopteran larvae Lepidopteran eggs (captivity)	One activity cycle per year: late June to late September (ee) but variable (e)	Adult (a)
Cymindis unicolor	Treeless country and north above tree line (a) Tundra (u)	??	??	??
Patrobus fovecollis	Rotten logs under bushes (*Alnus*) (a) Mixedwood forest (l; v) Aspen poplar forest (p) Spruce bog (p)	Mealworms (captivity)	??	Adult (a)
Platynus decentis	Under bark and logs, frequently near water (a) Mixedwood forest (l; v) Clearcut (r) Sugar maple (w) Aspen forest (e; h; i; k; p) Spruce forest (e) Fen & Bog (d)	Mealworms (captivity) Earthworms (captivity)	Two activity cycles per year: First in spring when reproduction occurs; Second in late summer to fall represent adults born of the spring generation (dd)	Adult (dd)

Table 17: (cont.)

Species	Adult habitats	Food	Adult activity / breeding period(s)	Overwinter stage
Pterostichus adstrictus	Not pronounced forest species but prefers open country on moderately moist to dry soil (a) Aspen forest (e; i; k; o; p) Spruce forest (e; o; p; y) Habitat generalist (p) Mixedwood (f; l; v; y) Open grassland (i) Agriculture field (t) Burned aspen and spruce (e; o) Woodland and open – independent of forest cover (x) White pine (y) Clearcut (m) Sugar Maple (w)	Bird excrement Lepidopteran eggs and larvae Live beetle Snails (captivity) (gg)	Two activity cycles per year; First spring when reproduction occurs. Second in late summer to fall (dd)	Adult (dd)
Pterostichus pensylvanicus	Under dead leaves and bushes (*Alnus*) (a) Mixedwood forest (f; l; v; z) Clearcut (f; m) Spruce bog (p; aa) Jack Pine (g) Agriculture field (bb) White Pine (y) Maple forest (w) Aspen forest (h; k; o; p) Under leaf litter, not under rotting logs; adults occur in most forest types (x) Lodgepole pine (j) Spruce forest (o) Burned spruce; burned aspen (o)	Mealworms (captivity) Dead *P. pensylvanicus* (captivity) Snails (captivity) (gg)	Two activity cycles per year; First spring when reproduction occurs. Second in late summer to fall (x)	Adult (x)

Table 17: (cont.)

Species	**Adult habitats**	**Food**	**Adult activity / breeding period(s)**	**Overwinter stage**
Sphaeroderus nitidicollis	Moist places with moss and dead leaves; under deciduous shrubs (a) Mixedwood forest (f; v; z) Clearcut (f; m; z) Aspen forest (e; k) Spruce forest (e) Burned spruce; burned aspen (e) Sugar maple forest (w)	Snails and slugs (a; ff)	One activity cycle per year; reproduction especially in the fall (dd); may be bimodal (e)	Adult (a; dd) Egg (a; dd)
Stereocercus haematopus	Most abundant on the tundra; on rather dry, sandy soil; northern coniferous forests (a) Lodgepole pine forests (q) White spruce forest (q) Spruce bog (p)	Earthworms (captivity)	??	??
Synuchus impunctatus	Open country and light forests on dry ground (a) Spruce/tamarack bog (aa) Jackpine forest (g) Clearcut (f; g; m; r) Mixedwood forest (f; j; l; r; v; y) Agriculture field (bb) White pine forests (y) Lodgepole Pine forest (j) Aspen forest (e; h; j; o; p) Spruce forest (e; o) Burned spruce (e; o) Burned aspen (e) Sugar Maple (w) Agriculture field (cc)	Plant seeds (Scrophulariaceae)	One activity cycle per year; mostly August and September (e; dd)	Larva (e; dd)

Table 17: (cont.)

References*:

a) Lindroth (1961-69)
b) Cárcamo (1995)
c) Gandhi et al. (2001)
d) Blades and Marshall (1994)
e) Holliday (1991)
f) Addison and Barber (1997)
g) Beaudry et al. (1997)
h) Ostaff and Freitag (1973)
i) Carter (1980)
j) Spence et al. (1996)
k) Pearce et al. (2003)
l) Digweed et al. (1995)
m) Levesque et al. (1976)
n) Spence and Niemelä (1994)
o) Richardson and Holliday (1982)
p) Niemelä et al. (1992)
q) Niemelä et al. (1993)
r) Duchesne et al. (1999)
s) Landry (1994)
t) Frank (1971a)
u) Holliday (1982)
v) Freitag et al. (1969)
w) Martel et al. (1991)
x) Goulet (1974)
y) Thompson et al. (1995)
z) Freitag and Poulter (1970)
aa) Runtz and Peck (1994)
bb) Rivard (1964)
cc) Frank (1971b)
dd) Bousquet and Pilon 1977
ee) Larochelle (1975)
ff) Larochelle (1972)
gg) Digweed (1993)

* Full citations are listed in the references section.

Summary and conclusions

1. Carabid beetle catch frequency changed with season. It was highest in early June and lowest in late August.
2. Carabid beetle catch frequency was highest in older sites and lowest in the most-recently disturbed sites.
3. Timber harvesting resulted in lower average catch frequency compared to forest fire, but there was considerable variation among plots within sites.
4. The number of species of carabid beetles was not affected by stand age, and was virtually the same in all age classes.
5. The diversity of carabid beetles was highest and the species dominance was lowest in recently disturbed sites.
6. In the most recently disturbed sites there was an increase in carabid beetle species that prefer open areas (e.g. *Agonum cupreum*, *Agonum cupripenne* and *Cymindis cribricollis*).
7. When compared to forest fire, timber harvesting had little affect on the species composition and diversity of carabid beetles, but did reduce the average overall catch frequency of carabid beetles.
8. Both fire and timber harvesting reduced the number and catch frequency of carabid beetle species that are considered forest generalists. These species returned as the stands matured, but did so more slowly in harvested stands.

9. Species that are considered mixedwood forest specialists were initially reduced or eliminated by disturbance, but returned, although not as quickly in harvested stands as in burned stands.
10. *Platynus decentis* was caught with very high frequencies, and would seem to a very important carabid beetle species in many of these forests, especially burned stands 20 years old or more.
11. Leaf litter and coarse woody debris are important carabid beetle habitat components in mixedwood boreal forests.

References

Addison, J.A. and K.N. Barber. 1997. Natural Resources Canada, Canadian Forest Service No. Information report GLC-X-1.

Adis, J. 1979. Problems of interpreting arthropod sampling with pitfall traps. *Zoologisher Anzeiger*. **202**: 177-187.

Alatalo, R.V. 1981. Problems in the measure of evenness in ecology. *Oikos*. **37**: 199-204.

Andersen, A. 1990. The use of ant communities to evaluate change in Australian terrestrial ecosystems: a review and a recipe. *Proceedings of the Ecological Society of Australia*. **16**: 347-357.

Anderson, R.C. 1992. The historic role of fire in the North American grassland. *In* Collis, S.L. and L.L. Wallace (eds.). *Fire in North American Tallgrass Prairie*. University of Oklahoma Press, Norman.

Apigian, K. and N.T. Wheelwright. 2000. Forest ground beetles (Coleoptera: Carabidae) on a boreal island: habitat preferences and the effects of experimental removal. *Canadian Entomologist*. **132**: 627-634.

Atzet, T., R.F. Powers and D.H. McNabb. 1989. Maintaining long-term forest productivity in Southwest Oregon and Northern California. *In* Perry, D.A., R. Meurisse and B. Thomas (eds.). *Maintaining the long-term productivity of Pacific Northwest forest ecosystems*. Timber Press, Portland, Oregon.

Barlow, C.A. 1970. Phenology and distribution of some *Pterostichus* (Coleoptera: Carabidae) of eastern Canada. *Journal of the New York Entomological Society*. **78**: 215-236.

Barnes, B. V. 1966. The Clonal Growth Habit of American Aspens. *Ecology*. **47**: 439-447.

Beaudry, S., L.C. Duchesne and B. Côté. 1997. Short-term effects of three forestry practices on carabid assemblages in a jack pine forest. *Canadian Journal of Forest Research*. **27**: 2065-2071.

Berger, W.H. and F.L Parker. 1970. Diversity of planktonic Foraminifera in deep sea sediments. *Science*. **168**: 1345-1347.

Bird, R.D. 1930. Biotic communities of the aspen parkland of central Canada. *Ecology*. **11**: 356-442.

Blades, D.C.A. and S.A. Marshall. 1994. Terrestrial arthropods of Canadian peatlands: synopsis of pan trap collections at four southern Ontario peatlands. *Memoirs of the Entomological Society of Canada*. **169**: 221-284.

Bonan, G.B. and H.H. Shugart. 1989. Environmental factors and ecological processes in boreal forests. *Annual Review of Ecology and Systematics*. **20**:1-28.

Boudreault, C., Y. Bergeron, S. Gauthier and P. Drapeau. 2002. Bryophyte and lichen communities in mature to old-growth stands in eastern boreal forests of Canada. *Canadian Journal of Forest Research*. **32**: 1080-1092.

Bousquet, Y. 1999. Supraspecific classification of the Nearctic Pterostichini (Coleoptera: Carabidae). *Association des entomologistes amateurs du Québec*. Suppliment 9.

Bousquet, Y. and A. Larochelle. 1993. Catalogue of the Geadephaga of America North of Mexico. *Memoirs of the Entomological Society of Canada*. Number 167.

Bousquet, Y. and J.G. Pilon. 1977. Activité saisonnière de quelques Coléoptères Carabidae du Québec. *Annals of the Entomological Society of Quebec*. **22**: 40-58.

Briggs, J.B. 1960. A comparison of pitfall trapping and soil sampling in assessing populations of two species ground beetles (Col.: Carabidae). *East Malling Research Station Annual Report*. **48**: 108-112.

Brown, A.A. and K.P. Davis. 1973. *Forest fire: control and use*. McGraw-Hill Book Company, New York.

Brown, L. 1985. *Grasslands*. Knopf, New York.

Brunson M.W. and B.A. Shindler. 2004. Geographic variation in social acceptability of wildland fuels management in the Western United States. *Society & Natural Resources*. **17**: 661-677.

Bultman, T.L. and G.W. Uetz. 1984. Effect of structure and nutritional quality of litter on abundances of litter-dwelling arthropods. *American Midland Naturalist*. **111**: 165-172.

Butterfield, J. 1997. Carabid community succession during the forestry cycle in conifer plantations. *Ecography*. **20**: 614-625.

Capar, L. 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 in eastern Manitoba*. M.Sc. Thesis, University of Manitoba, Winnipeg.

Cárcamo, H.A. and D. Parkinson. 1999. Distribution of ground beetle assemblages (Coleoptera, Carabidae) around sour gas processing plants in western Canada. *Pedobiologia*. **43**: 160-173.

Carter, A. 1980. *Agonum retractum* (Coleoptera: Carabidae) in aspen woodland in the Candain ROckeies: population biology and chemical cycling. *Pedobiologia*. **20**: 101-117

Clark, J.S. 1990. Fire and climate change during the last 750 yr in northwestern Minnesota. *Ecological Monographs*. **60**: 135-159.

Clements, F.E. 1936. Nature and the structure of climax. *Journal of Ecology*. **24**: 252-284.

Connell, J.H. and R.O. Slatyer 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist*. **111**: 1119-1144.

Conway, S. 1992. *Logging practices: Principles of timber harvesting systems*. Miller Freeman Publications, San Francisco.

Corns, I.G.W. and R.M. Annas. 1986. *Field guide to forest ecosystems of west-central Alberta*. Canadian Forest Service, Northern Forest Centre, Edmonton, Alberta.

Cowles, H.C. 1901. The physiographic ecology of Chicago and vicinity. *Botanical Gazette*. **31**: 73-108, 145-181.

Crins, W.J. 1980. Two aggregations of *Calosoma frigidum* (Coleoptera: Carabidae) in Ontario during 1976. *Entomological News*. **91**: 155-158.

Crowson, R.A. 1981. *The biology of the Coleoptera*. Academic Press, London.

Currie, C.R. and S.C. Digweed. 1996. Effect of substrate depth on predation of larval *Pterostichus adstrictus* Eschscholtz by adults of *P. melanarius* (Illiger). *Coleopterists Bulletin*. **50**: 291-296.

Danks, H.V. and R.H. Foottit. 1989. Insects of the boreal zone of Canada. *Canadian Entomologist*. **121**: 626-677.

Day, K.R. and J. Carthy. 1988. Changes in carabid beetle communities accompanying a rotation of Sitka spruce. Agricultural Ecosystems and Environments. **24**: 405–415.

Desender, K. and J.P. Maelfait. 1986. Pitfall trapping within enclosures: A method for estimating the relationship between abundance of coexisting carabid species (Coleoptera: Carabidae). *Holarctic Ecology*. **9**: 245-250.

Digweed, S.C. 1993. Selection of terrestrial gastropod prey by Cychrine and Pterostichine ground beetles (Coleoptera: Carabidae). *Canadian Entomologist*. **125**: 463-472.

Digweed, S.C., C.R. Currie, H.A. Cárcamo and J.R. Spence. 1995 Digging out the "diggin-in effect" of pitfall traps: influences of depletion and disturbance on catches of ground beetles (Coleoptera: Carabidae). *Pedobiologia*. **39**: 561-576.

Duchesne, L.C., R.A. Lautenschlager and F.W. Bell. 1999. Effects of clear-cutting and plant competition control methods on Carabid (Coleoptera: Carabidae) assemblages in northwestern Ontario. *Environmental Monitoring and Assessment*. **56**: 87-96.

Duchesne, L.C. and R.S. McAlpine. 1993. Using carabid beetles (Coleoptera: Carabidae) as a means to investigate the effect of forestry practices on soil diversity. Technical Report 16. *Forest Canada, Petawawa National Forestry Institute*.

Duffey, E. 1972. Ecological survey and the arachnologist. *Bulletin of the British Arachnological Society*. **2**: 69-82.

Dulge, R. 1994. Seasonal activity of carabid beetles in wooded habitats in northwest Germany (Coleoptera: Carabidae). *In* Desender, K. (ed.). *Carabid Beetles: Ecology and Evolution*. Kluwer Academic Publishers, The Netherlands.

Epstein, M.E. and H.M. Kulman. 1990. Habitat destruction and seasonal occurrence of carabid beetles in east-central Minnesota. *American Midland Naturalist*. **123**: 209-225.

Fernandes, P. and H. Botelho. 2004. Analysis of the prescribed burning practice in the pine forest of northwestern Portugal. *Journal of Environmental Management*. **70**: 15-26.

Fisher, R.A., A.S. Corbet and C.B. Williams. 1943. The relation 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.

Frank, J.H. 1971a. Carabidae (Coleoptera) as predators of the red-backed cutworm (Lepidoptera: Noctuidae) in Central Alberta. *Canadian Entomologist.* **103**: 1039-1044.

Frank, J.H., 1971b. Carabidae (Coleoptera) of an arable field in Central Alberta. *Quaestiones entomologicae.* **7**: 237-252.

Freitag, R., G.W. Ozburn, and R.E. Leech. 1969. The effects of Sumithion and Phosphamidon on populations of five carabid beetles and the spider Trochosa terricola in northwestern Ontario and including a list of collected species of carabid beetles and spiders. *Canadian Entomologist.* **101**: 1328-1333.

Freitag, R. and F. Poulter. 1970. The effects of the insecticides Sumithion and Phosphamidon on populations of five species of carabid beetles and two species of Lycosid spiders in northwestern Ontario. *Canadian Entomologist.* **102**: 1307-1311.

French, J.R.S. and R.M. Keirle. 1969. Studies in fire damaged radiata pine plantations. *Australian Forestry.* **33**: 175-180.

Froning, K. 1980. *Logging hardwoods to reduce damage to white spruce understory.* Information Report NOR-X-229. Northern Forest Research Centre, Edmonton.

Fryer, G.I. and E.A. Johnson. 1988. Reconstructing the fire behavior and effects in a subalpine forest. *Journal of Applied Ecology.* **25**: 1063-1072.

Gandhi, K.J.K., J.R. Spence, D.W. Langor and L.E. Morgantini. 2001. Fire residuals as habitat reserves for epigaeic beetles (Coleoptera: Carabidae and Staphylinidae). *Biological Conservation.* **102**: 131–141.

Government of Canada. Geography Division (1978-1995). *The national atlas of Canada, 5th edition.* Government of Canada, Ottawa.

Government of Canada. 1995. *Canadian biodiversity strategy.* Minister of Supply and Services Canada, Ottawa.

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

Gower, J.C. 1967. A comparison of some methods of cluster analysis. *Biometrics.* **23**: 623-637.

Gray, S., B. Wilsey and D. Simberloff. 2001 Empirical relationships between species richness, evenness and proportional diversity. *American Naturalist.* **158**: 286-298.

Greacen, E.L. and R. Sands. 1980. Compaction of forest soils. A review. *Australian Journal of Forest Research.* **18**: 163-189.

Greenslade, P.J.M. 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *Journal of Animal Ecology.* **33**: 301-310.

Greenslade, P.J.M. 1973. Sampling ants with pitfall traps: digging-in effects. *Insectes Sociaux.* **20**: 343-353.

Grossman, G.D. and D.M. Nickerson. 1991. Principal component analyses of assemblage structure data: Utility of tests based on eigenvalues. *Ecology.* **72**: 341-347.

Grossnickle, S.C. 2000. *Ecophysiology of northern spruce seedlings/: The performance of planted seedlings.* National Research Council of Canada Research Press, Ottawa.

Haeussler, S. and Y. Bergeron. 2004. Range of variability in boreal aspen plant communities after wildfire and clear-cutting. *Canadian Journal of Forest Research.* **34**: 274-288.

Hengeveld, R. 1981. Methodology of explaining differences in dietary composition of carabid beetles by competition. *Oikos.* **45**: 37-49.

Hill, M.O. 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology.* **54**: 427-432.

Holliday, N.J. 1982. Carabidae from Churchill, Manitoba with ecological notes and two new distribution records (Coleoptera). *Coleopterists Bulletin.* **36**: 116-117.

Holliday, N.J. 1991. Species responses of carabid beetles (Coleoptera: Carabidae) during post-fire regeneration of boreal forest. *Canadian Entomologist.* **123**: 1369-1389.

Howse, G.M. 1995. Forest pests in the Ontario region. *In* Armstrong J.A. and W.G.H. Ives (eds.). *Forest insect pests in Canada.* Natural Resources Canada, Canadian Forest Service, Ottawa, Canada.

Hurlbert, S.H. 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology.* **52**: 577-586.

Hwang, S. Y. and R. L. Lindroth. 1997. Clonal variation in foliar chemistry of aspen: effects on gypsy moths and forest tent caterpillars. *Oecologia.* **111**: 99-108.

Ilstedt, U., A. Malmer, A. Nordgren and P. Liau. 2004. Soil rehabilitation following tractor logging: early results on amendments and tilling in a second rotation *Acacia mangium* plantation in Sabah, Malaysia. *Forest Ecology and Management.* **194**: 215-222

Jackson, D.A. 1993. Stopping rules in principle component analysis: a comparison of heuristical and statistical approaches. *Ecology.* **74**: 2204-2214.

James, F.C. and C.E. McCulloch. 1990. Multivariate analysis in ecology and systematics: panacea or Pandora's box? *Annual Review of Ecology and Systematics.* **21**: 129-166.

Jennings, D.T., M.W. Houseweart and G.A. Dunn. 1986. Carabid beetles (Coleoptera: Carabidae) associated with strip clearcut and dense spruce-fir forests of Maine. *Coleopterists Bulletin.* **40**: 251-263.

Johnson, E.A. and C.P.S. Larsen. 1991. Climatically induced change in fire frequency in the southern Canadian Rockies. *Ecology.* **72**: 194-201

Johnson, E.A. and K. Miyanishi. 2004. *Forest fires: behavior and ecological effects.* Academic Press, San Diego, California.

Johnstone, J.F., F.S. Chapin III, J. Foote, S. Kemmett, K. Price and L. Viereck. 2004. Decadal observations of tree regeneration following fire in boreal forests. *Canadian Journal of Forest Research.* **34**: 267-273.

Kauppi, P.E. and M. Posch. 1985. Sensitivity of boreal forests to possible climate warming. *Climactic Change*, **7**: 45-54.

Kenkel, N.C., D.A. Derksen, A.G. Thomas and 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 development.* Prentice Hall, New Jersey.

Knapik, L.J., W.B. Russell, K.M. Riddell and N. Stevens. 1988. *Forest system classification and land system mapping pilot project: Duck Mountain, Manitoba.* Manitoba Natural Resources, Forestry Branch.

Koivula, M. P. Puntilla, Y. Haila and J. Niemelä. 1999. Leaf litter and the small scale distribution of carabid beetles (Coleoptera: Carabidae) in the boreal forest. *Ecography.* **22**: 424-435.

Krebs, C.J. 1989. *Ecological methodology*. HarperCollins Publishers, New York.

Krebs, C.J. 1994. *Ecology: the experimental analysis of distribution and abundance. 4th Edition*. HarperCollins College Publishers, New York.

Kurttila, M., T. Pukkala and J. Loikkanen. 2002. The performance of alternative spatial objective types in forest planning calculations: a case for flying squirrel and moose. *Forest Ecology and Management*. **166**: 245-260.

Lafrenière, R.C. 1994. *Impact of regeneration techniques on ecological diversity in panted and natural forests stands: species and ecosystem diversity among carabid beetles (Coleoptera: Carabidae) in Jack pine stands*. M.Sc. Thesis, University of Manitoba, Winnipeg.

Landry, J.F. 1994.Resource partitioning in a guild of marsh-dwelling *Agonum* (Coleoptera: Carabidae) in central Alberta. *Canadian Entomologist*. **126**: 706-728.

Larochelle, A. 1972. Notes on the food of Cychrini (Coleoptera: Carabidae). *Great Lakes Entomologist*. **5**: 81-83

Larochelle, A. 1975. Les Carabidae du Québec et du Labrador. *Département de biologie du Collège Bourget, Rigaud. Bulletin*. **1**: 1-255.

Larochelle, A. 1990. *The food of carabid beetles (Coleoptera: Carabidae, including Cicindelinae)*. Association des Entomologistes Amateurs du Québec. Supplement 5.

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

Legendre, P. and L. Legendre. 1998. *Numerical Ecology*. Elsevier Science, BV, Amsterdam.

Leidig, F.T. 1988. The conservation of diversity in forest trees. *BioScience*. **38**: 471-479.

Lemmon, P.E. 1956. A spherical densiometer for estimating forest overstory density. *Forest Science*. **2**: 314-320.

Lenski, R.E. 1982. The impact of forest cutting on the diversity of ground beetles (Coleoptera: Carabidae) in the southern Appalachians. *Ecological Monographs*. **7**: 385-390.

Levesque, C., J. Dubé and J.G. Pilon. 1976. Inventaire et étude des coléoptères carabidae de biotopes forestiers des Laurentides (Québec). *Naturaliste Canadien.* **103**: 569-582.

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. 1961-1969. *The ground beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Supplement 20 (1961), 24 (1963), 29 (1966), 33 (1968), & 35 (1969).* Opuscula Entomologica, Lund University, Sweden.

Lindroth, R. L. 1991. Biochemical ecology of aspen--Lepidoptera interactions. *Journal of the Kansas Entomological Society.* **64**: 372-380.

Looman, J. 1987. The vegetation of the Canadian Prairie provinces IV. The woody vegetation, part 4. *Phytocoenologia.* **15**: 289-327.

Loreau, M. 1985. Annual activity and life cycles of carabid beetles in two forest communities. *Holarctic Ecology.* **8**: 228-235.

Loreau, M. 1988. Determinants of the seasonal pattern in the niche structure of a forest carabid community. *Pedobiologia.* **31**: 75-87.

Loreau, M. 1990. The significance of intra- and interspecific competition in carabid beetles. *In* N.E. Stork (ed.). *Ground beetles: Their role in Ecological and Environmental Studies.* Intercept Publications, Andover, United Kingdom.

MacArthur, R.H. 1965. Patterns of species diversity. *Biological Reviews.* **40**: 510-533.

MacArthur, R.H. and E.O. Wilson. 1967. *The theory of island biogeography.* Princeton University Press, Princeton, New Jersey.

Magura, T., B. Tóthmérész and T. Molnár. 2001. Forest edge and diversity: carabids along forest-grassland transects. *Biodiversity and Conservation.* **10**: 287–300.

Magurran, A.E. 1988. *Ecological diversity and its measurement.* Princeton University Press, Princeton, New Jersey.

Mallik, A.U. and C.H Gimingham. 1985. The ecological effects of heather burning. *Ecology.* **73**: 633-644.

Manitoba Natural Resources. 1996. *Five year report on the status of forestry: Year ending March 31, 1996.* Report MG-14283. Manitoba Natural Resources, Manitoba.

Manitoba Natural Resources. 1997. *State of the environment report, 1997.* Manitoba Conservation, Manitoba.

Manitoba Natural Resources. 2001. *Five year report on the status of forestry: April 1996 – March 2001.* Report MG-14283. Manitoba Natural Resources, Manitoba.

Martel, J., Y. Mauffette and S. Tousignant. 1991. Secondary effects of canopy dieback: the epigeal carabid fauna in Quebec Appalachian maple forests. *Canadian Entomolgist.* **123**: 851–859.

Martell, D.L. 2001. Forest fire management. *In* Johnson, E.A. and K. Miyanishi (eds.). *Forest fires: behavior and ecological effects.* Academic Press, San Diego, California.

Matalin, A. V. 1994. The strategy of dispersal behaviour in some *Carabidae* species of Southeastern Europe. pp. 183-188. *In* K. Desender (ed.). *Carabid Beetles: Ecology and Evolution.* Kluwer Academic Publishers, The Netherlands.

May, R.M. 1975. Patterns of species abundance and diversity. *In* Cody, M.L. and J.M Diamond (eds.). *Ecology and Evolution of Communities.* Harvard University Press, Cambridge, MA.

May, R.M. 1986. The search for patterns in the balance of nature: advances and retreats. *Ecology.* **48**: 392-404.

McLeod, J. M. 1980. Forests, disturbances and insects. *Canadian Entomologist.* **112**: 1185-1192.

Moore, J.D., R. Ouimet, D. Houle and C. Camiré. 2004. Effects of two silvicultural practices on ground beetles (Coleoptera: Carabidae) in a northern hardwood forests, Quebec, Canada. *Canadian Journal of Forest Research.* **34**: 959-968.

Morley, P. M. 1986. Management and use of aspen poplar in North America. *The Forestry Chronicle.* **62**: 104-107.

Natural Resources, Canada. 2004. Canadian carabid habitat associations. Viewable at stable URL: http://www.glfc.cfs.nrcan.gc.ca/landscape/carabid_page_a_e.html

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

Niemelä, J., Y. Haila and P. Punttila. 1996. The importance of small-scale heterogeneity in boreal forests: variation in diversity in forest-floor invertebrates across the succession gradient. *Ecography*. **19**: 352-368.

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

Niemelä, J., J.R. Spence and D.H. Spence. 1992. Habitat associations and seasonal activity of ground-beetles (Coleoptera: Carabidae) in central Alberta. *Canadian Entomologist*. **124**: 521-540.

Ostaff, D.P. and R. Freitag. 1973. Phenology of carabid beetles of Thunder Bay and their associated mite population. *Proceedings of the Entomological Society of Ontario*. **104**: 34-36.

Palik, B.J., R.J. Mitchell and J.K. Hiers 2002. Modeling silviculture after natural disturbance to sustain biodiversity in the longleaf pine (*Pinus palustris*) ecosystem: balancing complexity and implementation. *Forest Ecology and Management*. **155**: 347-356.

Pande, Y.D. and P. Berthet. 1971. Comparison of the Tullgren funnel and soil section methods for surveying Oribatid populations. *Oikos*. **24**(3): 273-277.

Paquin, P. and N. Dupérré. 2001 Beetles of the boreal forest: a funistic survey carried out in western Québec. *Porceedings of the Entomological Society of Ontario*. **132**: 57-98.

Paulitz, T.C. and K.J. Adams. 2003. Composition and distribution of pythium communities from wheat fields in eastern Washington state. *Phytopathology*. **93**: 867-873.

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

Perala, D.A. 1990. Populus tremuloides Michx.: quaking aspen. *In* Burns, R.M. and B.H. Honkala (eds.). *Silvics of North America. Volume 2, Hardwoods*. Agricultural Handbook 654. U.S. Department pf Agriculture, Forest Service, Washington D.C.

Perry, D.A. 1994. *Forest ecosystems*. The Johns Hopkins University Press: Baltimore, Maryland.

Pickett, S.T.A., S.L. Collins and J.J. Armesto. 1987. Models, mechanisms and pathways of succession. *Botanical Review*. **53**: 335-371.

Pielou, E.C. 1975. *Ecological diversity*. John Wiley & Sons, New York.

Pielou, E.C. 1984. *The interpretation of ecological data*. J. Wiley, New York.

Reid, W.V. and K.R. Miller. 1989. *Keeping options alive: The scientific basis for conserving biodiversity*. World Resources Institute, Washington, D.C.

Richardson, R.J. and N.J. Holliday. 1982. Occurrence of carabid beetles (Coleoptera: Carabidae) in boreal forest damaged by fire. *Canadian Entomologist*. **114**: 509-514.

Ricklefs, R.E. 2001. *The economy of nature*. W.H Freedman and Company, United States of America.

Rivard, I., 1964. Observations on the breeding periods of some ground beetles (Coleoptera: Carabidae) in eastern Ontario. *Canadian Journal of Zoology*. **42**: 1081-1084.

Runtz, M.W.P. and S.B. Peck. 1994. The beetle fauna of a mature spruce-sphagnum bog, Algonquin Park, Ontario; ecological implications of the species composition. *Memoirs of the Entomological Society of Canada*. **129**: 161-171.

Rydgren, K., R.H. Økland and G. Hestmark. 2004. Disturbance severity and community resilience in a boreal forest. *Ecology*. **85**: 1906-1914.

Saravia, N.G., I. Segura, A.F. Holguin, C. Santrich, L. Valderrama and C. Ocampo. 1998. Epidemiologic, genetic, and clinical associations among phenotypically distinct populations of Leishmania (Viannia) in Colombia. *American Journal of Tropical Medicine and Hygiene*. **59**: 86-94.

Scott, G.A.J. 1995. *Canada's vegetation: a world perspective*. McGill-Queen's University Press, Montreal, Quebec.

Simon, N.P.P., C.B. Stratton, G.J. Forbes and F.E. Schwab. 2002. Similarity of small mammal abundance in post-fire and clearcut forests. *Forest Ecology and Management*. **165**: 163-172.

Sims, R.A., W.D. Towhill, K.A. Baldwin and G.M. Wickware. 1989. *Field guide to the forest ecosystem classification for northwestern Ontario*. Forestry Canada and Ontario Ministry for Natural Resources.

Smithers, L.A. 1961. *Lodgepole pine in Alberta*. Bulletin 127. Canada Department of Forestry, Ottawa.

Soil Classification Working Group. 1998. *The Canadian system of soil classification 3rd Edition*. Agriculture and Agri-Food Canada, Publication Number 1646.

Southwood, T.R.E. 1978. *Ecological methods: With particular reference to the study of insect populations*. John Wiley & Sons, Inc., New York.

Southwood, T.R.E. and V.K. Brown. 1979. The relationship of plant and insect diversities in succession. *Biological Journal of the Linnean Society*. **12**: 327-348.

Spence, J.R., D.W. Langor, J. Niemelä, H.A. Cárcamo, and 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. and J.K. Niemelä. 1994. Sampling carabid assemblages with pitfall traps: the madness and the method. *Canadian Entomologist*. **126**: 881-894.

Spence, J.R., R. Cartar, M. Reid, D.W. Langor and W.J.A. Volney. 2003. *Dynamics of arthropod assemblages in forests managed to emulate natural disturbance (BUGS)*. Sustainable Forest Management Network, University of Alberta, Edmonton, Alberta.

SPSS Inc. 2001. *SPSS Base 11.0 User's Guide*. SPSS Inc., Chicago, Illinois.

Stevens, M.T., M.G. Turner, G.A. Tuskan, W.H. Romme and D.M. Waller. 1999. Genetic variation in postfire aspen seedlings in Yellowstone National Park. *Molecular Ecology*. **8**: 1769-1780.

Taylor, L.R., R.A. Kempton and I.P. Woiwod. 1976. Diversity statistics and the log-series model. *Journal of Animal Ecology*. **45**: 255-71.

ter Braak, C.J.F. 1987. The analysis of vegetation-environmental relationships by canonical correspondence analysis. *Vegetation*. **69**: 69-77.

ter Braak, C.J.F. and P. Šmilauer. 2002. CANOCO reference manual and user's guide to CANOCO for Windows: Software for canonical community ordination (ver. 4.5). Microcomputer Power, New York.

Thiele, H.U. 1977. *Carabid beetles in their environments*. Springer-Verlag, Berlin

Thomas, A.W. 2001. *Moth diversity in a Northeastern, North American Red Spruce forest: I. Baseline Study.* Information Report M-X-210E. Forest Biodiversity Network, Fredericton, New Brunswick.

Thomas, C.F.G., L. Parkinson and E.J.P. Marshall. 1998. Isolating the components of activity-density for the carabid beetle *Pterostichus melanarius* in farmland. *Oecologia.* **116**: 103-112.

Thomas, G. 2000. *Bio~DAP: Ecological diversity and its measurement. A biodiversity analysis package.* [Computer Program]. Downloadable from stable URL http://nhsbig.inhs.vivc.edu/www/populations.html

Thompson, I. D., A. Applejohn, T.S. Jung, and L.A. Walton. 1995. Forest fragmentation and biodiversity project. – Unpublished data. (see Natural Resources, Canada 2004).

Triplehorn, C.A. and N.F. Johnson. 2004. *Borror and DeLong's Introduction to the Study of Insects.* Thomson, Belmont, California.

Uetz, G.W. 1979. The influence of variation in litter habitats on spider communities. *Oecologia.* **40**: 29-42.

Vance, C.C., and E. Nol. 2003. Temporal effects of selection logging on ground beetle communities in northern hardwood forests of eastern Canada. *Ecoscience.* **10**: 49–56.

Wang, G.G. 2003. Early regeneration and growth dynamics of *Populus tremuloides* suckers in relation to fire severity. *Canadian Journal of Forest Research.* **33**: 1998-2006.

Wardle, D.A., L.R. Walker and R.D. Bardgett. 2004. Ecosystem Properties and Forest Decline in Contrasting Long-Term Chronosequences. *Science.* **305**: 509-513.

Werner, S.M. and K.F. Raffa. 2000. Effects of forest management practices on the diversity of ground-occurring beetles in mixed northern hardwood forests of the Great Lakes Region. *Forest Ecology and Management.* **139**: 135-155.

Werner, S.M. and K.F. Raffa. 2003. Seasonal activity of adult, ground-occurring beetles (Coleoptera) in forests of northeastern Wisconsin and the upper peninsula of Michigan. *American Midland Naturalist.* **149**: 121-133.

White, P.S. and S.T.A. Pickett. 1985. Natural disturbance and patch dynamics: an introduction. *In* Picket, S.T.A. and S.T. White (eds.). *The ecology of natural disturbance and patch dynamics.* Academic Press, Orlando.

Whittaker, R.H. 1977. Evolution of species diversity in land communities. *In* Cody, M.L. and J.M Diamond (eds.). *Evolutionary biology*. Vol. 10 Harvard University Press, Cambridge, Massachusetts.

Wilkinson, L. 1998. *SYSTAT 9 for Windows*. SPSS Inc., Evanston, Illinois.

Wilkinson, L., L. Engelman, J. Corter and M. Coward. 2004. Cluster Analysis. *In* SYSTAT Software Inc. *SYSTAT 11: Statistics*. SYSTAT Software Inc., Richmond, California.

Wilson, E.O. (ed.) 1988. *Biodiversity*. National Academy Press, Washington.

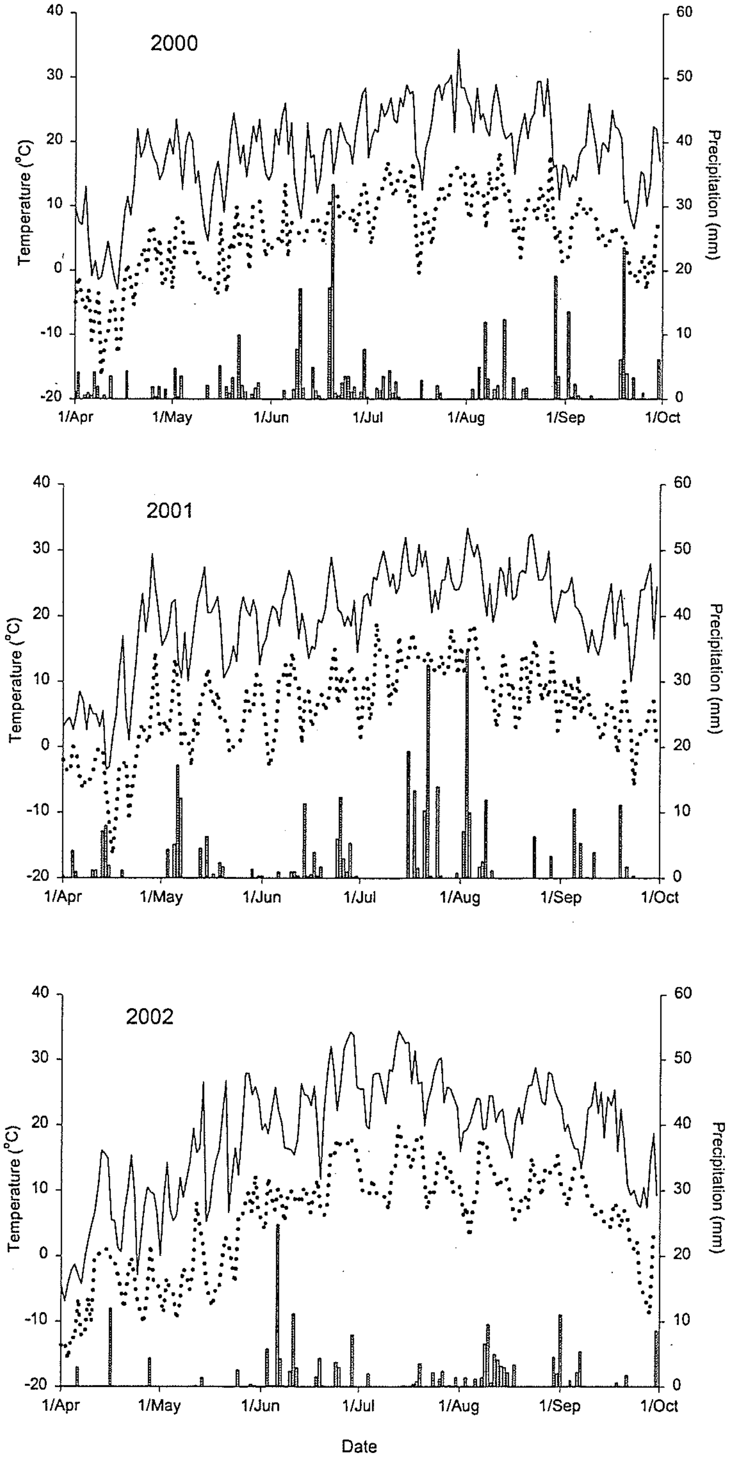
Wilson, E.O. 1992. *The diversity of life*. W.W. Norton, New York.

Wytrykush, C.M. 2003 *Implications of spruce budworm (Lepidoptera: Torticidae:* Choristoneura fumiferana *Clem.) management for the species diversity of moths (Lepidoptera) and carabid beetles (Coleoptera: Carabidae) in the Manitoba boreal forest*. M.Sc. Thesis, University of Manitoba, Winnipeg.

Zoladeski, C.A., G.M. Wickware, R.J. Delorme, R.A. Sims and I.G.W. Corns. 1995. *Forest Ecosystem Classification for Manitoba: Field Guide*. Canadian Forestry. Service and the Manitoba Forestry Branch.

Zoltai, S.C. 1975. *The southern limit of coniferous trees on the Canadian Prairies.* Information Report NOR-X-128. Northern Forest Research Centre, Edmonton.

Appendix I: Climate data from Swan River, Manitoba for the periods April 1 to October 1, 2000, 2001, 2002 and 30 year averages. Daily maximum (solid line) and minimum (dotted line) temperatures and daily precipitation (columns).



30 Year Monthly Averages (1971-2000)

Month	Daily Maximum Temp. (°C)	Daily Minimum Temp. (°C)	Precip. (mm)
April	8.8	-3.3	32.5
May	17.6	4.0	47.0
June	22.3	9.3	85.8
July	24.4	11.8	87.1
August	23.6	10.2	69.9
September	17.1	4.9	57.7
Mean Temp/ Tot. Precip.	19.0	6.2	380.0

2000 Monthly Averages

Month	Daily Maximum Temp. (°C)	Daily Minimum Temp. (°C)	Precip. (mm)
April	9.7	-3.2	28.4
May	16.5	3.5	41.2
June	19.3	7.7	111.4
July	24.6	11.3	22.1
August	22.8	10.0	67.6
September	16.9	4.8	62.2
Mean Temp/ Tot. Precip.	18.3	5.7	436.0

2001 Monthly Averages

Month	Daily Maximum Temp. (°C)	Daily Minimum Temp. (°C)	Precip. (mm)
April	9.1	-2.6	26.4
May	18.1	4.9	56.6
June	20.2	7.6	50.7
July	25.7	12.2	93.0
August	26.1	10.6	79.2
September	20.3	4.7	33.6
Mean Temp/ Tot. Precip.	19.9	6.2	339.5

2002 Monthly Averages

Month	Daily Maximum Temp. (°C)	Daily Minimum Temp. (°C)	Precip. (mm)
April	4.7	-5.8	194.
May	15.1	-0.6	4.8
June	23.5	10.8	73.2
July	26.9	12.6	14.4
August	22.4	11.0	48.4
September	17.1	5.3	30.6
Mean Temp/ Tot. Precip.	18.3	5.6	365.4

Appendix II: Plant species in each study plot by vegetation stratum with species and mean density (tree stratum) or mean percent cover (shrub stratum and herb/moss stratum).

	Stratum					
Plot	**Tree**	**Mean stem density (stems /m^2)[1]**	**Shrub**	**Mean percent cover[2]**	**Herb/Moss**	**Mean percent cover[3]**
B32A1	*Populus tremuloides* Michx.	6.8	*Corylus cornuta* Marsh.	16.1	*Viola pubescens* Ait	8.5
	Populus balsamifera L.	1.6	*Rosa acicularis* Lindl.	6.5	*Viburnum opulus* L.	6.5
	Corylus cornuta Marsh.	0.8	*Shepherdia canadensis* (L.) Nutt.	4.0		
	Pinus banksiana Lamb.	0.4	*Amelanchier alnifolia* Nutt.	3.3		
	Prunus spp.	0.4	*Symphiocarpus albus* (L.) Blake	2.8		
			Prunus spp.	1.6		
			Rubus idaeus L.	1.3		
			Viburnum edule (Michx.) Raf.	1.2		
			Viburnum opulus L.	1.0		
			Populus tremuloides Michx.	0.7		
			Prunus virginiana L.	0.5		
			Ribes triste Pall.	0.5		
B32A2	*Populus tremuloides* Michx.	4.0	*Rosa acicularis* Lindl.	5.7	*Aralia nudicaulis* L.	12.0
	Picea glauca (Moench) Voss	3.0	*Shepherdia canadensis* (L.) Nutt.	4.5	Grass spp.	7.0
	Populus balsamifera L.	1.4	*Rubus idaeus* L.	2.1		
	Picea mariana (Mill.) BSP.	1.2	*Abies balsamea* (L.) Mill.	2.0		
	Salix spp.	0.8	*Amelanchier alnifolia* Nutt.	1.8		
	Betula papyrifera Marsh.	0.6	*Symphiocarpus albus* (L.) Blake	1.7		
	Abies balsamea (L.) Mill.	0.4	*Viburnum edule* (Michx.) Raf.	1.5		
	Populus deltoides Marsh.	0.2	*Salix* spp.	1.0		
			Picea glauca (Moench) Voss	0.5		
			Populus tremuloides Michx.	0.5		
			Populus deltoides Marsh.	0.1		
			Rhamnus alnifolia L'Hér	0.1		
B61A1	*Populus tremuloides* Michx.	37.4	*Corylus cornuta* Marsh.	23.7	*Aralia nudicaulis* L	11.0
	Picea glauca (Moench) Voss	15.0	*Rosa acicularis* Lindl.	2.8	*Viola pubescens* Ait.	6.5
	Corylus cornuta Marsh.	3.6	*Viburnum edule* (Michx.) Raf.	1.1		
	Salix spp.	0.4	*Rubus idaeus* L.	0.6		
	Populus balsamifera L.	0.4	*Prunus pensylvanica* L. f.	0.5		
	Prunus spp.	0.2	*Apocynum androsaemifolium* L.	0.3		
			Disporum trachycarpum (Wats) B. & H.	0.2		
			Amelanchier alnifolia Nutt.	0.1		
			Prunus virginiana L.	0.1		
B61A2	*Populus tremuloides* Michx.	24.4	*Symphiocarpus albus* (L.) Blake	7.6	*Aralia nudicaulis* L	16.5
	Alnus crispa (Ait.) Pursh	5.6	*Rosa acicularis* Lindl.	5.3	*Cornus canadensis* L	4.0
	Picea glauca (Moench) Voss	2.8	*Rubus idaeus* L.	2.2		
	Salix spp.	0.8	*Alnus crispa* (Ait.) Pursh	2.0		
	Betula papyrifera Marsh.	0.4	*Amelanchier alnifolia* Nutt.	1.0		
	Prunus spp.	0.2	*Diervilla lonicera* Mill.	1.0		
	Populus balsamifera L.	0.2	*Salix* spp.	1.0		
			Viburnum edule (Michx.) Raf.	0.4		
			Disporum trachycarpum (Wats) B. & H.	0.2		
			Viburnum opulus L.	0.1		
B61B1	*Populus tremuloides* Michx.	30.8	*Rosa acicularis* Lindl.	10.6	Grass spp.	15.5
	Salix spp.	5.4	*Diervilla lonicera* Mill.	7.0	*Aralia nudicaulis* L.	13.5
	Alnus crispa (Ait.) Pursh	5.2	*Alnus crispa* (Ait.) Pursh	4.0		
	Betula papyrifera Marsh.	3.6	*Symphiocarpus albus* (L.) Blake	3.1		
	Picea glauca (Moench) Voss	1.2	*Viburnum edule* (Michx.) Raf.	2.5		
			Amelanchier alnifolia Nutt.	2.0		
			Corylus cornuta Marsh.	1.5		
			Rubus idaeus L.	0.2		
			Rubus acaulis Michx.	0.1		
			Viburnum opulus L.	0.1		
B61B2	*Populus tremuloides* Michx.	35.8	*Rosa acicularis* Lindl	12.6	*Aralia nudicaulis* L.	15.5
	Pinus banksiana Lamb.	5.8	*Viburnum opulus* L.	4.0	Grass spp.	8.5
	Salix spp.	3.6	*Rubus idaeus* L.	3.7		
	Populus balsamifera L.	2.2	*Symphiocarpus albus* (L.) Blake	2.1		
	Alnus crispa (Ait.) Pursh	1.2	*Ribes triste* Pall.	0.6		
	Picea glauca (Moench) Voss	1.2	*Alnus crispa* (Ait.) Pursh	0.3		
	Betula papyrifera Marsh.	0.8	*Disporum trachycarpum* (Wats) B. & H.	0.1		
			Populus tremuloides Michx.	0.1		
			Salix spp.	0.1		

---

[1] Derived from five 10 m x 10 m sampling quadrats per plot.

[2] Derived from ten 2m x 2 m sampling quadrats per plot.

[3] Derived from ten 1 m x 1 m sampling quadrats per plot.

Appendix II: cont.

Plot	Stratum					
	Tree	**Mean stem density (stems /m²)**	**Shrub**	**Mean percent cover**	**Herb/Moss**	**Mean percent cover**
B80A1	*Betula papyrifera* Marsh.	82.6	*Rosa acicularis* Lindl.	4.0	*Rubus pubescens* Raf.	8.5
	Populus tremuloides Michx.	21.6	*Rubus idaeus* L.	3.8	*Aster ciliolatus*	7.0
	Salix spp.	18.0	*Picea glauca* (Moench) Voss	1.0		
	Populus balsamifera L.	6.4	*Amelanchier alnifolia* Nutt.	0.1		
	Picea glauca (Moench) Voss	4.4	*Salix* spp.	0.1		
	Alnus crispa (Ait.) Pursh	0.8				
B80A2	*Populus tremuloides* Michx.	87.2	*Rosa acicularis* Lindl.	10.3	*Aralia nudicaulis* L	15.5
	Populus balsamifera L.	10.8	*Viburnum edule* (Michx.) Raf.	8.1	Grass spp.	10.0
	Salix spp.	4.0	*Viburnum opulus* L.	1.1		
	Alnus crispa (Ait.) Pursh	1.0	*Amelanchier alnifolia* Nutt.	1.0		
			Apocynum androsaemifolium L.	0.8		
			Shepherdia canadensis (L.) Nutt.	0.6		
			Rubus idaeus L.	0.2		
B80B1	*Populus tremuloides* Michx.	111.8	*Rosa acicularis* Lindl.	9.6	Grass spp.	9.0
	Salix spp.	8.8	*Viburnum edule* (Michx.) Raf.	6.0	*Rubus pubescens* Raf.	6.5
	Populus balsamifera L.	6.8	*Shepherdia canadensis* (L.) Nutt.	4.0		
	Betula papyrifera Marsh.	0.8	*Salix* spp.	3.5		
			Viburnum opulus L.	2.8		
			Picea glauca (Moench) Voss	2.6		
			Apocynum androsaemifolium L.	2.3		
			Populus tremuloides Michx.	0.2		
			Lonicera dioica L.	0.1		
			Populus balsamifera L.	0.1		
B80B2	*Populus tremuloides* Michx.	99.6	*Rosa acicularis* Lindl.	9.6	Grass spp.	9.0
	Populus balsamifera L.	15.6	*Apocynum androsaemifolium* L.	2.0	*Viola pubescens* Ait.	5.0
	Salix spp.	5.8	*Shepherdia canadensis* (L.) Nutt.	1.6		
			Salix spp.	1.0		
			Symphiocarpus albus (L.) Blake	1.0		
			Viburnum opulus L.	1.0		
			Rubus idaeus L.	0.3		
			Viburnum edule (Michx.) Raf.	0.1		
H67A1	*Populus tremuloides* Michx.	15.4	*Alnus crispa* (Ait.) Pursh	6.5	*Rubus idaeus* L.	11.0
	Populus balsamifera L.	8.2	*Symphiocarpus albus* (L.) Blake	2.1	*Viola pubescens* Ait.	5.0
	Alnus crispa (Ait.) Pursh	7.6	*Corylus cornuta* Marsh	2.0		
	Prunus spp.	1.4	*Viburnum opulus* L.	1.7		
	Salix spp.	1.0	*Salix* spp.	1.6		
			Populus balsamifera L.	1.5		
			Cornus stolonifera Michx.	1.0		
			Disporum trachycarpum (Wats) B. & H.	1.0		
			Rhamnus alnifolia L'Hér	1.0		
			Rubus idaeus L.	1.0		
			Prunus virginiana L.	0.7		
			Ribes triste Pall.	0.7		
			Ribes oxyacanthoides L.	0.2		
			Prunus pensylvanica L. f.	0.1		
			Rosa acicularis Lindl.	0.1		
			Lonicera dioica L.	0.1		
			Ribes lacustre (Pers.) Poir.	0.1		
			Streptopus roseus Michx.	0.1		
H67A2	*Populus tremuloides* Michx.	33.0	*Rosa acicularis* Lindl.	7.6	*Aralia nudicaulis* L.	13.0
	Populus balsamifera L.	2.6	*Alnus crispa* (Ait.) Pursh	5.5	Grass spp.	9.0
	Salix spp.	1.4	*Symphiocarpus albus* (L.) Blake	2.6		
	Prunus spp.	1.2	*Viburnum opulus* L.	1.7		
	Alnus crispa (Ait.) Pursh	1.0	*Prunus virginiana* L.	0.1		
			Rubus idaeus L.	0.1		
			Ribes oxyacanthoides L.	0.1		
H67B1	*Populus tremuloides* Michx.	12.4	*Corylus cornuta* Marsh.	26.1	*Aralia nudicaulis* L.	12.0
	Alnus crispa (Ait.) Pursh	7.8	*Rubus idaeus* L.	6.1	*Viburnum edule* (Michx.) Raf	3.5
	Populus balsamifera L.	7.2	*Rosa acicularis* Lindl.	4.6		
	Salix spp.	3.0	*Symphiocarpus albus* (L.) Blake	3.1		
	Prunus spp.	1.4	*Prunus virginiana* L.	2.0		
	Betula papyrifera Marsh.	0.4	*Amelanchier alnifolia* Nutt.	1.5		
	Corylus cornuta Marsh.	0.2	*Prunus pensylvanica* L. f.	1.0		
	Picea glauca (Moench) Voss	0.2	*Viburnum opulus* L.	0.6		
			Alnus crispa (Ait.) Pursh	0.5		
			Salix spp.	0.2		
			Ribes triste Pall.	0.1		
			Populus tremuloides Michx.	0.1		
			Rhamnus alnifolia L'Hér	0.1		
H67B2	*Populus tremuloides* Michx.	20.4	*Corylus cornuta* Marsh.	14.0	*Aralia nudicaulis* L.	16.0
	Populus balsamifera L.	6.6	*Rosa acicularis* Lindl.	6.1	*Rubus pubescens* Raf.	6.0
	Salix spp.	1.4	*Rubus acaulis* Michx.	1.5		
	Picea glauca (Moench) Voss	0.6	*Rubus idaeus* L.	1.5		
	Prunus spp.	0.2	*Picea glauca* (Moench) Voss	1.0		
			Viburnum opulus L.	1.0		
			Disporum trachycarpum (Wats) B. & H.	0.6		
			Prunus pensylvanica L. f.	0.5		
			Salix spp.	0.1		
			Symphiocarpus albus (L.) Blake	0.1		

Appendix II: cont.

Plot	Stratum					
	Tree	Mean stem density (stems /m^2)	Shrub	Mean percent cover	Herb/Moss	Mean percent cover
H80A1	*Populus tremuloides* Michx.	38.6	*Diervilla lonicera* Mill.	20.5	*Aralia nudicaulis* L.	12.5
	Corylus cornuta Marsh.	11.0	*Corylus cornuta* Marsh.	6.1	*Diervilla lonicera* Mill.	9.0
	Alnus crispa (Ait.) Pursh	6.0	*Rosa acicularis* Lindl.	3.7		
	Acer spicatum Lam.	5.2	*Viburnum opulus* L.	2.0		
	Prunus spp.	3.0	*Viburnum edule* (Michx.) Raf.	1.7		
	Betula papyrifera Marsh.	2.4	*Ribes lacustre* (Pers.) Poir.	1.6		
	Salix spp.	1.2	*Symphiocarpus albus* (L.) Blake	1.1		
	Amelanchier alniflolia Nutt.	0.8	*Rubus idaeus* L.	0.2		
	Populus balsamifera L.	0.2				
H80A2	*Populus tremuloides* Michx.	20.8	*Rubus idaeus* L.	5.6	*Rubus pubescens* Raf.	6.5
	Alnus crispa (Ait.) Pursh	9.8	*Diervilla lonicera* Mill.	4.5	*Viburnum edule* (Michx.) Raf.	6.0
	Salix spp.	2.4	*Symphiocarpus albus* (L.) Blake	4.5		
	Betula papyrifera Marsh.	1.8	*Rosa acicularis* Lindl.	4.2		
	Corylus cornuta Marsh.	1.8	*Alnus crispa* (Ait.) Pursh	3.0		
	Populus balsamifera L.	1.0	*Ribes triste* Pall.	2.7		
	Prunus spp.	0.8	*Prunus virginiana* L.	2.1		
			Rubus acaulis Michx.	2.0		
			Ribes oxyacanthoides L.	0.2		
H95A1	*Populus tremuloides* Michx.	322.0	*Salix* spp.	8.2	Grass spp.	32.0
	Populus balsamifera L.	138.7	*Corylus cornuta* Marsh.	7.0	*Anemone canadensis* L.	6.0
			Populus tremuloides Michx.	6.0		
			Rosa acicularis Lindl.	5.2		
			Populus balsamifera L.	0.7		
			Symphiocarpus albus (L.) Blake	0.2		
			Rubus idaeus L.	0.1		
			Prunus pensylvanica L. f.	0.1		
H95A2	*Populus tremuloides* Michx.	416.0	*Rosa acicularis* Lindl.	29.0	Grass spp.	19.0
	Populus balsamifera L.	138.8	*Populus tremuloides* Michx.	26.5	*Fragaria virginiana* Duchesne	18.0
			Corylus cornuta Marsh.	7.0		
			Salix spp.	6.0		
			Cornus stolonifera Michx.	2.0		
			Prunus pensylvanica L. f.	1.0		
			Symphiocarpus albus (L.) Blake	0.5		
			Rubus idaeus L.	0.3		
			Populus balsamifera L.	0.1		
			Prunus virginiana L.	0.1		
			Amelanchier alnifolia Nutt.	0.1		
H95B1	*Populus tremuloides* Michx.	546.4	*Corylus cornuta* Marsh.	12.5	*Rosa acicularis* Lindl.	7.5
	Populus balsamifera L.	119.7	*Populus tremuloides* Michx.	11.5	Grass spp.	6.0
			Rosa acicularis Lindl.	10.3		
			Rubus idaeus L.	3.7		
			Prunus pensylvanica L. f.	3.6		
			Diervilla lonicera Mill.	1.5		
			Prunus virginiana L.	0.7		
			Alnus crispa (Ait.) Pursh	0.5		
			Symphiocarpus albus (L.) Blake	0.5		
			Amelanchier alnifolia Nutt.	0.1		
			Populus balsamifera L.	0.1		
H95B2	*Populus tremuloides* Michx.	454.0	*Populus tremuloides* Michx.	26.5	Grass spp.	18.5
	Populus balsamifera L.	176.4	*Corylus cornuta* Marsh	25.1	*Aralia nudicaulis* L.	9.5
			Rosa acicularis Lindl.	5.2		
			Salix spp.	5.0		
			Diervilla lonicera Mill.	3.5		
			Amelanchier alnifolia Nutt.	2.2		
			Prunus virginiana L.	1.1		
			Symphiocarpus albus (L.) Blake	0.6		
			Populus balsamifera L.	0.5		
			Rubus idaeus L.	0.1		
			Prunus pensylvanica L. f.	0.1		
			Viburnum edule (Michx.) Raf.	0.1		

Appendix III: Vegetation measurements for tree, shrub and herb/moss strata for all burn plots

Stratum	B32A1	B32A2	B61A1	B61A2	B61B1	B61B2	B80A1	B80A2	B80B1	B80B2
Tree										
Mean Tree Age (n)	69 (10)	69 (10)	40 (10)	40 (10)	40 (10)	40 (10)	21 (10)	21 (10)	21 (10)	21 (10)
Mean Tree Height (m) (n)	20.5 (55)	11.7 (63)	9.7 (289)	10.6 (177)	9.5 (236)	9.6 (258)	4.2 (647)	7.7 (518)	6.3 (646)	6.3 (600)
Mean Tree Density (/m^2)[1]	0.11	0.14	0.57	0.40	0.47	0.52	1.34	1.10	1.36	1.23
Number Tree Species	6	8	7	8	5	7	6	6	4	3
% *Populus* spp.	80.0	43.1	81.5	69.5	65.7	73.6	20.8	95.2	92.4	90.3
% Conifer	5.5	36.5	8.8	7.9	2.5	14.7	3.3	0.0	0.0	0.0
% Other tree spp.	14.6	17.5	10.3	22.6	31.8	11.6	76.0[2]	4.8	7.6	9.7
Mean Diameter *Populus* spp (n)	27.0 (44)	21.2 (29)	10.5 (189)	12.2 (123)	9.8 (155)	8.1 (190)	4.3 (140)	4.9 (493)	3.8 (597)	4.3 (542)
Mean Diameter Conifer (n)	14.2 (3)	17.3 (23)	4.8 (76)	7.0 (14)	6.9 (6)	8.8 (38)	2.5 (22)	NA	NA	NA
Mean Diameter Other tree spp. (n)	2.1 (8)	11.4 (11)	2.3 (24)	2.4 (40)	2.4 (75)	2.7 (30)	2.5 (512)	3.3 (25)	2.0 (49)	1.9 (58)
Mean Canopy Closure[1]	87.1	80.9	93.1	92.1	91.3	92.7	86.1	82.9	81.3	81.9
C.V.(X) Canopy Closure	3.0	17.0	1.0	3.3	2.1	2.8	5.1	8.2	5.4	10.5
Log-Series α	1.38	2.52	1.07	1.47	0.90	1.33	0.91	0.59	0.57	0.41
Mean % Light Intensity[3]	19.8	22.8	18.3	14.6	15.8	20.3	7.8	13.3	41.2	24.3
C.V.(X) Light Intensity	40.1	23.9	16.0	27.0	28.5	23.7	29.5	28.7	63.7	36.5
Shrub										
% Shrub Cover[4]	39.4	24.5	29.4	20.8	31.2	23.6	9.0	22.1	31.9	16.6
Number Shrub Species	12	12	9	10	11	9	5	7	10	8
Shrub Shannon-Weiner Index	2.13	1.99	1.40	1.59	1.62	1.58	0.98	1.49	1.84	1.36
Herbaceous/Moss										
% Bare Ground[5]	40.5	35.5	32.5	41.5	48.0	43.5	56.6	37.0	42.0	46.5
% Herb Cover[5]	59.5	64.5	67.5	58.5	52.0	56.5	44.0	63.0	58.0	53.5

NA: Not applicable

[1] Mean of five 10 m x 10 m quadrats per plot.

[2] The majority of these stems were *Betula papyrifera*.

[3] Mean of ten randomly located readings per plot.

[4] Mean of ten 2 x 2 quadrats per plot.

[5] Mean of ten 1 m x 1 m quadrats per plot.

Appendix IV: Vegetation measurements for tree, shrub and herb/moss strata for all harvest plots

Stratum	H67A1	H67A2	H67B1	H67B2	H80A1	H80A2	H95A1	H95A2	H95B1	H95B2
Tree										
Mean Tree Age	34	34	34	34	21	21	6	6	6	6
Mean Tree Height (m)	9.4	13.1	9.2	12.2	7.5	7.7	2	2	2	2
Mean Tree Density (/m^2)	0.35	0.40	0.35	0.36	0.70	0.40	8.18	9.87	11.82	11.20
Number Tree Species	5	5	8	6	9	8	2	2	2	2
% *Populus* spp.	68.2	90.1	58.3	91.4	55.9	54.8	100	100	100	100
% Conifer	0.0	0.0	0.6	2.7	0.0	0.0	0.0	0.0	0.0	0.0
% Other tree spp.	31.8	10.0	41.1	6.0	44.1	45.2	0.0	0.0	0.0	0.0
Mean Diameter *Populus* spp	12.2	9.7	10.9	10.8	6.6	10.5	NM	NM	NM	NM
Mean Diameter Conifer	NA	NA	9.0	4.0	NA	NA	NA	NA	NA	NA
Mean Diameter Other tree spp.	3.1	3.1	4.4	2.9	2.9	3.5	NA	NA	NA	NA
Canopy Closure	90.4	92.5	87.3	87.7	74.6	80.0	NM[1]	NM	NM	NM
C.V.(X) Canopy Closure	4.5	8.8	8.6	12.2	8.4	7.4	NM	NM	NM	NM
Log-Series α	0.97	0.93	1.76	1.00	1.47	1.43	NA	NA	NA	NA
Mean % Light Intensity	21.8	2.7	8.3	8.2	32.7	28.9	64.6	29.4	48.3	90.0
C.V.(X) Light Intensity	155.8	74.4	74.0	49.2	115.7	57.8	75.13	69.9	51.9	10.5
Shrub										
% Shrub Cover	21.4	17.6	45.9	26.4	36.9	28.8	27.5	72.6	45.0	69.9
Number Shrub Species	18	7	13	10	8	9	8	11	11	12
Shrub Shannon-Weiner Index	2.53	1.54	1.84	1.69	1.60	1.98	1.56	1.52	1.94	4.60
Herbaceous/Moss										
% Ground Cover	36.5	37.5	34.0	39.0	58.5	46.0	30.5	24.5	30.5	25.5
% Herb Cover	63.5	62.5	66.0	61.0	41.5	54.0	69.5	75.5	69.5	74.5

NA: Not applicable
NM: Not measured

[1] It was determined that the trees in the H95 plots were not tall enough to constitute a 'canopy' (see Materials and Methods for further explanation).

Appendix V: Vegetation measurements (mean ± s.e.) for tree, shrub and herb/moss strata for all sites (the number of plots follows the name of each site).

Stratum	Site (n)					
	B32 (2)	B61 (4)	B80 (4)	H67 (4)	H80 (2)	H95 (4)
Tree						
Mean Age	69.0 ± 0.0	40.0 ± 0.0	21.0 ± 0.00	34.0 ± 0.00	21.0 ± 0.00	6.0 ± 0.00
Mean Height (m)	16.1 ± 4.40	9.9 ± 0.25	6.1 ± 0.72	11.0 ± 0.99	7.6 ± 0.10	2.0 ± 0.10
Mean Tree Density (/m^2)	0.13 ± 0.02	0.49 ± 0.04	1.26 ± 0.06	0.37 ± 0.01	0.55 ± 0.15	10.27 ± 0.81
Number Species	7.0 ± 1.00	6.8 ± 0.63	4.8 ± 0.75	6.0 ± 0.71	8.5 ± 0.50	2.0 ± 0.00
% *Populus* spp.	61.5 ± 18.47	72.6 ± 3.39	74.7 ± 18.00	77.0 ± 8.18	55.3 ± 0.57	100 ± 0.00
% Conifer	21.0 ± 15.53	8.5 ± 2.50	0.8 ± 1.63	0.8 ± 0.89	0.0 ± 0.00	0.0 ± 0.00
% Other tree spp.	16.0 ± 1.45	19.1 ± 5.06	24.5 ± 17.18	22.2 ± 8.48	44.7 ± 0.56	0.0 ± 0.00
Mean Diameter *Populus* spp	24.1 ± 2.88	10.2 ± 0.85	4.3 ± 0.23	10.9 ± 0.51	8.5 ± 1.91	NM
Mean Diameter Conifer	15.8 ± 1.57	6.9 ± 0.83	2.5 ± NA[1]	6.5 ± 2.50	NA	NA
Mean Diameter Other tree spp.	6.7 ± 4.66	2.5 ± 0.10	2.5 ± 0.31	3.4 ± 0.33	3.2 ± 0.31	NA
Canopy Closure	84.0 ± 3.10	92.3 ± 0.39	83.1 ± 1.07	89.5 ± 1.22	77.3 ± 2.70	NM[2]
C.V.(X) Canopy Closure	10.0 ± 6.99	2.3 ± 0.49	7.3 ± 1.26	8.5 ± 1.58	7.9 ± 0.52	NM
Log-Series α	1.95 ± 0.566	1.19 ± 0.127	0.62 ± 0.104	1.17 ± 0.199	1.45 ± 0.022	NA
Mean % Light Intensity	21.3 ± 1.50	17.3 ± 1.28	21.7 ± 7.36	10.3 ± 4.07	30.8 ± 1.90	58.1 ± 12.84
C.V.(X) Light Intensity	32.0 ± 8.06	23.8 ± 2.78	39.6 ± 8.22	88.4 ± 23.23	86.7 ± 28.94	51.9 ± 14.65
Shrub						
% Shrub Cover	32.0 ± 7.48	26.2 ± 2.44	19.7 ± 4.67	27.9 ± 6.28	32.8 ± 4.04	53.8 ± 10.73
Number Species	12.0 ± 0.00	9.8 ± 2.44	7.5 ± 1.04	12.0 ± 2.35	8.5 ± 0.50	10.5 ± 0.87
Shannon-Weiner Index	2.06 ± 0.070	1.55 ± 0.050	1.42 ± 0.178	1.90 ± 0.219	1.79 ± 0.190	2.41 ± 0.738
Herbaceous/ Moss						
% Bare Ground	38.0 ± 2.50	41.4 ± 3.26	45.4 ± 4.04	36.8 ± 1.05	52.3 ± 6.25	27.8 ± 1.60
% Herb Cover	62.0 ± 2.50	58.6 ± 3.26	54.6 ± 4.04	63.3 ± 1.05	47.8 ± 6.25	72.3 ± 1.60

NA: Not applicable
NM: Not measured

[1] Conifers were recorded in only one of the four plots.

[2] It was determined that the trees in the H95 plots were not high enough to constitute a 'canopy'.

Appendix VI: Stem counts for all species in the tree and shrub strata by plot. Percent cover values for shrub stratum species are listed below the number of stems.

Tree stratum species	Burn Sites										Harvest Sites									
	B32A1	B32A2	B61A1	B61A2	B61B1	B61B2	B80A1	B80A2	B80B1	B80B2	H67A1	H67A2	H67B1	H67B2	H80A1	H80A2	H95A1	H95A2	H95B1	H95B2
Abies balsamea (L.) Mill.	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acer spicatum Lam.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	26	0	0	0	0	0
Alnus crispa (Ait.) Pursh	0	0	0	28	26	6	4	5	0	0	38	5	39	0	30	49	0	0	0	0
Amelanchier alnifolia Nutt.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0
Betula papyrifera Marsh.	0	3	0	2	18	4	413	0	4	0	0	0	2	0	12	9	0	0	0	0
Corylus cornuta Marsh.	4	0	18	0	0	0	0	0	0	0	0	0	1	0	55	9	0	0	0	0
Picea glauca (Moench) Voss	0	15	75	14	6	6	22	0	0	0	0	0	1	3	0	0	0	0	0	0
Picea mariana (Mill.) BSP.	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pinus banksiana Lamb.	2	0	0	0	0	29	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Populus deltoides Marsh.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prunus spp.	2	0	1	1	0	0	0	0	0	0	7	6	7	1	15	4	0	0	0	0
Salix spp.	0	4	2	4	27	18	90	20	44	29	5	7	15	7	6	12	0	0	0	0
Populus balsamifera L.	8	7	2	1	0	11	32	54	34	78	41	13	36	33	1	5	0	0	0	0
Populus tremuloides Michx.	34	20	187	122	154	179	108	436	559	498	77	165	62	102	193	104	2300	2775	3325	3150
Number of species	5	8	6	7	5	7	6	4	4	3	5	5	8	5	9	7	1	1	1	1

Appendix VI: cont.

Shrub stratum species	Burn Sites										Harvest Sites									
	B32A1	B32A2	B61A1	B61A2	B61B1	B61B2	B80A1	B80A2	B80B1	B80B2	H67A1	H67A2	H67B1	H67B2	H80A1	H80A2	H95A1	H95A2	H95B1	H95B2
Abies balsamea (L.) Mill.	0	2 (2.0)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alnus crispa (Ait.) Pursh	0	0	0	3 (2.0)	12 (4.0)	6 (0.3)	0	0	0	0	15 (6.5)	5 (5.5)	1 (0.5)	0	0	7 (3.0)	0	0	1 (0.5)	0
Amelanchier alnifolia Nutt.	17 (3.3)	16 (1.8)	1 (0.1)	7 (1.0)	5 (2.0)	0	1 (0.1)	9 (1.0)	0	0	0	0	2 (1.5)	0	0	0	0	1 (0.1)	4 (0.1)	25 (2.2)
Apocynum androsaemifolium L.	0	0	8 (0.3)	0	0	0	0	11 (0.8)	25 (2.3)	37 (2.0)	0	0	0	0	0	0	0	0	0	0
Cornus stolonifera Michx.	0	0	0	0	0	0	0	0	0	0	4 (1.0)	0	0	0	0	0	0	10 (2.0)	0	0
Corylus cornuta Marsh.	57 (16.1)	0	60 (23.7)	0	3 (1.5)	0	0	0	0	0	1 (2.0)	0	39 (26.1)	40 (14.0)	9 (6.1)	0	31 (7.1)	32 (7.0)	44 (12.5)	241 (25.1)
Diervilla lonicera Mill.	0	0	0	4 (1.0)	80 (7.0)	0	0	0	0	0	0	0	0	0	58 (20.5)	16 (4.5)	0	0	15 (1.5)	18 (3.5)
Disporum trachycarpum (Wats.) B & H	0	0	3 (0.2)	4 (0.2)	3 (0.2)	2 (0.1)	0	0	0	0	2 (1.0)	0	0	2 (0.6)	0	0	0	0	0	0
Lonicera dioica L.	0	0	0	0	0	0	0	0	1 (0.1)	0	1 (0.1)	0	0	0	0	0	0	0	0	0
Picea glauca (Moench) Voss	0	2 (0.5)	0	0	0	0	2 (1.0)	0	5 (2.6)	0	0	0	0	1 (1.0)	0	0	0	0	0	0
Populus balsamifera L.	0	0	0	0	0	0	0	0	1 (0.1)	0	3 (1.5)	0	0	0	0	0	4 (0.7)	1 (0.1)	1 (0.1)	4 (0.5)
Populus tremuloides Michx.	8 (0.7)	2 (0.5)	0	0	0	1 (0.1)	0	0	2 (0.2)	0	0	0	1 (0.1)	0	0	0	24 (6.0)	85 (26.5)	44 (11.5)	163 (26.5)
Prunus pensylvanica L. f.	6 (1.6)	0	1 (0.5)	0	0	0	0	0	0	0	2 (0.1)	0	1 (1.0)	3 (0.5)	0	0	1 (0.1)	5 (1.0)	13 (3.6)	2 (0.1)
Prunus virginiana L.	3 (0.5)	0	2 (0.1)	0	0	0	0	0	0	0	5 (0.7)	1 (0.1)	1 (2.0)	0	0	3 (2.1)	0	2 (0.1)	7 (0.7)	9 (1.1)

Appendix VI: (cont.)

Shrub stratum species	Burn Sites										Harvest Sites									
	B32A1	B32A2	B61A1	B61A2	B61B1	B61B2	B80A1	B80A2	B80B1	B80B2	H67A1	H67A2	H67B1	H67B2	H80A1	H80A2	H95A1	H95A2	H95B1	H95B2
Rhamnus alnifolia L'Hér.	0	1 (0.1)	0	0	0	0	0	0	0	0	3 (1.0)	0	1 (0.1)	0	0	0	0	0	0	0
Ribes lacustre (Pers.) Poir.	0	0	0	0	0	0	0	0	0	0	1 (0.1)	0	0	0	7 (1.6)	0	0	0	0	0
Ribes oxyacanthoides L.	0	0	0	0	0	0	0	0	0	0	4 (0.2)	1 (0.1)	0	0	0	5 (0.2)	0	0	0	0
Ribes triste Pall.	5 (0.5)	0	0	0	0	3	0	0	0	0	5 (0.7)	0	5 (0.1)	0	0	33 (2.7)	0	0	0	0
Rosa acicularis Lindl.	50 (6.5)	32 (5.7)	39 (2.8)	49 (5.3)	80 (10.6)	56 (12.6)	30 (4.0)	50 (10.3)	38 (9.6)	62 (9.6)	1 (0.1)	21 (7.6)	21 (4.6)	25 (6.1)	16 (3.7)	15 (4.2)	46 (5.2)	126 (29.0)	59 (10.3)	27 (5.2)
Rubus acaulis Michx.	0	0	0	0	1 (0.1)	0	0	0	0	0	0	0	0	7 (1.5)	0	5 (2.0)	0	0	0	0
Rubus idaeus L.	11 (1.3)	19 (2.1)	5 (0.6)	31 (2.2)	3 (0.2)	27 (3.7)	33 (3.8)	5 (0.2)	0	4 (0.3)	3 (1.0)	3 (0.1)	16 (6.1)	6 (1.5)	3 (0.2)	15 (5.6)	2 (0.1)	4 (0.3)	28 (3.7)	1 (0.1)
Salix spp	0	5 (1.0)	0	7 (1.0)	0	1 (0.1)	2 (0.1)	0	10 (3.5)	2 (1.0)	5 (1.6)	0	2 (0.2)	1 (0.1)	0	0	10 (8.2)	17 (6.0)	0	27 (5.0)
Shepherdia canadensis (L.) Nutt.	14 (4.0)	11 (4.5)	0	0	0	0	0	5 (0.6)	16 (4.0)	4 (1.6)	0	0	0	0	0	0	0	0	0	0
Streptopus roseus Michx.	0	0	0	0	0	0	0	0	0	0	1 (0.1)	0	0	0	0	0	0	0	0	0
Symphoricarpos albus (L.) Blake	38 (2.8)	32 (1.7)	0	91 (7.6)	36 (3.1)	18 (2.1)	0	0	0	10 (1.0)	14 (2.1)	12 (2.6)	24 (3.1)	3 (0.1)	6 (1.1)	16 (4.5)	3 (0.2)	5 (0.5)	8 (0.5)	35 (0.6)
Viburnum edule (Michx.) Raf.	17 (1.2)	18 (1.5)	6 (1.1)	6 (0.4)	13 (2.5)	0	0	48 (8.1)	47 (6.0)	1 (0.1)	0	0	0	0	9 (1.7)	0	0	0	0	2 (0.1)
Viburnum opulus L.	10 (1.0)	0	0	2 (0.1)	1 (0.1)	15 (4.0)	0	5 (1.1)	14 (2.8)	5 (1.0)	9 (1.7)	8 (1.7)	3 (0.6)	10 (1.0)	6 (2.0)	0	0	0	0	0
Number of species	12	11	9	10	11	9	5	7	10	8	18	7	13	10	8	9	8	11	11	12
Total mean percent cover	39.44	24.4	29.3	20.7	31.2	23.6	9.0	22.0	31.1	16.5	21.4	17.6	45.9	26.4	36.8	28.7	27.5	72.5	44.9	69.93

Appendix VII: Description of the vegetation types (v-types) found in this study (based on Zoladeski et al. 1995).

V-Type	Type Name	Overstory[1]	Understory[2]	Soils[3]	General Description
V4	White birch hardwood and mixedwood	*Betula papyrifera, Pinus banksiana, Populus tremuloides, Populus balsamifera*	**(S)** *Rubus pubescens, Diervilla lonicera, Corylus cornuta* **(H)** *Aralia nudicaulis, Cornus canadensis, Viola renifolia*	• Brunisols, Luvisols • **L**, **F**, **Ae**, Bfj, **Bm**, BC, C • Luvisols • **L**, **F**, Ahe, **Ae**, **Bt**, BC, C(k)	Mixedwood stands with a canopy dominated by *Betula papyrifera*. Stands are herb and shrub rich. Occur on fresh to moist, well to rapidly drained, fine to coarse-textured mineral soils.
V5	Aspen hardwood	*Populus tremuloides, Betula papyrifera, Populus balsamifera, Pinus banksiana*	**(S)** *Amelanchier* spp., *Vaccinium myrtilloides, Corylus cornuta* **(H)** *Aralia nudicaulis, Maianthemum canadense, Cornus canadensis*	• Brunisols, Luvisols • L, **F**, H, **Ah**, Ae, Bm, Bt, C(k) • Luvisols • L, **F**, **A(h)e**, **Bt**, Bm, **C(k)**	Hardwood stands of *Populus tremuloides*, sometimes with a small mixture of other species. The understory is relatively herb and shrub rich. Occur on deep, moist, upland mineral soils, mostly on flat to slightly undulating terrain.
V8	Trembling aspen mixedwood/tall shrub	*Populus tremuloides, Picea glauca, Picae mariana, Populus balsamifera*	**(S)** *Acer spicatum, Corylus cornuta, Abies balsamea* **(H)** *Aster ciliolatus, Aralia nudicaulis, Mitella nuda*	• Gleysols, Brunisols, Luvisols • L, F, H, Ahe, Ae, **Bt**, Bg, Ckg, Cg	Hardwood mixedwoods with *Populus tremuloides* as the main deciduous tree species, often with a mix of *Picea glauca*. Dense thickets of *Acer spicatum* or *Corylus cornuta* and a herb-rich understory. Occur on deep, moist, well-drained mineral soils.
V9	Trembling aspen mixedwood/low shrub	*Populus tremuloides, Pinus banksiana, Picea mariana, Picea glauca*	**(S)** *Alnus crispa, Viburnum edule, Viburnum opulus* **(H)** *Cornus canadensis, Maianthemum canadense, Aralia nudicaulis*	• Brunisols, Luvisols • L, **F**, H, **Ah**, Ae, Bm, Bt, C(k) • Luvisols • **L**, **F**, Ahe, **Ae**, **Bt**, BC, C(k)	Hardwood mixedwood with *Populus tremuloides* and conifers including *Pinus banksiana, Picea mariana* or *Picea glauca*. The herb and shrub layers are usually rich in broadleaf species. Occur mainly on deep, moist to fresh, well to rapidly drained mineral soils.
V10	Trembling aspen mixedwood/ feather moss	*Populus tremuloides, Picea mariana, Picea glauca, Populus balsamifera*	**(S)** *Alnus crispa, Rubus pubescens, Rosa acicularis* **(H)** *Cornus canadensis, Aralia nudicaulis, Epilobium, augustifolium*	• Gleysols, Brunisols, Luvisols • L, F, H, Ahe, Ae, **Bt**, Bg, Ckg, Cg • Luvisols • L, **F**, **A(h)e**, **Bt**, Bm, **C(k)**	Hardwood mixedwood stands of *Populus tremuloides*, with *Picea mariana, Picea glauca* or *Pinus banksiana* as conifer components. The shrub understory is typically dominated by *Alnus crispa*. Occur on fresh, well-drained soils.
V13	White spruce mixedwood	*Picea glauca, Populus tremuloides, Abies balsamea, Betula papyrifera*	**(S)** *Abies balsamea, Rubus pubescens, Acer spicatum* **(H)** *Aralia nudcaulis, Cornus canadensis, Maianthemum canadense*	• Brunisols, Luvisols • **L**, **F**, **Ae**, Bfj, **Bm**, BC, C • Luvisols • **L**, **F**, Ahe, **Ae**, **Bt**, BC, C(k)	The tree canopy consists of *Picea glauca* with an admixture of *Populus tremuloides, Abies balsamea*, or *Betula papyrifera* in the secondary canopy. The understory varies from shrub- and herb-poor to moderately rich. Usually on deep, moist, mineral soils.

---

[1] The four most common overstory (tree) species.
[2] Three most common shrub **(S)** and three most common herbaceous **(H)** species.
[3] Commonly occurring soil types followed by the soil horizons that may be present. The most commonly occurring horizons are in bold type.

Appendix VIII: Total number of individuals of the most frequently caught species of carabid beetles by plot and year of collection (the catch frequency of species listed was each ≥ 5% of the total catch from that study plot).

Plot	2000	n	2001	n	2002	n
B32A1	*Calathus ingratus*	30	*Platynus decentis*	558	NS[1]	
	Pterostichus adstrictus	17	*Pterostichus adstrictus*	203		
	Pterostichus pensylvanicus	13	*Calathus ingratus*	70		
	Platynus decentis	6				
	Stereocercus haematopus	6				
	Carabus taedatus	6				
B32A2	*Carabus taedatus*	32	*Platynus decentis*	356	NS	
	Stereocercus haematopus	19	*Pterostichus adstrictus*	172		
	Calathus ingratus	12	*Stereocercus haematopus*	101		
	Pterostichus adstrictus	7	*Carabus taedatus*	56		
	Pterostichus pensylvanicus	7				
	Sphaeroderus nitidicollis	6				
B61A1	*Carabus taedatus*	45	*Platynus decentis*	536	NS	
	Agonum retractum	33	*Pterostichus pensylvanicus*	149		
	Calathus ingratus	21	*Pterostichus adstrictus*	80		
	Pterostichus pensylvanicus	15	*Carabus taedatus*	69		
	Sphaeroderus nitidicollis	11				
B61A2	*Calathus ingratus*	40	*Platynus decentis*	484	NS	
	Pterostichus adstrictus	21	*Pterostichus adstrictus*	165		
	Pterostichus pensylvanicus	15	*Calathus ingratus*	115		
	Carabus taedatus	13	*Pterostichus pensylvanicus*	67		
	Platynus decentis	10				
	Agonum retractum	6				
	Sphaeroderus nitidicollis	6				
B61B1	*Calathus ingratus*	82	*Platynus decentis*	301	NS	
	Carabus taedatus	38	*Pterostichus pensylvanicus*	133		
	Agonum retractum	30	*Pterostichus adstrictus*	110		
	Platynus decentis	27	*Calathus ingratus*	80		
			Carabus taedatus	59		
B61B2	*Carabus taedatus*	26	*Platynus decentis*	328	NS	
	Calathus ingratus	24	*Pterostichus pensylvanicus*	141		
	Pterostichus pensylvanicus	8	*Pterostichus adstrictus*	121		
	Pterostichus adstrictus	7	*Calathus ingratus*	58		
	Sphaeroderus nitidicollis	5	*Carabus taedatus*	54		
B80A1	*Calathus ingratus*	21	*Platynus decentis*	86	*Platynus decentis*	97
	Synuchus impunctatus	15	*Pterostichus pensylvanicus*	63	*Pterostichus pensylvanicus*	54
	Sphaeroderus nitidicollis	12	*Calathus ingratus*	26	*Calathus ingratus*	28
	Agonum retractum	3	*Synuchus impunctatus*	19	*Synuchus impunctatus*	21
			Pterostichus adstrictus	14		
B80A2	*Calathus ingratus*	16	*Platynus decentis*	603	*Platynus decentis*	1004
	Agonum retractum	13	*Pterostichus pensylvanicus*	77	*Pterostichus pensylvanicus*	114
	Platynus decentis	8	*Agonum retractum*	54	*Agonum retractum*	45
	Sphaeroderus nitidicollis	7			*Calathus ingratus*	45
	Synuchus impunctatus	6				
	Carabus taedatus	3				
	Pterostichus adstrictus	3				
B80B1	*Calathus ingratus*	7	*Platynus decentis*	184	*Platynus decentis*	297
	Sphaeroderus nitidicollis	7	*Calathus ingratus*	58	*Calathus ingratus*	79
	Agonum retractum	3	*Pterostichus pensylvanicus*	30	*Pterostichus pensylvanicus*	44
	Agonum sordens	3	*Agonum retractum*	22	*Agonum retractum*	43
	Platynus decentis	3				
B80B2	*Platynus decentis*	18	*Platynus decentis*	48	*Platynus decentis*	231
	Calathus ingratus	11	*Agonum retractum*	32	*Calathus ingratus*	38
	Sphaeroderus nitidicollis	8	*Pterostichus pensylvanicus*	29	*Pterostichus pensylvanicus*	38
			Calathus ingratus	22	*Agonum retractum*	22

---

[1] NS: Plots were not sampled that year

Appendix VIII: cont.

Plot	2000	n	2001	n	2002	n
H67A1	*Sphaeroderus nitidicollis*	4	*Platynus decentis*	165	NS	
	Synuchus impunctatus	2	*Carabus maeander*	14		
	Carabus maeander	2	*Calosoma frigidum*	11		
	Agonum gratiosum	1	*Synuchus impunctatus*	11		
	Agonum superioris	1				
	Calathus ingratus	1				
	Carabus taedatus	1				
	Patrobus septentrionis	1				
	Pterostichus adstrictus	1				
	Pterostichus pensylvanicus	1				
H67A2	*Synuchus impunctatus*	17	*Platynus decentis*	165	NS	
	Platynus decentis	4	*Calathus ingratus*	39		
	Calathus ingratus	3	*Synuchus impunctatus*	33		
			Pterostichus pensylvanicus	26		
			Agonum retractum	18		
H67B1	*Calathus ingratus*	16	*Platynus decentis*	227	NS	
	Sphaeroderus nitidicollis	5	*Pterostichus adstrictus*	63		
	Pterostichus adstrictus	3	*Calathus ingratus*	61		
	Agonum retractum	2	*Agonum retractum*	32		
	Platynus decentis	2	*Pterostichus pensylvanicus*	29		
	Pterostichus pensylvanicus	2				
H67B2	*Synuchus impunctatus*	16	*Platynus decentis*	379	NS	
	Calathus ingratus	12	*Calathus ingratus*	100		
	Sphaeroderus nitidicollis	7	*Calosoma frigidum*	86		
	Platynus decentis	6	*Pterostichus adstrictus*	68		
	Pterostichus adstrictus	5	*Pterostichus pensylvanicus*	51		
	Pterostichus pensylvanicus	4				
	Agonum gratiosum	3				
H80A1	NS		*Platynus decentis*	55	*Platynus decentis*	532
			Pterostichus pensylvanicus	46	*Pterostichus pensylvanicus*	121
			Calathus ingratus	36	*Calathus ingratus*	89
H80A2	NS		*Calathus ingratus*	13	*Platynus decentis*	305
			Synuchus impunctatus	9	*Pterostichus pensylvanicus*	70
			Platynus decentis	8	*Calathus ingratus*	39
			Sphaeroderus nitidicollis	7		
			Patrobus fovecollis	7		
			Agonum gratiosum	5		
			Pterostichus pensylvanicus	4		
			Agonum sordens	4		
H95A1	*Agonum cupreum*	2	*Platynus decentis*	30	NS	
	Agonum cupripenne	2	*Agonum gratiosum*	25		
	Agonum gratiosum	1	*Pterostichus pensylvanicus*	16		
	Amara cupreolata	1	*Carabus maeander*	15		
	Carabus maeander	1	*Agonum retractum*	12		
	Patrobus septentrionis	1	*Synuchus impunctatus*	8		
			Agonum sordens	8		
H95A2	*Agonum gratiosum*	4	*Carabus maeander*	33	NS	
	Agonum sordens	3	*Agonum gratiosum*	20		
	Agonum cupreum	1	*Agonum cupreum*	10		
	Agonum retractum	1	*Synuchus impunctatus*	8		
	Patrobus septentrionis	1				
	Pterostichus pensylvanicus	1				
	Synuchus impunctatus	1				
H95B1	NS		*Synuchus impunctatus*	72	NS	
			Platynus decentis	71		
			Calathus ingratus	28		
			Pterostichus pensylvanicus	25		
			Agonum retractum	24		
H95B2	*Sphaeroderus nitidicollis*	10	*Platynus decentis*	135	NS	
	Calathus ingratus	5	*Pterostichus pensylvanicus*	38		
	Carabus taedatus	3	*Calathus ingratus*	27		
	Pterostichus patruelis	2				
	Pterostichus pensylvanicus	2				

Appendix IX: The number of carabid beetles caught, number of species caught, log-series α and evenness of carabid beetles in 2000 by plot.

Species	Burn Plots										Harvest Plots							Total
	B32A1	B32A2	B61A1	B61A2	B61B1	B61B2	B80A1	B80A2	B80B1	B80B2	H67A1	H67A2	H67B1	H67B2	H95A1	H95A2	H95B2	
Agonum affine Kirby	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	0	0	0	2	1	0	3
Agonum cupripenne Say	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2
Agonum gratiosum Mannerheim	0	0	0	0	0	0	0	0	0	0	1	0	0	3	1	4	0	9
Agonum placidum Say	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	2
Agonum propinquum Gemminger and Harold	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
Agonum puncticeps	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Agonum retractum LeConte	0	0	33	6	30	3	3	13	3	2	0	0	2	2	0	1	0	98
Agonum simile Kirby	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	3
Agonum sordens Kirby	0	0	0	0	0	0	1	1	3	0	0	0	0	0	0	3	0	8
Agonum superioris Lindroth	0	0	0	0	0	0	0	1	0	2	1	0	1	0	0	0	0	5
Agonum thoreyi Dejean	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Agonum trigeminum Lindroth	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Amara cupreolata Putzeys	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Anisodactylus sanctaecrucis Fabricus	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1

Appendix IX: (cont.)

Species	Burn Sites										Harvest Sites							Total
	B32A1	B32A2	B61A1	B61A2	B61B1	B61B2	B80A1	B80A2	B80B1	B80B2	H67A1	H67A2	H67B1	H67B2	H95A1	H95A2	H95B2	
Calathus ingratus Dejean	30	12	21	40	82	24	21	16	7	11	1	3	16	12	0	0	5	**301**
Carabus chamissonis Fischer von Wadlheim	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	**2**
Carabus maeander Fischer von Wadlheim	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	**3**
Carabus taedatus LeConte	5	32	45	13	38	26	2	3	0	0	1	0	1	0	0	0	3	**169**
Cymindis unicolor Kirby	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	**2**
Harpalus erythropus Dejean	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Harpalus fulvilabris Mannerheim	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**2**
Harpalus sp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	**1**
Patrobus septentrionis Dejean	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	**4**
Platynus decentis Say	6	1	3	10	27	0	0	8	3	18	0	4	2	6	0	0	0	**88**
Pterostichus adstrictus Eschscoltz	17	7	0	21	5	7	1	3	1	0	1	0	3	5	0	0	0	**71**
Pterostichus corvinus LeConte	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**2**
Pterostichus luctousis Dejean	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**2**
Pterostichus patruelis Dejean	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	**3**
Pterostichus pensylvanicus LeConte	13	7	15	15	6	8	1	0	0	0	1	1	2	4	0	1	2	**76**

Appendix IX: (cont.)

Species	Burn Sites										Harvest Sites							Total
	B32A1	B32A2	B61A1	B61A2	B61B1	B61B2	B80A1	B80A2	B80B1	B80B2	H67A1	H67A2	H67B1	H67B2	H95A1	H95A2	H95B2	
Pterostichus punctatissimus Randall	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Sphaeroderus nitidicollis LeConte	2	6	11	6	9	5	12	7	7	8	4	0	5	7	0	0	10	99
Stereocercus haematopus Dejean	6	19	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	30
Synuchus impunctatus Say	2	0	0	1	2	2	15	6	1	0	2	17	1	16	0	1	0	66
Total individuals caught	86	88	131	118	199	79	56	59	28	43	15	27	33	56	8	12	23	1061
Total species caught	11	10	9	10	8	10	8	10	10	6	10	6	9	9	6	7	6	34
Log-series α	2.40	2.30	2.20	2.30	2.08	2.30	2.08	2.30	2.30	1.79	2.30	1.79	2.20	2.20	1.79	1.95	1.79	
Evenness	-0.14	-0.18	-0.24	-0.17	-0.22	-0.17	-0.22	-0.15	-0.11	-0.22	-0.05	-0.24	-0.13	-0.13	-0.07	-0.10	-0.18	

Appendix X: The number of carabid beetles caught, number of species caught, log-series α and evenness of carabid beetles in 2001 by plot.

Species	Burn Plots										Harvest Plots										**Total**
	B32A1	B32A2	B61A1	B61A2	B61B1	B61B2	B80A1	B80A2	B80B1	B80B2	H67A1	H67A2	H67B1	H67B2	H80A1	H80A2	H95A1	H95A2	H95B1	H95B2	
Agonum cupreum Dejean	0	0	0	1	0	0	1	4	0	4	1	0	0	0	0	0	2	10	1	6	**30**
Agonum gratiosum Mannerheim	0	0	0	0	0	0	2	0	0	0	3	0	0	0	0	5	25	20	3	1	**59**
Agonum placidum Say	6	0	1	4	0	6	2	4	0	3	1	1	0	3	0	1	3	2	2	1	**40**
Agonum quinquepunctatum Motschulsky	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Agonum retractum LeConte	1	8	35	10	17	12	2	54	22	32	10	18	32	6	5	1	12	2	24	9	**312**
Agonum simile Kirby	0	0	1	0	0	0	0	1	3	2	0	2	0	3	0	0	0	0	0	0	**12**
Agonum sordens Kirby	0	0	1	2	0	3	0	2	0	0	1	0	0	0	0	4	8	1	11	1	**34**
Agonum trigeminum Lindroth	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	**3**
Amara lunicollis Schiødte	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	**1**
Badister obtusus LeConte	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	**2**
Bradycellus semipubescens Lindroth	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	**2**
Calathus ingratus Dejean	70	24	33	115	80	58	26	37	58	22	9	39	61	100	36	13	2	0	28	27	**838**
Calosoma frigidum Kirby	6	0	0	21	11	10	5	24	1	4	11	8	16	86	0	1	0	0	0	0	**204**
Carabus chamissonis Fischer von Wadleheim	15	24	44	11	1	13	0	4	15	1	0	0	4	2	0	0	0	0	0	0	**134**
Carabus maeander Fischer von Wadleheim	0	0	0	0	0	0	0	0	1	0	14	0	1	0	0	0	15	33	0	0	**64**
Carabus taedatus LeConte	8	56	69	29	59	54	5	0	1	1	1	0	7	1	0	0	0	0	6	2	**299**

Appendix X: (cont.)

Species	Burn Sites										Harvest Sites										Total
	B32A1	B32A2	B61A1	B61A2	B61B1	B61B2	B80A1	B80A2	B80B1	B80B2	H67A1	H67A2	H67B1	H67B2	H80A1	H80A2	H95A1	H95A2	H95B1	H95B2	
Cymindis cribricollis Dejean	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	**1**
Cymindis unicolor Kirby	1	1	0	1	1	1	2	1	0	0	0	0	0	1	0	0	0	0	1	0	**10**
Dicaelus sculptilis Say	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	**3**
Diplocheila striatopunctata Dejean	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	**1**
Harpalus fulvilabris Mannerheim	0	1	0	0	0	0	0	2	1	2	0	0	0	0	0	0	0	0	0	0	**6**
Harpalus ochropus Kirby	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	**1**
Loricera pilicornis Fabricus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	**1**
Notiophilus intermedius Lindroth	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	**2**
Patrobus fovecollis Eschscholtz	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	7	0	0	1	1	**13**
Patrobus lecontei Chaudoir	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3	0	1	0	**6**
Patrobus septentrionis Dejean	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	**1**
Platynus decentis Say	558	356	536	484	301	328	86	603	184	48	165	165	227	379	55	8	30	4	71	135	**4723**
Poecilus corvinus LeConte	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Poecilus lucublandus Say	0	1	0	2	0	2	0	0	1	0	0	0	0	1	0	0	0	0	0	0	**7**
Pterostichus adstrictus Eschscholtz	203	172	80	165	110	121	14	10	3	0	2	8	63	68	7	0	1	0	7	6	**1040**
Pterostichus pensylvanicus LeConte	2	9	149	67	133	141	63	77	30	29	9	26	29	51	46	4	16	2	25	38	**946**

Appendix X: (cont.)

Species	Burn Sites										Harvest Sites										**Total**
	B32A1	B32A2	B61A1	B61A2	B61B1	B61B2	B80A1	B80A2	B80B1	B80B2	H67A1	H67A2	H67B1	H67B2	H80A1	H80A2	H95A1	H95A2	H95B1	H95B2	
Pterostichus punctatissimus Randall	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Sphaeroderus nitidicollis LeConte	2	3	8	4	11	1	0	9	7	3	6	5	8	10	4	7	1	0	0	8	97
Stereocercus haematopus Dejean	23	101	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	138
Synuchus impunctatus Say	1	0	0	2	0	2	19	3	0	1	11	33	7	7	1	9	8	8	72	4	188
Total individuals caught	**896**	**761**	**957**	**932**	**724**	**753**	**227**	**836**	**330**	**155**	**245**	**305**	**456**	**718**	**155**	**63**	**128**	**86**	**254**	**243**	**9224**
Total species caught	**13**	**14**	**11**	**16**	**10**	**15**	**12**	**16**	**16**	**15**	**15**	**10**	**12**	**14**	**8**	**13**	**14**	**12**	**15**	**15**	**36**
Log-series α	**2.15**	**2.44**	**1.74**	**2.74**	**1.64**	**2.65**	**2.70**	**2.81**	**3.51**	**4.10**	**3.53**	**1.98**	**2.26**	**2.47**	**1.79**	**4.97**	**4.01**	**3.79**	**3.49**	**3.53**	
Evenness	**-0.22**	**-0.21**	**-0.27**	**-0.17**	**-0.27**	**-0.19**	**-0.17**	**-0.16**	**-0.15**	**-0.13**	**-0.13**	**-0.21**	**-0.20**	**-0.20**	**-0.28**	**-0.10**	**-0.12**	**-0.14**	**-0.15**	**-0.14**	

Appendix XI: The number of carabid beetles caught, number of species caught, log-series α and evenness of carabid beetles in 2002 by plot.

Species	**Burn Plots**				**Harvest Plots**		**Total**
	B80A1	B80A2	B80B1	B80B2	H80A1	H80A2	
Agonum cupreum Dejean	0	1	0	0	0	0	**1**
Agonum cupripenne Say	0	1	0	0	0	0	**1**
Agonum gratiossum Mannerheim	1	0	0	0	0	3	**4**
Agonum placidum Say	1	1	0	2	1	0	**5**
Agonum retractum LeConte	11	45	43	22	2	9	**132**
Agonum sordens Kirby	0	2	3	0	0	4	**9**
Agonum trigeminum Lindroth	0	0	0	0	0	2	**2**
Amara cupreolata Putzeys	0	0	1	0	0	0	**1**
Amara impuncticollis Say	0	1	0	0	0	0	**1**
Badister obtusus LeConte	0	0	0	0	1	0	**1**
Bradycellus semipubescens Lindroth	0	0	0	0	0	1	**1**
Calathus ingratus Dejean	28	45	79	38	89	39	**318**
Calosoma frigidum Kirby	4	7	2	5	18	16	**52**
Carabus chamissonis Fischer von Wadlheim	0	8	8	0	0	0	**16**
Carabus maender Fischer von Wadlheim	0	0	1	0	0	3	**4**
Carabus taedatus Fabricus	1	3	3	0	2	0	**9**

Appendix XI: (cont.)

Species	**Burn Sites**				**Harvest Sites**		**Total**
	B80A1	B80A2	B80B1	B80B2	H80A1	H80A2	
Cymindis unicolor Kirby	1	0	0	0	1	1	**3**
Dicaelus sculptilis Say	1	0	0	0	0	0	**1**
Harpalus fulvilabris Mannerheim	0	0	0	1	0	1	**2**
Patrobus fovecollis Eschscholtz	0	2	1	0	0	1	**4**
Patrobus longicornus Say	0	0	0	0	0	1	**1**
Patrobus septentrionis Dejean	0	0	3	0	0	0	**3**
Platynus decentis Say	97	1004	297	231	532	305	**2466**
Poecilus lucublandus Say	0	1	1	0	0	0	**2**
Pterostichus adstrictus Eschscholtz	3	14	3	1	7	5	**33**
Pterostichus pensylvanicus LeConte	54	114	44	38	121	70	**441**
Sphaeroderus nitidicollis LeConte	2	4	3	2	6	4	**21**
Synuchus impunctatus Say	21	9	2	1	6	15	**54**
Total individuals caught	**225**	**1262**	**494**	**341**	**786**	**480**	**3588**
Total species caught	13	17	16	10	12	17	**28**
Log-series α	3.00	2.78	3.16	1.93	2.01	3.44	
Evenness	-0.41	-0.37	-0.34	-0.61	-0.55	-0.31	